Evolutionary dynamics of habitat use

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Summary

I examine the evolution of alternate genotypes that use two habitats that differ in vegetative cover, focusing on the interplay between ecological dynamics of the community and changes in selective advantage. Facultative habitat choice can stabilize a predator population that would cycle if isolated in the more open habitat. This has important implications for the evolution of habitat use strategies. Local stability arising from facultative habitat use allows any number of behavioural genotypes to co-exist: selective use of the open habitat, selective use of the dense habitat, opportunistic use of both habitats in proportion to availability, and facultative switching between habitats to maximize energy gain. Co-existence occurs because the fitness landscape is flat at the ecological equilibrium imposed by the facultative genotype. In contrast, ecological instability favours the evolution of genotypes with behavioural flexibility to avoid being in the wrong place at the wrong time or selective exploitation of one of the habitats. Uncertain information about habitat quality erodes the adaptive advantage of otherwise 'optimal' behaviours, favouring a bet-hedging behavioural strategy synonymous with partial habitat preferences. These results suggest that ecological dynamics could have a strong influence on behavioural heterogeneity within forager populations and that a mixed ESS for habitat use should predominate.

Keywords: foraging; genetics; habitat; optimal; population dynamics; predator; stability

Introduction

In their landmark 1966 paper, MacArthur and Pianka proposed that complex behavioural decisions made by foragers should be shaped by natural selection in ways that mimic economic decision-making. One of their primary motivations for developing what has come to be known as optimal foraging theory was to provide a conceptual framework for predicting community dynamics under different ecological and physiological constraints (MacArthur and Pianka, 1966). Although by no means pervasive in the empirical literature, there are numerous applications of optimal foraging theory to theoretical models of predator–prey dynamics (e.g. Abrams, 1982, 1987a,b, 1990; Sih, 1984; Schwinning and Rosenzweig, 1990; Bernstein *et al.*, 1991; Mangel and Roitberg, 1992; Abrams and Matsuda, 1993; Fryxell and Lundberg, 1993, 1994; Van Baalen and Sabelis, 1993; Werner and Anholt, 1993; Schmitz, 1995; Krivan, 1996). There have also been numerous applications of optimal foraging to theoretical models of competition and community structure (Rosenzweig, 1981, 1986, 1991; Holt, 1983, 1985, 1987; Gleeson and Wilson, 1986; Brown, 1988, 1990; Kotler and Holt, 1989; Abramsky *et al.*, 1990; Mitchell and Brown, 1990; Brown *et al.*, 1994).

This considerable body of work suggests that an understanding of processes of natural selection shaping individual behaviour is essential in predicting dynamical interactions in ecological communities. It is just as relevant to invert this line of inquiry, to examine how community dynamics might affect the outcome of natural selection for alternate foraging strategies. Great strides in this direction have been made in recent years (Matsuda, 1985; Matsuda and Namba, 1989; Brown, 1990, 1996; Brown and Pavlovic, 1992; Brown and Vincent, 1992; Abrams *et al.*, 1993; Saloniemi, 1993; Vincent *et al.*, 1993, 1996; Abrams and Matsuda, 1994; Abrams, 1995; Doebeli,

1996). Most of this work has been confined to communities that are dynamically stable and few models actually incorporate explicit genetic mechanisms for trait evolution (but see Clark and Yoshimura, 1993b; Doebeli, 1996). In this paper, I relax these assumptions, to consider how the evolution of simple Mendelian traits for habitat use strategies might be shaped by community dynamics.

   As the genetic model of habitat use is somewhat complex, I first consider the optimal behavioural strategy, then develop a suitable model for the genetic basis of alternate habitat use behaviours and, finally, imbed the behavioural model in a population genetic framework.

