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SOME CRUCIAL CONSEQUENCES OF ADAPTIVE HABITAT SELECTION BY PREDATORS AND PREY: APPARENT MUTUALISMS, COMPETITIVE GHOSTS, HABITAT ABANDONMENT, AND SPATIAL STRUCTURE

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ABSTRACT

Numerous ecological models evaluate how predators influence the abundance of their prey. Prey dynamics in these models often reflect a compromise between prey reproductive potential, density-dependent competition, and the direct consumption of prey by predators. But predators and prey play a complex evolutionary game where prey behavior, and its effect on distribution and abundance, depends on predation risk. Risk is subsequently modified by adaptive predator responses. Many of the co-adaptive behaviors are likely to involve a spatial component where density-dependent habitat selection can mask prey competition. I explored the consequences of the predator–prey habitat-selection game with numerical simulations of two classical predator–prey models. Two species of prey and their predator attempted to maximize their fitness by choosing between two distinctly different habitats. The simulations included exogenous stochastic effects on prey density and explored large changes in individual parameters. Several common themes emerge from both models. (1) Habitat selection promotes community persistence. (2) Predators and prey often persist at an ideal-free "equilibrium". (3) Single habitats often include only a single food chain (predator and one prey species), whereas pairs of habitats always include the complete web of three species. (4) Habitat selection can cause rapid and occasional reciprocal reversals in predator habitat use and habitat abandonment. (5) Predators reduce prey numbers. (6) Predators reinforce prey habitat preferences that further reduce their net competitive interaction. The adaptive behaviors played out in the evolutionary games among interacting species are thereby etched deeply into the dynamics of their populations and the structure of their emergent communities.

INTRODUCTION

Ecological models of species interactions have often concentrated on either competition among species within a single trophic guild, or on the joint dynamics of predators and their prey. The polarity in ecological theory is reflected in empirical studies that also

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tend to emphasize only one type of interaction. But competitive interactions are embedded in communities where predators and their prey play intriguing evolutionary games that have crucially important consequences on distribution and abundance, and on subsequent evolution (Brown et al., 1999). It is thus crucial that we investigate whether a more thorough understanding of these complex interactions will modify our general perspectives on the dynamics of populations and the structure of ecological communities.

Several community models integrate behavior implicitly through the functional responses of predators (e.g., Oksanen et al., 1981; Fryxell and Lundberg 1998), and a few have even modelled behavior explicitly (Abrams, 1996, 1999; Křivan and Schmitz, 2003). Predator–prey interactions are heterogeneous in space, as well as in time, and a growing number of models have included a spatial component (Oksanen, 1990; Oksanen et al., 1992, 1995; Fryxell and Lundberg, 1998; Holt, 1984, 1985, 1993; Abrams, 1999; Křivan and Schmitz, 2003). Despite these advances, phenomenological models often ignore spatial influences associated with habitat and habitat choice.

But habitat and habitat selection are bound to be important. All species vary in their specialization on habitat, few occupy a single habitat, and the evolution of habitat preference must surely depend on interactions with other species (Svärdsson, 1949; Fretwell and Lucas, 1970; Fretwell, 1972; Rosenzweig, 1974, 1981, 1985, 1991; Morris, 1988, 1989, 1999a,b; Brown and Pavlovic, 1992; Morris et al., 2000a,b). Theories of habitat selection, and their empirical tests, demonstrate habitat's pervasive role in obscuring competition from species that would otherwise be intense competitors (the ghost of competition, Rosenzweig, 1974, 1981, 1985; Abramsky et al., 1991, 1992, 1994; Morris, 1999a; Morris et al., 2000a,b). It would be surprising if trophic models that include habitat selection yield the same outcomes as those that have ignored it.

Initial theories reveal a panoply of habitat-dependent effects. An early model by Hugie and Dill (1994), for example, revealed the novel insight that the density of prey in a habitat will often depend only on how risky the habitat is, and not on its productivity. The Hugie–Dill game captured the essence of habitat selection by predators and prey, but did not incorporate population dynamics. Abrams (1999) included the dynamic perspective in models that also allowed adaptive habitat selection by predators. Predator populations often failed to reach an ideal-free distribution (IFD) and their habitat selection destabilized predator–prey dynamics. Grand (2002) used a complementary approach with dynamic prey populations in an IFD model of coexistence (Grand and Dill, 1999). The dynamic-prey model supported the conclusions of the earlier work; adaptive habitat selection by prey, in response to predation risk, reinforces prey coexistence.

New models that view habitat choice as a dynamic evolutionary game played by both competing prey and their predators demonstrate an even greater potential significance of habitat to our understanding of whole ecosystems. Habitat-selecting predators, and the risks associated with them, can augment habitat preferences of competing prey species, and further increase the role of Rosenzweig's competitive ghosts (Morris, 2003a). Prey species that otherwise co-occupy habitats are forced, by their predator, to restrict their habitat preferences. Habitat separation between the prey reduces their competition, reinforces their habitat preferences, and yields patterns (no competition among prey) identical to those of exploitation theory. But models have so far assessed only a small subset of predator–prey parameters where, in the absence of stochastic effects on population regulation, all species coexist in both habitats. It is thus important to explore the potential influences of predator–prey habitat selection across a much wider range of possible patterns of coexistence.

I imagine a landscape where two adjoining habitats are selected by both a predator and its two competing prey species. Each species possesses a life history with discrete pulses of reproduction. I simulate the predator–prey/habitat-selection game for two different plausible alternative models. I explore a range of parameter values to find a set of initial "control" conditions where all three species coexist in the two habitats. I then manipulate the values of each parameter across an equivalent range of possible alternative values (proportional to initial conditions) to assess the sensitivity of predator–prey habitat selection to different parameters in the models. My main interest is to assess if the habitat-selection game tends to eliminate competition between otherwise competing prey species. Accordingly, I summarize patterns in abundance of all three species across simulations, and measure the competition between prey in each simulated community. I conclude by summarizing the potential of habitat selection to structure ecological communities and ecosystems.

THEORY

SIMULATED COMMUNITIES

I used two different models to simulate habitat-selecting predators and prey. First, I modified the Comins and Hassell (1976) host-parasitoid equation (Hassell, 1978) (hereafter referred to as the CH model) such that

$$N_{1(t+1)A} = \lambda_{1A} N_{1tA} \left(\exp\left[-\frac{r_{1A}}{K_{1A}} \left\{ N_{1tA} + \alpha_{12A} N_{2tA} \right\} - \frac{a'_A T P_{tA}}{1 + a'_A T_{h1A} N_{1tA} + a'_A T_{h2A} N_{2tA}} \right] \right) \tag{1}$$

where $N_{1(t+1)A}$ is the future population size of species 1 in habitat A, λ_{1A} is the species' maximum net reproductive rate, N_{1A} is the current number of individuals, 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 (one year if set equal to unity as in my simulations), P is the number of predators, and T_h is the predator's handling time. The extreme right-hand term is a two-species equivalent of the predator's

Holling Type II functional response (Holling, 1959). The predator's consumption of prey species 1 also depends on the number of individuals of the second species occupying that habitat (search efficiency is assumed to depend on habitat, not on the prey species consumed). A similar equation applies to prey species 2. The "predator's" dynamics in habitat *A* are given by

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

$$+\,c_{2A}N_{2tA}\left(1-\exp\left[-\frac{a'_A TP_{tA}}{1+a'_A T_{h2A}N_{2tA}+a'_A T_{h1A}N_{1tA}}\right]\right) \qquad (2)$$

where *c* is the number of predator offspring produced by each individual of prey species *i* in habitat *j*. Similar equations apply to each species in habitat *B* and for the second prey species.

The host–parasitoid equations simplify our ability to calculate future population sizes because, unlike predator–prey equivalents, they do not require an estimate of the predator's prey consumption. The limitation does not apply to a linear functional response, so I also investigated the behavior of classical predator–prey models using Comins and Hassell's (1976) two-prey equivalent of the Nicholson–Bailey (1935) equation [NB model] such that

$$N_{1(t+1)A} = \lambda_{1A}N_{1tA}\left(\exp\left[-\frac{r_{1A}}{K_{1A}}\{N_{1tA}+\alpha_{12A}N_{2tA}\}-a'_A P_{tA}\right]\right) \qquad (3)$$

and

$$P_{(t+1)A} = N_{1tA}\left(1-\exp\left[-a'_A P_A\right]\right) + N_{2tA}\left(1-\exp\left[-a'_A P_A\right]\right) \qquad (4)$$

respectively. Again, similar equations apply to habitat *B*, and to prey species 2. I elected to use eqs 2 and 3 because their behavior, in a single habitat, is reasonably well understood (e.g., Morin, 1999). A somewhat more realistic version would vary the conversion of prey into predator offspring (as in eq 2).

I used each set of predator–prey equations to calculate the expected population sizes at time $t + 1$ for each species in each habitat. The general protocol of the simulations mimicked those I used previously (Morris, 2003a):

Step 1: At time *t* the habitats were colonized by all three species (except when modelling control situations without predators).

Step 2: Individuals of each species then attempted to equalize their fitness in the two habitats by dispersing between them until they attained an ideal distribution (or as close as possible given the constraints of the simulation, below).

Step 3: Population density of each prey species in each habitat was adjusted at random (but in the same direction in both habitats).
Step 4: The populations grew according to the respective predator–prey eqs 1–4.

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 exogenous stochasticity.

I mimicked stochastic changes in density (non-regulating stochasticity, Morris, 2003a) by allowing current population size of each prey species to fluctuate. Current density was multiplied by unity plus-or-minus a normally distributed random variable with mean of zero (values ranged from –0.3 to +0.3). I then repeated the calculations of population size to determine the sizes of each species expected at time $t + 2$ should the environment remain the same. I calculated a prey individual's expected fitness in each habitat as

$$\frac{N_{t+2} - N_{t+1}}{N_{t+1}}$$

and similarly for the predator. My definition of fitness ignores complications associated with temporally varying environments (e.g., Metz et al., 1992; Holt and Barfield, 2001) and assumes, therefore, (1) that habitat-selection decisions occur much more rapidly than changes in population size, and (2) that individuals cannot "bank" their fitness by trading off a currently sub-optimal habitat choice against its future value (because other individuals will invade [the "Conquistador effect"], Morris et al., in press). The assumptions appear reasonable for the purposes of these models because the stochastic effects are totally random, and because the direction and limits to stochasticity are identical in the two habitats (Morris, 2003a).

COMPETITIVE COEXISTENCE OF PREY

I searched for competition between prey species via isodar analysis (Morris, 1988, 1989, 1999a, 2003b,c; Rodríguez, 1995; Morris et al., 2000a,b). To visualize the analysis, imagine two competing species with discrete intervals of reproduction. Imagine that the two species occupy a landscape with two adjacent habitats, that each species has a distinct preference for a different habitat (Pimm and Rosenzweig, 1981), and that the two species strive to achieve an ideal-free distribution (Fretwell and Lucas, 1970). The dynamics for species 1 can be modelled by a pair of habitat-specific discrete-logistic equations,

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

and

$$N_{1,A(t+1)} = N_{1,A(t)} + r_{1,A} N_{1,A(t)} \left(1 - \frac{N_{1,A(t)} + \alpha_{1,2A} N_{2,A(t)}}{K_{1,A}} \right) \quad (6)$$

where N_{ij} is population size of species i in habitat j at times t and $t + 1$, 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,

$$\frac{N_{B(t+1)} - N_{B(t)}}{N_{B(t)}} = \frac{N_{A(t+1)} - N_{A(t)}}{N_{A(t)}} \tag{7}$$

Substituting eqs 5 and 6 into eq 7 yields the linear isodar

$$N_B = K_B\left(\frac{r_B - r_A}{r_B}\right) + \frac{r_A}{r_B}\frac{K_B}{K_A}N_A + \frac{r_A}{r_B}\frac{K_B}{K_A}\alpha_{1,2A}N_{2A} - \alpha_{1,2B}N_{2B} \tag{8}$$

and similarly for species 2 (Morris, 1988, 1989, 1999a,b, 2003b,c; Morris et al., 2000a,b). Equation 8 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., 2000a,b).

METHODS

Each simulation ran for 250 "generations". I deleted the first 50 generations to eliminate the effects of initial conditions, then assessed the rest of the time series. I began by exploring approximately 50 different combinations of parameter values for each of the two predator–prey/habitat-selection models. I stopped when I found a set of values that allowed the three species to persist, and to jointly occupy both habitats most of the time.

I ran each "control" simulation in the absence of predators to demonstrate that isodars are capable of estimating the actual competition between prey. I then varied each parameter sequentially to assess its possible effect on prey coexistence. It would be interesting to explore the sensitivity of predator–prey dynamics to manipulation of each parameter, but such a detailed analysis is premature until we know the general features that emerge from predator–prey habitat selection. My primary purpose, then, was to assess the effect of predator and prey habitat-selection on prey competition. So I manipulated individual parameters to either 1/2 or 1 1/2 times their initial "control" values and examined the outcomes. I allowed all parameters other than attack rates (a'_j) and conversion of prey biomass into predators (c_{ij}) to vary between species and habitats. Thus, I assume that search rates are a function of habitat only, and that the value of a single prey individual, once captured, is independent of the habitat in which it occurs. I list the parameter values used to simulate the "control" communities in Appendix I. The manipulated parameter values for the 31 different pairs of simulations contrasting eqs 1 and 2 (CH model, Type II functional response) with eqs 3 and 4 (NB model, linear functional response) are listed in Appendix II. Appendix II also includes the values for the 12 simulations unique to the CH model (handling time [T_h] and prey conversion [c]).

The dispersal algorithm allowed individuals to move to whichever habitat increased their fitness. Following population growth, I calculated the expected fitness values of individuals of each species in both habitats. 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 was 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 ten different occasions, or when 250 movement iterations (750 individual movements, the number of potential movements always exceeded the total number of individuals (e.g., Fig. 1)) were completed. I classified the resulting outcomes as either ideal free (IFD) or non-ideal free (non-IFD) distributions (Morris, 2003a). After all movements were complete, each prey subpopulation experienced stochastic variation in size (above). Stochastic variation in predator populations occurred through their dependence on prey density. Populations then entered the next generation and either increased or declined according to their population growth parameters.

The random assignment of movement to species, and the two stages of dynamics (dispersal separate from population growth), overcome many of the limitations associated with "event-timing" in individual-based models (Hugie and Grand, 2003; Ruxton and Humphries, 2003). And while the movement rule is necessarily based on integers, an individual of each species has an opportunity to respond instantaneously to the decisions of the other species. It is nevertheless possible that alternative distributions could arise if groups of individuals tend to move together, or if movements by the different species are contingent on prior (or ordered) movements by others.