Optimal behaviour

Assume that a hypothetical predator is faced with a single species of prey that occurs in either of two distinct habitats with different cover characteristics. Further assume, as is usually the case, that the predator has a monotonically decelerating functional response to changes in prey density – Holling's (1959) type II response. If habitats are close enough together that travel time between habitats is trivially small, then the total time available for foraging is composed of search time in each habitat type $(\beta T_s + [1 - \beta]T_s)$ and handling time in each habitat type $(h\beta T_s a_1 N_1 + h[1 - \beta]T_s a_2 N_2)$, where T_s = total search time, β = the proportion of search time spent in the first habitat, $1 - \beta$ = the proportion of time spent in the second habitat, N_1 or N_2 = prey density in each habitat, a_1 or a_2 = the area searched per unit time by the predator in each habitat, and h = the time it takes to handle each prey item (Lawlor and Maynard Smith, 1976; Rosenzweig, 1981; Hubbard *et al.*, 1982). Note the logical necessity that time spent searching for prey in habitat 1 (β) must be inversely related to the time devoted to prey search in habitat 2 $(1 - \beta)$. Following the same logic used in deriving the functional response (Holling, 1959; Murdoch, 1973), predator fitness can be calculated according to the following equation:

$$w = \frac{e(\beta a_1 N_1 + (1 - \beta)a_2 N_2)}{1 + h(\beta a_1 N_1 + (1 - \beta)a_2 N_2)} \tag{1}$$

where e = the rate of conversion of prey into new offspring.

   Perhaps the simplest way to analyse the optimal allocation of search time in each habitat is to take the derivative of Equation 1 with respect to β, to determine how fitness changes with an increasing proportion of time spent searching for prey in habitat 1:

$$\frac{dw}{d\beta} = \frac{e(a_1 N_1 - a_2 N_2)}{[\beta h(a_1 N_1 - a_2 N_2) + 1 + a_2 h N_2]^2} \tag{2}$$

From this equation, one can see that $dw/d\beta > 0$ when $N_1/N_2 > a_2/a_1$ and, conversely, that $dw/d\beta < 0$ when $N_1/N_2 < a_2/a_1$. These mathematical characteristics dictate that fitness is either a convex or concave function of β, but the function never has a local maximum on the interval $0 < \beta < 1$. Hence, the optimal strategy is to conditionally exploit either habitat 1 exclusively or habitat 2 exclusively, but never use both habitats (Lawlor and Maynard Smith, 1976; Rosenzweig, 1981; Hubbard *et al.*, 1982). The optimal choice of habitat depends on the densities of prey and the efficiency of search in each habitat.

Genetic basis of behaviour

To understand the circumstances under which different patterns of habitat use might be selectively advantageous, it is helpful to have a simple behavioural model that is nonetheless general enough to span a realistically wide range of alternative strategies, without being based on fundamentally different structure. The following sigmoid function for β provides such a simple behavioural model:

$$\beta = \frac{\exp{(iN_1)}}{\exp{(iN_1)} + \exp{\left(i\left(\frac{a_2 N_2}{a_1} + j - 1\right)\right)}} \tag{3}$$

where i specifies the magnitude of behavioural variability around the switching function and j specifies the central location of the switching function. The β function has a symmetrical sigmoid shape and is centred at prey ratios yielding equal fitness (Fig. 1). One can view the β function as a simple means of modelling statistical variability around a threshold value, which one might expect in any empirical realization of even intensely selected traits (Stephens, 1985). The shape of the β function reflects the energetic (fitness) cost of deviation from the optimal pattern of habitat choice (McNamara and Houston, 1987).

The parameter j specifies the switch point by the predator. When $j = 1$, then the predator facultatively switches at the appropriate prey ratio to maximize energy gain. When $j = 0$, the
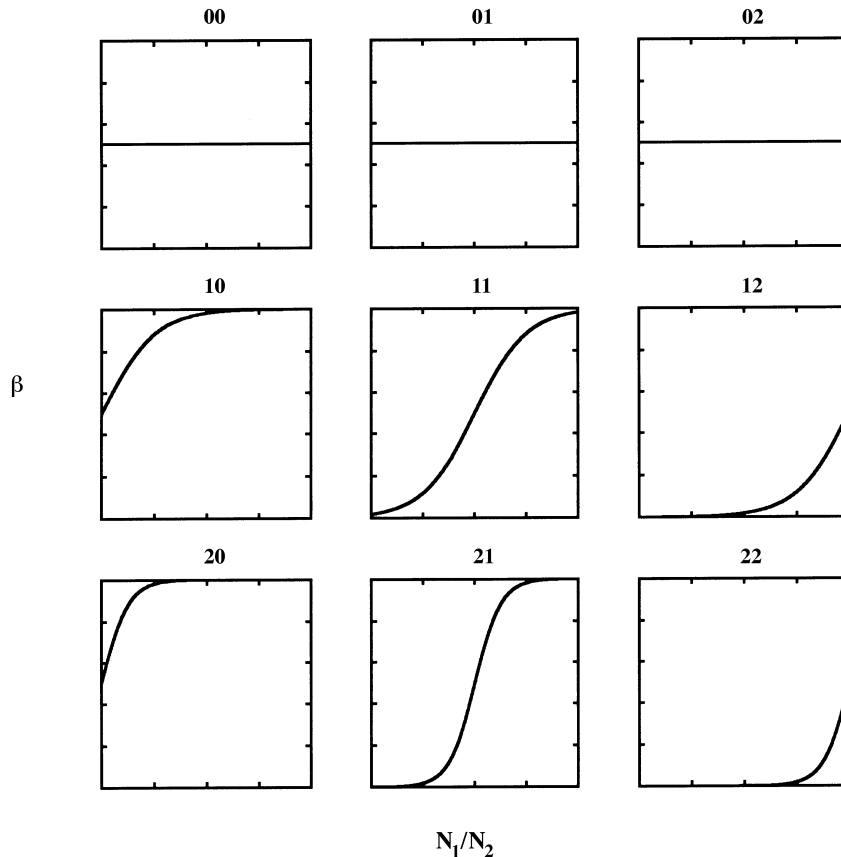