The stochastic effects had two purposes: (1) They guaranteed that populations departed from their ideal-free distribution. (2) They mimicked local and regional (exogenous) processes that alter densities independent of the process of habitat selection. The stochastic dynamics included in each simulation are thus likely to reduce (but on some occasions increase) my chances of finding significant influences on population persistence and interspecific competition. While such effects could bias my initial screening of parameters, they are unlikely to create any consistent bias across the range of values used to assess any single parameter's influence. A more detailed screening would replicate each simulation numerous times, and contrast the confidence intervals about the mean densities of each species. Such a process would require many thousands of replicates, would use an excessive amount of computer time, and is beyond the primary focus of this contribution.

There are several additional nuances of the predator–prey interaction that are important for us to differentiate and understand in the context of habitat selection. In the classical predator–prey scenario, predators and prey live in a homogeneous landscape. Predation reduces prey density below carrying capacity, so the average competition between prey species is reduced. If predators are capable only of habitat selection (e.g., Abrams, 1999), they occupy whichever habitat yields the greatest fitness return. The resulting predator–prey communities seldom reach an ideal-free distribution and often exhibit chaotic dynamics. But when habitat-selection between predators and prey is visualized as an evolutionary game, each individual, regardless of species, responds to the adaptive decisions of the other players. It is not immediately obvious whether the game should reduce or increase prey competition. A predator species that concentrates on a particularly profitable prey species in an easily searched habitat might facilitate an increase in density of the competitor (reduced density of species *A* allows an increase in the density of species *B*, apparent competition, Holt, 1977). Apparent competition could also emerge if the predator's prey preference is independent of habitat.

Alternatively, the predator's initial concentration in a single habitat, and the associated reduction in prey density, may subsequently cause the predator to increase its density in the other habitat, that preferred by the second prey species. Competition could be increased because the prey species no longer possess a habitat refuge, or competition could be reduced because the predator also limits the density of each species in its secondary habitat. Perhaps more importantly, the predator's response to the abundant prey species may result in habitat-dependent short-term apparent competition (Holt and Kotler, 1987). Large numbers of predators keying on species 1 in its preferred habitat may increase predation on the less abundant species (species 2), and thus reinforce its preference for the other habitat. The restriction of species 2 to its preferred habitat will increase competition with species 1 there, and force species 1 into its preferred habitat, even though the predator is abundant. The two species will live primarily in different habitats and their competition will disappear because they are spatially segregated. Thus, I am not interested simply in the reduction in density by the predator that yields the classic interpretation of reduced competition between prey, but rather how adaptive habitat selection alters competition and our ability to measure it.

I examined the role of predator and prey habitat selection on prey coexistence by summarizing simulations for both "control" and "manipulated" communities. I assessed whether the community of three species persisted for all 200 generations. I then determined, (1) the number of generations in which a sub-population was "extinct", (2) the number of generations that either did, or did not, attain an IFD, (3) the mean and standard error of each species' density in each habitat, and, (4) the estimate of competition obtained from the isodar analysis. I also screened the data for novel patterns that might emerge when both generalist predators and their prey are capable of habitat selection. My goal was to evaluate whether habitat selection across trophic levels alters fundamental mechanisms (and our ability to measure them) of prey coexistence. If predation risk from habitat-selecting predators reinforces prey habitat preferences, average competition between prey species will be reduced, even though the potential for competition has not changed.

RESULTS

THE PLAYERS

Final parameter values (Appendix I) corresponded to a community of two competing prey with distinct habitat preferences. Species 1 had a higher carrying capacity and population growth rate in habitat *A* than did species 2. Species 1 was not only the superior competitor in habitat *A*, it also was a stronger competitor in its preferred habitat *A* than was species 2 in its preferred habitat *B*. Species 2 specialized on habitat *B*, where it had a higher carrying capacity and growth rate than species 1. Note, however, that the relative advantage of each species varied throughout the simulations. The range of manipulations guaranteed that each species had a turn at being superior to the other. Likewise, the higher "control" attack rate of the predator in habitat *A* was reversed in simulations that either reduced that rate by 50%, or that increased the attack rate in habitat *B* by 50%. Nevertheless, the control community, against which all others were judged, was composed of two competing habitat specialists exposed to a generalist predator with a slight preference for species 2 ($c_1 < c_2$; CH model only) that was capable of more effective search ($a'_A > a'_B$) and prey capture ($T_{hiA} < T_{hiB}$; CH model) in habitat *A*.

One pair of simulations (model 31) imagined that the landscape was composed of a single habitat. In this instance, all parameters for a given species were identical in the two habitats (Appendix II).

CONTROL COMMUNITIES

Populations of all species fluctuated but nevertheless persisted through time

Habitat-selecting predator–prey communities exhibited pronounced fluctuations in abundance (Fig. 1), regardless of which model was used to evaluate their dynamics. Despite occasional local extinctions within a single habitat, each species was rescued rapidly by immigration. Prey extinctions occurred only within secondary habitats. Predator numbers mirrored one another in the CH model, whereas predators were substantially less abundant and prone to extinction in habitat *B* in the NB model. Yet, the NB model also reveals a novel but repeating phenomenon (see below). Local extinction caused by low growth and emigration of the predator in habitat *B* (generations 154–161) is followed by an immediate reversal where the predator, even though abundant, completely abandons habitat *A* (local extinction) to reoccupy habitat *B* (generations 162–165).

Note that the predator's reversal in habitat choice is reflected in the dynamics of each prey species. The habitat switch from *B* to *A* by predators was associated with the highest density of species 2 in its less preferred habitat *A*, and with its minimum density in habitat *B*. Species 1 responded with its maximum density in habitat *A*, but there was no obvious effect in habitat *B* (Fig. 1). The shifts in density highlight the point that habitat switching by predators is the result of a dynamic evolutionary game among the three species. The density shifts also highlight the possibility of using otherwise unusual "imbalances" of prey between habitats to begin the search for habitat switching by their predators.

Isodars correctly estimated competition between prey in their preferred habitats

When predators were absent, isodars of prey alone were highly significant for both classes of simulations (Table 1). Isodars were identical for the two models (both models collapse on identical competition equations when predators are absent) and yielded