Figure 1. Graphical depiction of behavioural differences among nine genotypes based on foraging preference for the better habitat as a function of prey ratio (N_1/N_2) in two habitats. Genotypes 00, 01 and 02 (where the first numeral refers to parameter i and the second numeral to parameter j) are opportunists, genotypes 10 and 20 selectively use the open habitat, genotypes 11 and 21 are facultative foragers choosing between habitats, and genotypes 12 and 22 selectively use the dense habitat. Algebraic expressions for each of these genotypes are indicated in Equation 3.

predator tends to forage selectively in habitat 1, whereas $j = 2$ implies selective foraging in habitat 2 (Fig. 1). The parameter i specifies whether the predator exhibits partial habitat preferences. When i is small, then the degree of correlation between the sigmoid β function and the optimal step function is relatively crude, implying partial habitat preferences, whereas exclusive habitat use becomes the norm when $i \to \infty$ (Fig. 1). Hence, small values of i would mimic behaviour of an opportunistic forager that forages indiscriminately in each habitat it encounters, whereas higher values of i mimic foragers that discriminate between habitats.

The primary advantage of this approach is that the predator–prey equations for each behavioural strategy have identical structural form, differing only in the magnitude of simple parameters. This is intended to mimic the kind of quantitative differences one might expect from alternate alleles for simple Mendelian traits.

To model this behavioural process using principles of population genetics, I assumed that habitat use behaviour arises from simple Mendelian assortment of two alleles at each of two independent loci, the first locus specifying the parameter i and the second locus the parameter j in the behavioural model described by Equation (3). At each locus, both genotype and phenotype are fully described by the simple addition of pairwise alleles valued 0 or 1. Hence, an individual having one allele for 0 and a second allele for 1 would have a phenotype score of 1. Two alleles can therefore generate three different behavioural phenotypes (0, 1 and 2) corresponding to three combinations, two homozygous and one heterozygous. These quantitative characters have straightforward fitness consequences when calculated according to Equations (1) and (3).

The foregoing β model assumes that foragers base their habitat choices on perfect knowledge of fitness in the two habitats. I also examined evolutionary dynamics when foragers have imprecise information on habitat quality, because perfect knowledge is obviously unrealistic. Uncertain habitat assessment was simulated by generating random normal deviates drawn from a Gaussian distribution with 50% coefficient of variation around the true N_1/N_2 ratio. This is intended to mimic uncertain estimates of the true threshold for optimal habitat switching, thereby applying a stochastic penalty to foragers that switch habitats at inappropriate prey densities.