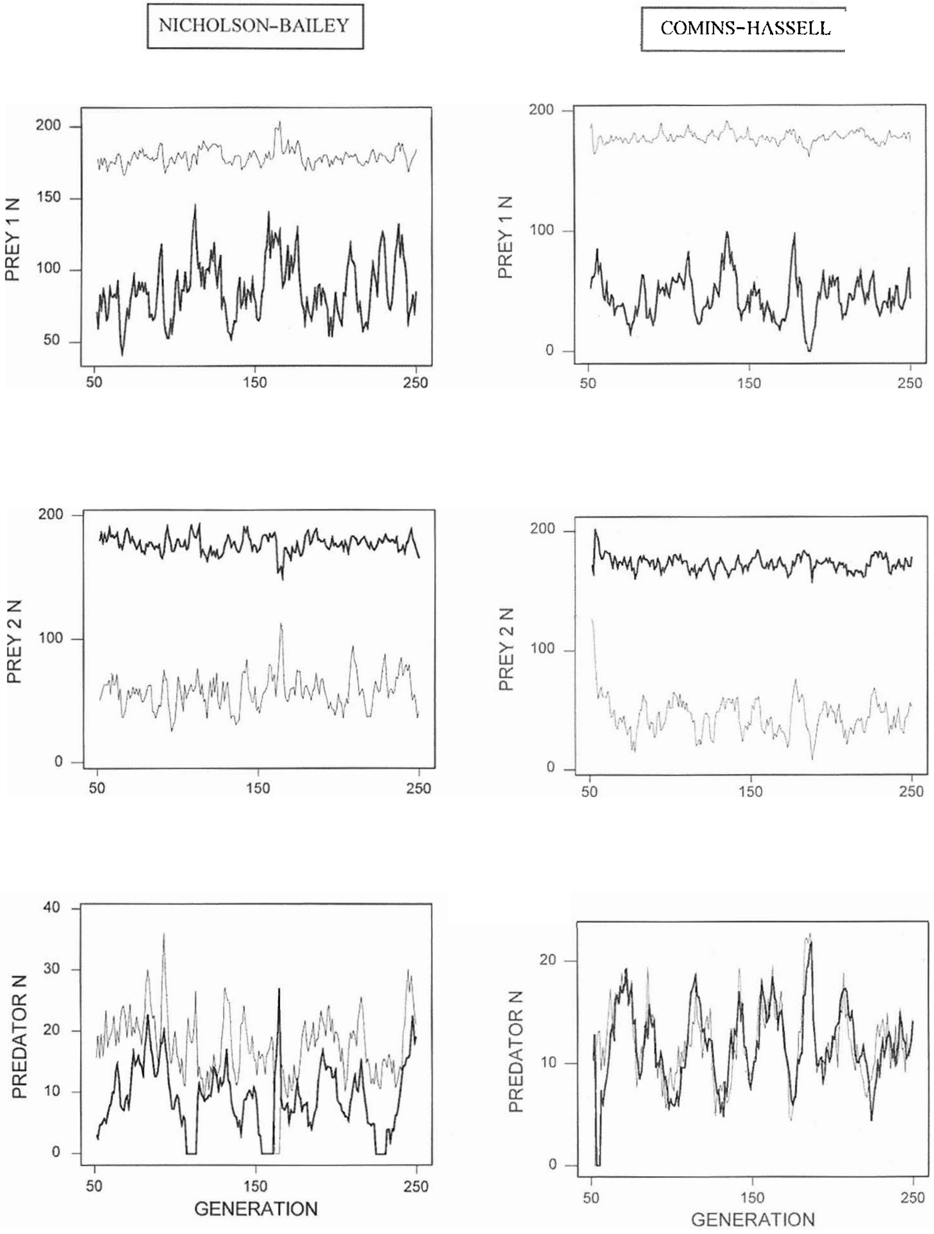

Fig. 1. Population numbers of all three species fluctuated dramatically but nevertheless persisted in both Nicholson–Bailey and Commins–Hassell simulations. The number of individuals in habitat *A* is indicated with the narrow solid line, that in habitat *B* is indicated with the bold line. Parameter values for this "control" simulation are listed in Appendix I.

accurate estimates of competition within the prey species' preferred habitat. Density in the secondary habitat, and the density of the competitor within the preferred habitat, accounted for virtually all of the variance in the target species' isodar. The result, for the parameter values used here, is unsurprising. The expected regression coefficients for the density of the competitor in secondary habitat (0.02 and 0.04 for species 1 and 2 respectively; Table 1) are too small to be statistically significant. These small coefficients also account for the minor departures of the isodar intercepts from their expected values (Table 1). We can thus be confident that any departures from our ability to measure competition in manipulated communities is caused by the predator and its density-dependent habitat response.

MANIPULATED COMMUNITIES

The majority of communities yielded three-species ideal-free distributions

Despite large changes in input parameters, all three species frequently co-occupied both habitats (53 of the 74 different simulations produced sample sizes [all species in both habitats] greater than 100) and most of those communities attained ideal-free distributions of all three interacting species (Fig. 2). The number of non-ideal-free

Table 1

Isodars calculated for simulated communities with two competing and habitat-selecting prey species (no predators) were highly significant and yielded accurate estimates of interspecific competition in preferred habitats (expected values calculated from eq 8)

Empirical data	Expected value
Model (CH) including a type II functional response (eq 1)	
$N_{1A} = 175 + 0.19N_{1B} - 0.09N_{2A}$ $F_{2,197} = 20{,}510; p < 0.001; R^2 = 0.995$	$N_{1A} = 172 + 0.19N_{1B} + 0.02N_{2B} - 0.1N_{2A}$
$N_{2B} = 165 + 0.23N_{2A} - 0.12N_{1A}$ $F_{2,197} = 32{,}615; p < 0.001; R^2 = 0.997$	$N_{2B} = 158 + 0.24N_{2A} + 0.04N_{1A} - 0.12N_{1B}$
Model (NB) including a linear functional response (eq 3)	
$N_{1A} = 175 + 0.19N_{1B} - 0.10N_{2A}$ $F_{2,197} = 12{,}413; p < 0.001; R^2 = 0.992$	$N_{1A} = 172 + 0.19N_{1B} + 0.02N_{2B} - 0.1N_{2A}$
$N_{2B} = 165 + 0.23N_{2A} - 0.12N_{1A}$ $F_{2,197} = 19{,}739; p < 0.001; R^2 = 0.995$	$N_{2B} = 158 + 0.24N_{2A} + 0.04N_{1A} - 0.12N_{1B}$

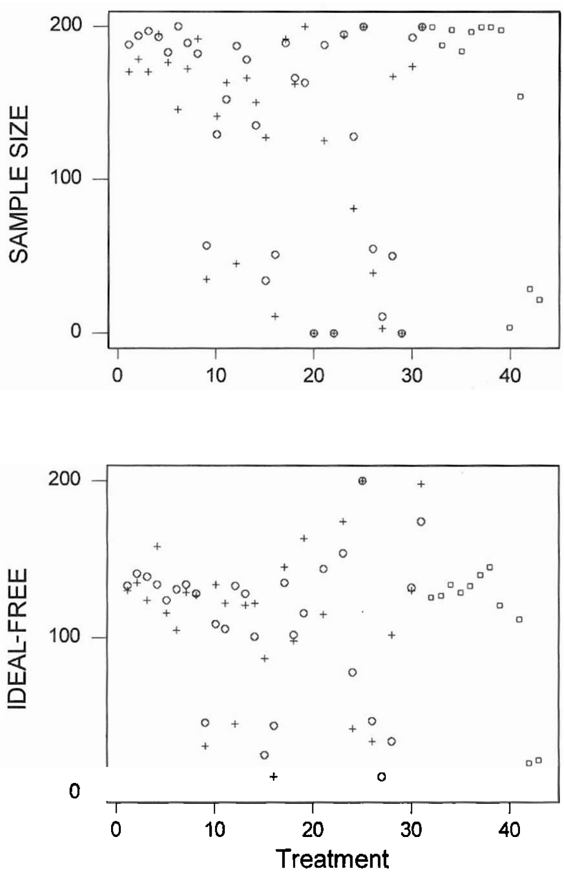

Fig. 2. An illustration of how most communities, whether modeled by the two-species Nicholoson–Bailey model (plus signs) or the modified Comins–Hassell equation (circles), attained ideal-free distributions of all three species (data include only those generations where all three species were present in both habitats). Squares represent Comins–Hassell simulations for which there is no Nicholson–Bailey analogue. Top: The number of "communities" where all three species occurred simultaneously in both habitats. Bottom: The actual number of the same communities (only those cases where all three species occupied both habitats) that attained an ideal-free distribution. Treatment values are listed in Appendix II.

distributions never exceeded the number of IFD communities for any simulation. Constant persistence of all species in both habitats (nine cases) was uncommon, as was total exclusion of a species for all 200 generations (six cases).

Predator–prey communities were resistant to changes in parameters

All three species persisted in each simulation, even though abundances fluctuated through time (Fig. 1). Communities modelled on the Nicholson–Bailey equation converged on a solution more slowly than did those obeying the Comins–Hassell model (Table 2). Despite differences in attack rates in the two models, both types of communities maintained similar mean numbers of prey species 1 in its preferred habitat *A*, and of predators in habitat *B*. Nicholson–Bailey communities supported more predators (and prey species 2) in habitat *A*, and concomitantly higher numbers of both prey species in habitat *B* (Table 2). Nevertheless, the two models often yielded comparable populations of each species, and responded to manipulations of parameters in the same direction (Fig. 3).

Predators were more prone to abandon a habitat than were prey

Neither prey species abandoned its preferred habitat in any of the 74 simulations (14,800 generations). Predators were locally extinct in one habitat approximately 20% of the time (3,293 generations), and were more than twice as likely to abandon habitat *B* (2,317 generations) than habitat *A* (976). Prey species abandoned their secondary habitats approximately 7% of the time (1,005 extinctions of species 1 in habitat *B*, 1,252 extinctions of species 2 in habitat *A*).

Reduced attack rates and prey carrying capacities forced predators to abandon habitats

I examined all simulations with sample sizes <100 to search for repeated patterns in habitat abandonment (Table 3). In both sets of simulations, predators always abandoned habitats within which their attack rates were reduced (absent in 786 of 800 possible

Table 2

Communities modeled with a linear functional response using the modified Nicholson–Bailey (NB) equation tended to maintain higher population sizes than those where predators exhibited a type II functional response (modified Comins–Hassell equation, CH). Data from 27 different model communities for which all species occupied each habitat simultaneously for at least part of the 200-generation simulation

Model	Species	Habitat	Mean population size	Paired-T	p
CH	Prey 1	*A*	175.9	0.81	0.43
NB	Prey 1	*A*	176.5		
CH	Prey 1	*B*	54.5	12.2	<0.001
NB	Prey 1	*B*	82.5		
CH	Prey 2	*A*	48.8	10.1	<0.001
NB	Prey 2	*A*	58.4		
CH	Prey 2	*B*	166.2	5.1	<0.001
NB	Prey 2	*B*	172.8		
CH	Predator	*A*	13.3	10.4	<0.001
NB	Predator	*A*	21.4		
CH	Predator	*B*	13.1	0.3	0.78
NB	Predator	*B*	13.3		

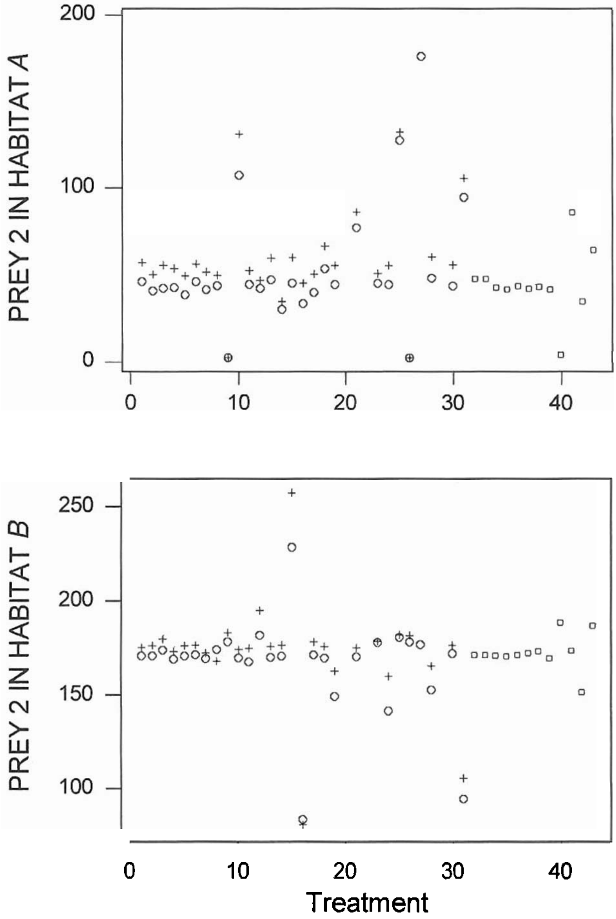

Fig. 3. An illustration of similarities between the outcomes of two different predator–prey models (Nicholson–Bailey, plus signs; Comins–Hassell, circles) on prey distribution in two different habitats. Each treatment represents a separate manipulation of the parameters shared in common by the two models (Appendix II). Data are the mean number of prey occupying each habitat from those generations when all three species were present in both.

observations). Predators were also often absent from habitats with low carrying capacities (and especially so for reduced carrying capacity of species 2 in its preferred habitat *B* [CH model—149 instances; NB model—189 instances; Table 3]). Predators also tended to abandon habitat when prey recruitment (prey population growth rate) declined (Table 3).

Variation in several parameters can cause prey to abandon secondary habitats

Prey species were most prone to abandon secondary habitats when their competitor's carrying capacity in its preferred habitat was increased (three of the four possible scenarios; Table 3). Increased attack rates also caused local extinction in prey secondary habitats (Table 3). Reductions in prey growth rates were always associated with local prey extinction (Table 3), and prey also abandoned secondary habitats when their value to predators was increased. Thus, changes in several different parameters force habitat specialization that nests the niche of one prey species within that of another. Nested habitat niches reduce net competition between prey, even though the reciprocal effect of increased competition does not lead to nested niches (below).

Habitat abandonment was insensitive to changes in competition coefficients and handling time

None of the modified competition coefficients (treatments 1–8) was associated with high rates of habitat abandonment (Fig. 2). The same was true for manipulations of prey handling times (treatments 32–39, Fig. 2). All three species often attained their respective ideal-free distributions in both sets of scenarios (Fig. 2). Thus, differences in competitive

Table 3
A listing of all simulations where at least one species was absent from a single habitat for at least 100 generations

Treatment #	Parameter	Manipulation	Model[a]	Species	Habitat	Generations
26	a'_A	× 1.5	CH	Prey 2	*A*	145
27	a'_A	× 0.5	CH	Predator	*A*	189
28	a'_B	× 1.5	CH	Prey 1	*B*	150
29	a'_B	× 0.5	CH	Predator	*B*	200
26	a'_A	× 1.5	NB	Prey 2	*A*	145
27	a'_A	× 0.5	NB	Predator	*A*	197
29	a'_B	× 0.5	NB	Predator	*B*	200
40	c_1	× 1.5	CH	Prey 2	*A*	195
42	c_2	× 1.5	CH	Prey 1	*B*	161
43	c_2	× 0.5	CH	Predator	*B*	178
20	λ_{1B}	× 0.5	CH	Prey 1	*B*	200
22	λ_{2A}	× 0.5	CH	Prey 2[b]	*A*	200
20	λ_{1B}	× 0.5	NB	Prey 1	*B*	200
22	λ_{2A}	× 0.5	NB	Prey 2	*A*	200
24	λ_{2B}	× 0.5	NB	Predator	*B*	102
9	K_{1A}	× 1.5	CH	Prey 2	*A*	142
15	K_{2B}	× 1.5	CH	Prey 1	*B*	166
16	K_{2B}	× 0.5	CH	Predator	*B*	149
9	K_{1A}	× 1.5	NB	Prey 2	*A*	151
12	K_{1B}	× 0.5	NB	Predator	*B*	155
16	K_{2B}	× 0.5	NB	Predator	*B*	189

[a] CH = Modified Comins–Hassell equation; NB = Modified Nicholson–Bailey equation.
[b] The predator was also absent from habitat *A* in 150 generations.

ability and the predator's foraging cost have relatively little effect on the presence and absence of species within habitats. But search efficiency, prey value, prey reproductive rates, and prey carrying capacity can all result in local habitat extinction of either predator or prey.