Population and genetic dynamics

This simple algorithm for habitat choice behaviour can be readily imbedded in a modified set of Lotka-Volterra equations, such that density-dependent recruitment would serve to regulate prey density in the absence of predation:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - N_1/K_1) - P \sum_{i=0}^{2} \sum_{j=0}^{2} \frac{\beta_{ij} a_1 N_1 g_{ij}}{1 + \beta_{ij} a_1 h N_1 + (1 - \beta_{ij}) a_2 h N_2} \tag{4}$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - N_2/K_2) - P \sum_{i=0}^{2} \sum_{j=0}^{2} \frac{(1 - \beta_{ij}) a_2 N_2 g_{ij}}{1 + \beta_{ij} a_1 h N_1 + (1 - \beta_{ij}) a_2 h N_2} \tag{5}$$

$$\frac{dP}{dt} = P \sum_{i=0}^{2} \sum_{j=0}^{2} \frac{g_{ij} e (\beta_{ij} a_1 N_1 + (1 - \beta_{ij})(a_2 N_2)}{1 + \beta_{ij} a_1 h N_1 + (1 - \beta_{ij}) a_2 h N_2} - dP \tag{6}$$

where r_1 and r_2 are the maximum per capita rates of prey recruitment in each habitat, K_1 and K_2 are the carrying capacity of prey in each habitat, $g_{ij} =$ proportion of genotype ij in the predator population, and d is the per capita mortality rate of the predators (P). Using this approach, one can simulate both the ecological consequences of particular behavioural attributes as well as examine the evolution of predator genotypes in the predator population.

If each genotype has a fitness of w_{ij} and mating is non-assortative with respect to foraging genotype, then the proportion of haploid genotypes among gametes can be calculated by the following set of equations:

$$h_{11} = \left(w_{22}g_{22} + \frac{w_{21}g_{21} + w_{12}g_{12}}{2} + \frac{w_{11}g_{11}}{4} \right) \left(\frac{1}{\overline{w}} \right) \tag{7}$$

$$h_{10} = \left(w_{20}g_{20} + \frac{w_{21}g_{21} + w_{10}g_{10}}{2} + \frac{w_{11}g_{11}}{4} \right) \left(\frac{1}{\overline{w}} \right) \tag{8}$$

$$h_{01} = \left(w_{02}g_{02} + \frac{w_{12}g_{12} + w_{01}g_{01}}{2} + \frac{w_{11}g_{11}}{4} \right) \left(\frac{1}{\overline{w}} \right) \tag{9}$$

$$h_{00} = \left(w_{00}g_{00} + \frac{w_{10}g_{10} + w_{01}g_{01}}{2} + \frac{w_{11}g_{11}}{4} \right) \left(\frac{1}{\overline{w}} \right) \tag{10}$$

where the mean fitness of individuals in the predator population $(\overline{w}) = \sum_i \sum_j w_{ij}g_{ij}$. The frequency of offspring genotypes that can be produced through randomly mixing these gametes (γ_{ij}) is calculated as follows: $\gamma_{00} = h_{00}^2, \gamma_{01} = 2h_{01}h_{00}, \ \gamma_{10} = 2h_{10}h_{00}, \gamma_{11} = 2h_{11}h_{00} + 2h_{10}h_{01}, \ \gamma_{20} = h_{10}^2,$ $\gamma_{02} = h_{01}^2, \gamma_{21} = 2h_{10}h_{11}, \gamma_{12} = 2h_{11}h_{01},$ and $\gamma_{22} = h_{11}^2$. It is subsequently straightforward to calculate changes in the proportion of each genotype by adding recruits $(P\gamma_{ij}\Sigma_i\Sigma_j w_{ij}g_{ij})$, subtracting deaths (Pdg_{ij}), and dividing by the new population density. All simulations were run for 3000 time steps, using a discrete time Euler approximation with 25 substeps to model the continuous Lotka-Volterra differential equations. I assumed equal initial frequencies of each genotype in the population and started simulations with prey near carrying capacity and predators 1/10 as common as prey. To ensure the possibility of reinvasion of rare genotypes with higher-than-average fitness (to be consistent with Maynard Smith's, 1982, definition of an ESS), I set a lower limit of 10^{-5} for the density of each genotype.

Results

Before considering the dynamics of structured predator communities, it is useful to reconsider the dynamical properties of predator–prey systems restricted to a single habitat type, because the dynamics of the two-habitat system reflect the aggregate properties of the simpler subsystems. The stability of simple predator–prey systems of this kind have been treated in great detail elsewhere (Rosenzweig, 1971; Gilpin, 1972; May, 1972; Murdoch and Oaten, 1975), so I only briefly review these previous results. Co-existing populations of predators and prey will be locally stable provided that $A_{NN} + A_{PP} < 0$ and $A_{NN}A_{PP} > A_{NP}A_{PN}$, where A is the partial derivative of the rate of change of a given species with respect to increase in population density at the joint equilibria of both populations. Hence $A_{NN} = \partial(dN/dt)/\partial N$, $A_{NP} = \partial(dN/dt)/\partial P$, $A_{PN} = \partial(dP/dt)/\partial N$, and $A_{PP} = \partial(dP/dt)/\partial P$ at equilibrium values for N and P. These values are often termed the 'coefficients of the community matrix' in ecological jargon.