Even when prey coexisted in both habitats, habitat selection eliminated interspecific competition between them

The vast majority of "competition coefficients" calculated by prey isodars were opposite expectation (Fig. 4, and see eq 8). Thus, for example, an increase in the number

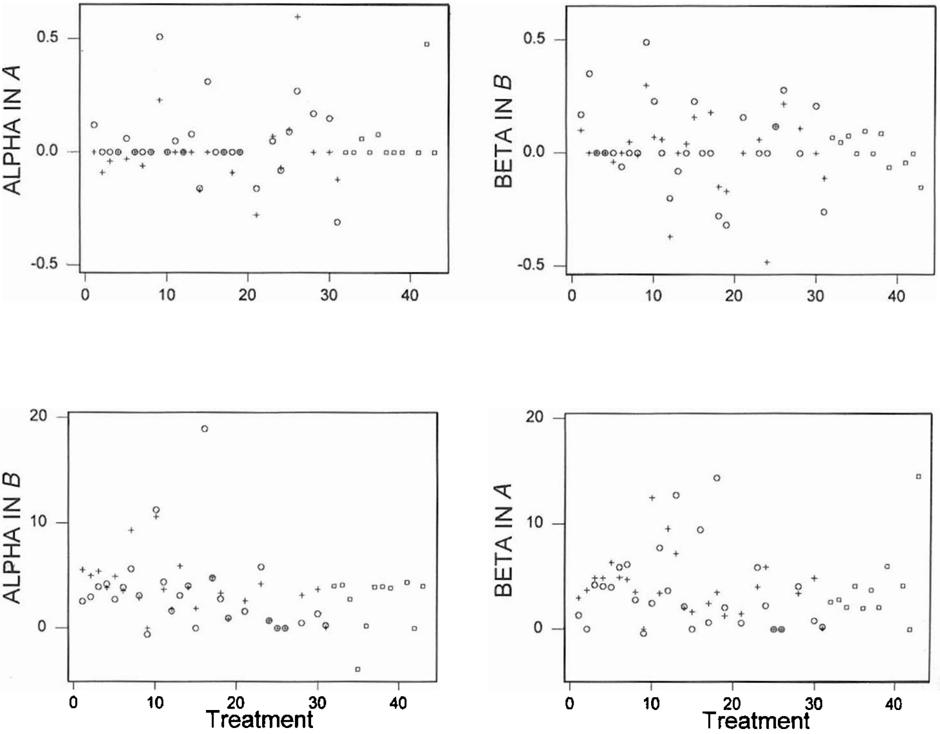

Fig. 4. Estimates of competition coefficients of simulated communities were characteristically biased when both predators and prey were capable of density-dependent habitat selection. "Alpha" refers to the effect of species 2 on 1 ($\alpha_{1,2}$). "Beta" is the effect of species 1 on 2 ($\alpha_{2,1}$). The estimate of competition in preferred habitats was frequently zero, while estimates in secondary habitats were characteristically large and opposite in sign (apparent mutualism) from their actual values in the simulations. Simulations based on a modified Nicholson–Bailey model (plus signs) yielded outcomes similar to those based on manipulating the same parameters in the Comins–Hassell equation (circles). Manipulations of handling time and conversion efficiency (Comins–Hassell model only) also produced biased estimates. Data were calculated from statistically significant regression coefficients of isodar analyses (eq 8) from generations where both habitats were occupied by all three species. Note that the figures are drawn to different scales.

of species 2 in habitat B should have been associated with an increased number of species 1 in habitat A ($\alpha_{1,2B}$ should be negative, eq 8; high densities of the competitor in its preferred habitat reinforce habitat choice in the target species). But most simulations revealed a large and opposite effect (Fig. 4). Net interactions between prey were often opposite the competitive effect on its own. The target species was usually abundant in its preferred habitat only when its competitor was relatively low.

Predator habitat selection reinforced prey habitat preference

The target species also tended to be abundant in its preferred habitat only when the predator had low abundance in that habitat. I tested for the significance of this effect by calculating correlation coefficients between the abundance of prey and that of the predator. The effect was most evident for the less profitable prey species (1). There were 51 significant correlations between prey 1 and the predator in habitat A, and 50 were negative. Only 27 correlations between prey 2 and its predator in habitat B were significant; 19 of these were negative. When the numbers of predators in the two habitats were contrasted by isodar analysis, 61 were significant, all of which had positive slopes (the number of predators in habitat A was significantly and positively related to the number in habitat B).

Thus, prey tend to cycle out of phase with their predators and with each other (e.g., Fig. 1). Overall dynamics and distribution are modulated by habitat and habitat selection such that the net interaction between competitors in their preferred habitats is positive. Even though the two prey species compete with one another, their behavioral response to the predator swamps the competitive signal. Each species tends to be abundant only when its competitor and its predator both exist at low density, and vice versa. Adaptive movements by all three species tend to reinforce each prey species' habitat preference and thereby reduce the potential for competition. In the CH "control" model when predators were absent, 61% of the expected 301 individuals of prey species 1 lived in habitat A (based on the mean numbers present throughout the simulation) and a similar proportion (59% of 309 individuals) of species 2 occupied habitat B. In the control with predators, 80% of the individuals of both species occupied their preferred habitats (Fig. 1). A similar but somewhat less dramatic pattern occurred with the NB model; no predators—62% of 297 individuals of species 1 in A, 58% of 315 individuals of 2 in B; predators present—68% of 263 individuals for species 1 and 76% of 233 individuals for species 2.

I attempted to assess the importance of adaptive habitat-selecting behavior by running a simulation (treatment 31, Appendix II) where, for a given prey species, each habitat was identical to the other. I eliminated differential effects of competition by setting all coefficients to the same value (0.125), but maintained a slight difference in carrying capacity ($K_{1A} = K_{1B} = 200$, $K_{2A} = K_{2B} = 175$). Thus, prey numbers differed between habitats, and their value to predators, that could choose between them, varied. Prey, however, responded only to the habitat differences induced by adaptive habitat selection practiced by predators. For species 1, the results were similar to those of the other simulations. Isodars revealed all three coefficients (e.g., eq 8), but those for the competitor were opposite their expected sign (CH model: $\alpha_{1,2A} = 0.31$, $\alpha_{1,2B} = 0.30$; NB model: $\alpha_{1,2A} = 0.12$, $\alpha_{1,2B} = 0.11$). Isodars did reveal the competition of species 1 on 2, but not necessarily its proper magnitude (CH model: $\alpha_{2,1A} = -0.26$, $\alpha_{2,1B} = -0.26$; NB model: $\alpha_{2,1A} = -0.11$, $\alpha_{2,1B} = -0.11$).

Stochastic prey populations can initiate cycles of habitat abandonment by predators

The control simulation (Fig. 1) revealed a novel pattern. When predators restrict themselves to a single habitat, they occasionally switch their preference within a single generation, abandon the original habitat, and occupy, exclusively, the alternative one. The pattern can reverse within a few generations. When such episodes occur, all species alter their distribution.

I explore an interesting example of predator habitat reversal in Figs. 5 and 6. The simulation responsible for the reversal increased the carrying capacity of species 1 in

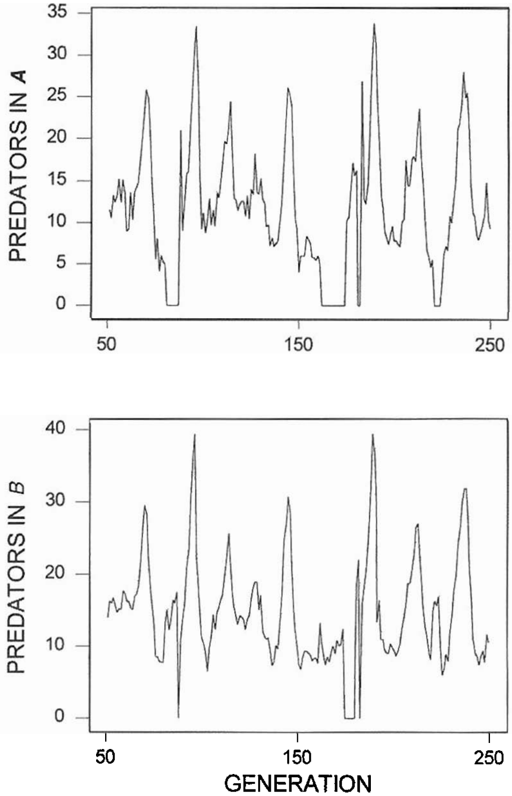

Fig. 5. An example of cycling habitat abandonment by habitat-selecting predators coexisting with two habitat-selecting prey species. In this example, the extinct population in habitat *A* (generations 87–88) is rescued by immigration that causes extinction in habitat *B*. Generations 162–183 reveal two episodes of cycling habitat abandonment (162–174, extinct in *A*; 175–180, extinct in *B*; 181–182, extinct in *A*; 183, extinct in *B*). Data represent those from a simulation that increased the carrying capacity of species 1 in its secondary habitat (× 1.5; treatment 11, CH model).

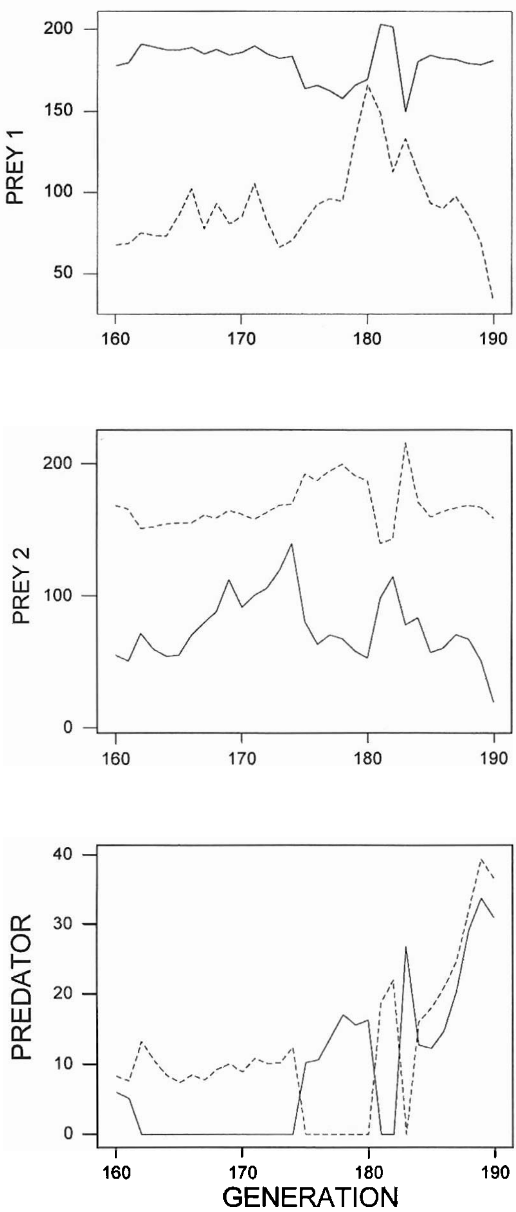

Fig. 6. A "close-up" view of the joint dynamics of habitat-selecting predators and prey when predator extinctions cycle between habitats (illustrated at a larger scale in Fig. 5). Note that habitat reversals by predators (steeply-sloped lines) are rapid single-generation changes in habitat preference. The number of individuals in habitat *A* is illustrated with solid lines, dashed lines represent those in habitat *B*.

habitat *B* by 50% (treatment 11, Appendix II). Beginning in generation162 there are two sequential "cycles" of habitat reversal. The predator first abandons habitat *A*, then *B*, *A*, and *B* again, before increasing and occupying both. The first reversal in habitat use by the predator from being absent in *A*, to being absent from *B*, corresponds to an increase in the most profitable species (2), and most especially so in habitat *A*. The next cycle, from *B*, back to *A*, occurs because species 1 has increased disproportionately in habitat *B*. The example makes it clear that absolute habitat reversals by predators emerge from a combination of intrinsic dynamics and exogenous stochasticity that alters prey population size, and most importantly, from the adaptive habitat choices made by members of each species.

DISCUSSION

Adaptive habitat-selection by predators and their prey reduces prey competition. The pattern is general. It applies to a wide range of parameter values, and to at least two different models of predator–prey interaction.

Predators reinforce prey habitat preferences that, in turn, reduce the potential for competition (the ghost of competition, Rosenzweig, 1974, 1981; Morris, 1999b). A field ecologist assessing interactions between the prey species could be misled by the net positive (mutualistic) interaction. The apparent mutualism between the prey species is driven by the predator's adaptive habitat selection that allows prey species to masquerade as mutualists despite their pervasive and underlying competitive interaction. Competition disappears as all species strive to achieve their own ideal-free distribution. The constraints placed on habitat choice by the simulations dictated that it would not always be possible for all three species to reach, simultaneously, an ideal-free state. Even so, ideal-free distributions dominated the simulated communities, and suggest that predators and prey may frequently "equilibrate" around their joint IFD. As they attempt to do so, their adaptive habitat selection masks competitive interactions between prey.

The role of adaptive behaviors was emphasized in my simulation where prey could respond only to predator-induced differences in habitat quality. Even here, competition between prey could be hidden by habitat selection. Adaptive behavior alone obscured the competition of species 2 on 1, but not necessarily that of 1 on 2. The ability of habitat selection to hide competition by prey is thereby most likely when prey species recognize habitat differences in addition to those caused by predator habitat choice.

Field biologists are often puzzled by (but seldom publish) the rapid appearance or disappearance of species from study plots. Long-term studies of desert small-mammal communities, for example, have revealed intriguing incidents of invading and disappearing species (e.g., Valone and Brown, 1995; Brown et al., 2001; Ernest and Brown, 2001). Many of these events probably represent a combination of isolation, stochastic influences, climate change, and habitat alteration through time. Yet the stunning habitat reversals by predators that occur occasionally in simulated communities demonstrate a clear and profound connection between stochastic changes in prey abundance, and the potential for a rapid adaptive shift in predator distribution.

If field biologists are confused about the rapid appearance and disappearance of species, they may also be confused by habitat-driven apparent mutualisms. Ecologists have known for a long time that predator dynamics, and prey behavioral responses, can mimic the effects of competitive interactions (long- and short-term apparent competition, Holt, 1977; Holt and Kotler, 1987). But it is now clear that ecologists must also be wary of behaviorally-induced apparent mutualisms that demonstrate, once more, the crucial importance that food webs (and predation risk) play in determining net interactions among species.