Three non-trivial dynamics are possible in the long term: extinction of the predator but stable persistence of prey at carrying capacity; stable co-existence of predators and prey; or an endlessly repeated limit cycle in which prey and predator populations oscillate slightly out of phase. Habitats having a low rate of search or low carrying capacity cannot sustain predators. Predators and prey are stable at moderate search rate and prey carrying capacity, but become unstable when either the search rate or carrying capacity is increased.

For example, consider a hypothetical habitat in which $r = d = h = 1, e = 2$, and $a = 1.5$. Substituting these parameter values into the community matrix elements under equilibrium conditions, $A_{NN} + A_{PP} < 0$ when $K < 2$ and $A_{NN}A_{PP} > A_{NP}A_{PN}$ when $K > 0.67$, hence the system is locally stable

when $0.67 < K < 2$. It is instructive to compare these values to that of predator and prey populations confined to a second habitat with identical parameters except for a reduced rate of search ($a = 1$), due perhaps to increased cover or topographical relief. The second habitat will support stable predator and prey populations provided that $1 < K < 3$ (i.e. under a wider range of conditions than for the first habitat).

Now consider the properties of a population of precise facultative predators ($i = 2, j = 1$) with access to both habitat types. The zero population growth isoclines for predators specializing in either habitat 1 or habitat 2 have a common point of intersection at the prey densities at which marginal gains are identical in both habitats (Fig. 2; Brown, 1990), which of course is the point at which the perfect predator would switch between habitats (Fig. 3). The zero isocline for a precise facultative predator therefore combines the isoclines of each of the genotypes using habitats selectively, yielding the horizontal line when $N_1 < 0.67$ and the vertical line when $N_2 < 1$ (Fig. 2).

The local stability properties for a facultative predator using both habitats is dictated by aggregate dynamical characteristics of each of its habitats (Fryxell and Lundberg, 1997). If a selective predator confined to the dense habitat is stable, whereas a selective predator confined to the open habitat is unstable, a facultative predator optimally switching between habitats is also stable (Fig. 4). Hence, a facultative predator can stably co-exist with its prey in two habitats, an open habitat in which $a_1 = 1.5$ and a second dense habitat in which $a_2 = 1$, provided that $0.67 < K < 3$. In this sense, facultative use of an alternate habitat can sometimes have a stabilizing influence on trophic dynamics. If both habitats are stable or if both habitats are unstable, however, facultative habitat use has little effect on community stability. I accordingly restrict my descriptions of evolutionary dynamics to the following three scenarios: parameters permitting (1) a sustainable and stable population of predators in the open habitat but not allowing a sustainable population in the dense habitat ($K = 1$ in both habitats); (2) a sustainable but unstable predator population in the
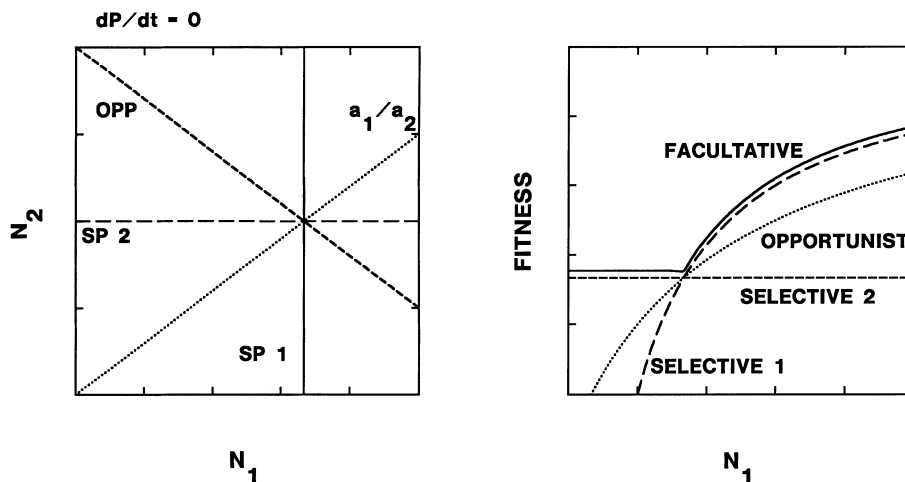