If apparent mutualisms are widespread, it should be difficult to measure competitive interactions between prey with isodars. Yet isodars have measured competition effectively between competing rodents living under widely different conditions (lemmings in Canada's Arctic, herbivores in Australian heathlands; Morris et al., 2000a,b). If anything, interaction coefficients should have revealed net positive interactions for these species that typically support relatively specialized predator communities. Three counter points deserve emphasis: (1) The habitat choices by rodents in both systems were far more complicated than the distinct preferences analyzed here. Lemmings appear to alter their habitat preference during different phases of their cyclical dynamics (Morris et al., 2000a; this does not exclude the possibility of predator-induced habitat preference at low prey population size). Habitat preferences by heathland rodents also undergo cyclical changes as habitat varies with pyric succession (Morris et al., 2000b). (2) Though predators are abundant in both systems, cyclical changes in habitat preference complicate the possible role of exploitation by predators. (3) Cyclical dynamics (most especially for lemmings) suggest that, at least during periods of population growth by prey, the system is primarily one of donor control when predators should have little influence on prey habitat use, and associated estimates of competition.

Future analyses should, therefore, contrast a wider variety of community types. Comparisons between species sharing the same habitat preference would appear to be especially interesting because opportunities to hide competitive interactions are far more limited than in distinct-preference communities (e.g., Rosenzweig, 1981, 1991; Rosenzweig and Abramsky, 1986; but see Brown and Rosenzweig, 1986, and Morris, 1999a).

Křivan and Schmitz (2003), in an enlightening and important paper, also explored the consequences of ideal-free distributions (albeit on a different scale than here) on predator–prey coexistence, and on the topology of food-webs. When only consumers (prey) are allowed ideal-free choice, (e.g., as with sit-and-wait predators) food-web topologies can be either linear chains with a single consumer and prey species, or webs where the predator consumes both prey. The linear chains disappear in two-patch systems employing an active predator–prey game similar to what I model here. All three species coexist in both patches, and the predator consumes both prey species. Yet it is also clear from my simulations that the general conclusion depends on habitat. A field study might concentrate on a single habitat. The resulting community could, depending on recent history and dynamics, appear to be one without trophic interactions (when the predator abandons one habitat for another), a linear food chain when only the predator and one of the prey species is present, or a web containing the generalist predator and both prey species. But the dynamics and stability of the overall community are expressed on a larger scale incorporating both habitats. Any experiment hoping to discover the underlying processes of food-web structure, and of the interactions among species, would need to include the relevant scales of habitat choice that define the limits of the predator–prey game.

In the short term, adaptive habitat selection by prey in response to foraging, and other fitness opportunities, including predation risk, reinforce habitat preferences and obscure competition between coexisting species. Moreover, by altering parameter values, we can begin to assess how short-term changes in prey behavior can also influence their coexistence, and patterns in the overall community. The preliminary results here (e.g., by altering prey conversion efficiencies [*c*] and handling times) suggest that those responses are insufficient to reverse predator-induced habitat selection.

In the long term, the predator-induced habitat preference will reinforce habitat specialization (e.g, Rosenzweig, 1987; Brown and Pavlovic, 1992; Holt and Gaines, 1992) and reduce competition further. Evolutionary divergence between prey, and their associated habitat displacement, would arise primarily through the effects of the predator, but occur only because the two species also competed with one another.

Thus, over short intervals of time, habitat-selecting predators and prey play in a world where spatially-varying population dynamics and their associated adaptive games reduce prey abundance, alter habitat distribution, and eliminate much of the competition that otherwise forces prey into alternative habitats. In the long term, the habitat selection game co-evolves as a strategy that not only drives adaptive behavior, but that also reduces the potential for competition through habitat specialization. It would be reasonable to speculate that those specializations also result in the divergence of less-plastic characters than behavior motivated by predation risk. It is noteworthy that recent studies on the divergence of sympatric stickleback species (Vamosi and Schluter 2002; Vamosi 2003) implicate a predominant role for habitat-dependent predation. Adaptive behavior by predators and prey not only helps to eliminate competition between prey species, it may very well be responsible for long-term morphological divergence that might otherwise be attributed to competitive character displacement.

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APPENDIX I

List of control values for simulating predator/prey habitat selection. Initial numbers of prey were set equal to the respective carrying capacities. All simulations began with 12 predators in habitat *A*, and 15 in *B*

Parameter	Value (CH model)[a]	Value (NB model)
$\alpha_{1,2A}$	0.1	0.1
$\alpha_{1,2B}$	0.125	0.125
$\alpha_{2,1A}$	0.15	0.15
$\alpha_{2,1B}$	0.125	0.125
a'_A	0.009	0.0045
a'_B	0.008	0.004
c_1	0.5625	(NA)[b]
c_2	0.7	(NA)
K_{1A}	200	200
K_{1B}	150	150
K_{2A}	175	175
K_{2B}	200	200
λ_{1A}	3.6	3.6
λ_{1B}	1.2	1.2
λ_{2A}	1.2	1.2
λ_{2B}	2.4	2.4
T_{h1A}	0.055	(NA)
T_{h1B}	0.056	(NA)
T_{h2A}	0.05	(NA)
T_{h2B}	0.06	(NA)

[a] CH = Modified Comins–Hassell equation, NB = Modified Nicholson–Bailey equation.

[b] The value for prey conversion in the NB model is implicitly set at 1; there is no handling time.

See Appendix II next page

APPENDIX II

Treatments for the 74 simulated communities and their respective parameter changes

Treatment	Modification	Model[a]
1	$\alpha_{1,2A} \times 1.5$	CH & NB
2	$\alpha_{1,2A} \times 0.5$	CH & NB
3	$\alpha_{1,2B} \times 1.5$	CH & NB
4	$\alpha_{1,2B} \times 0.5$	CH & NB
5	$\alpha_{2,1A} \times 1.5$	CH & NB
6	$\alpha_{2,1A} \times 0.5$	CH & NB
7	$\alpha_{2,1B} \times 1.5$	CH & NB
8	$\alpha_{2,1B} \times 0.5$	CH & NB
9	$K_{1A} \times 1.5$	CH & NB
10	$K_{1A} \times 0.5$	CH & NB
11	$K_{1B} \times 1.5$	CH & NB
12	$K_{1B} \times 0.5$	CH & NB
13	$K_{2A} \times 1.5$	CH & NB
14	$K_{2A} \times 0.5$	CH & NB
15	$K_{2B} \times 1.5$	CH & NB
16	$K_{2B} \times 0.5$	CH & NB
17	$\lambda_{1A} \times 1.5$	CH & NB
18	$\lambda_{1A} \times 0.5$	CH & NB
19	$\lambda_{1B} \times 1.5$	CH & NB
20	$\lambda_{1B} \times 0.5$	CH & NB
21	$\lambda_{2A} \times 1.5$	CH & NB
22	$\lambda_{2A} \times 0.5$	CH & NB
23	$\lambda_{2B} \times 1.5$	CH & NB
24	$\lambda_{2B} \times 0.5$	CH & NB
25	Control with 0 predators	CH & NB
26	$a'_A \times 1.5$	CH & NB
27	$a'_A \times 0.5$	CH & NB
28	$a'_B \times 1.5$	CH & NB
29	$a'_B \times 0.5$	CH & NB
30	Control	CH & NB
31	Values for $A = B$; all αs $= 0.125$, $K_1 = 200$, $K_2 = 175$	CH and NB
32	$T_{h1A} \times 1.5$	CH
33	$T_{h1A} \times 0.5$	CH
34	$T_{h1B} \times 1.5$	CH
35	$T_{h1B} \times 0.5$	CH
36	$T_{h2A} \times 1.5$	CH
37	$T_{h2A} \times 0.5$	CH
38	$T_{h2B} \times 1.5$	CH
39	$T_{h2B} \times 0.5$	CH
40	$c_1 \times 1.5$	CH
41	$c_1 \times 0.5$	CH
42	$c_2 \times 1.5$	CH
43	$c_2 \times 0.5$	CH

[a] CH = Modified Comins–Hassell equation, NB = Modified Nicholson–Bailey equation.