Figure 2 (left). Zero growth isoclines for opportunists (OPP) and two genotypes selectively using a single habitat (SP1 and SP2 denote selectors of habitats 1 and 2 respectively) as well as the switching point (a_1/a_2) for a facultative predator.

Figure 3 (right). Fitness of individuals selectively concentrating in either habitat, an opportunist, and a facultative forager switching between habitats in relation to prey density in habitat 1, holding prey density in habitat 2 constant. Note that the fitness line for the facultative forager has been displaced slightly to clarify its position relative to the other fitness curves.
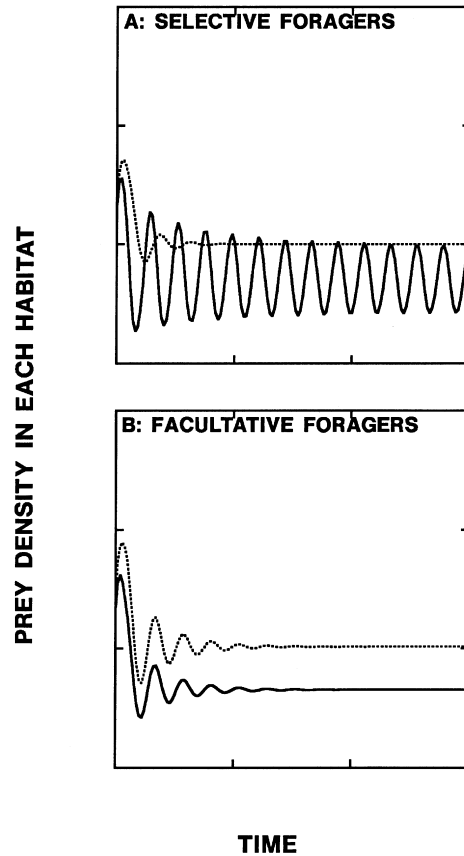
Figure 4. Prey population dynamics over time according to three behavioural scenarios: (A) selective use of an open habitat (dotted line), selective use of a dense habitat (solid line); or (B) facultative use of either habitat. The following parameter values were used: $e = 2$, $a_1 = 1.5$, $a_2 = h = d = r = 1$, $K = 2$ in all cases, and $i = 2$ and $j = 1$ for the facultative forager.

open habitat and a sustainable and stable predator population in the dense habitat ($K = 2$ in both habitats); and (3) sustainable but unstable predator populations in both habitats ($K = 4$ in both habitats).

I first consider the outcomes for the simplest model, involving nine behavioural genotypes (but only seven phenotypes, as shown in Fig. 1) with perfect habitat assessment. In unproductive environments $(K_1 = K_2 = 1)$, genotypes that selectively use the open habitat $1(j = 0)$ quickly eliminate all but a scattering of other genotypes (Fig. 5a). This is probably not surprising, given that the dense habitat 2 is incapable of sustaining predators, hence any degree of use of the dense habitat is bound to decrease predator fitness. Highly productive environments $(K_1 = K_2 = 4)$ favour genotypes with either facultative habitat switching $(j = 1)$ or selective use of the dense habitat $(j = 2)$, with individuals that selectively choose the open habitat persisting at much lower frequency (Fig. 5c).

In moderately productive environments $(K_1 = K_2 = 2)$, however, all genotypes persist indefinitely (Fig. 5b). At first glance, this seems a remarkable result: despite gross differences in behaviour, no genotype is at a disadvantage. The explanation for this oddity is that the system itself is

stabilized by the facultative individuals in this parameter range. Recall from our isocline analysis that even though fitness differs considerably among genotypes at prey densities away from the equilibrium, under stable conditions they all have identical fitness (Figs 2, 3). Co-existence of all genotypes under stability imposed by the action of facultative foragers occurs regardless of starting frequencies of each genotype, but does not necessarily evolve to the same genotype frequencies, indicative of a neutral equilibrium. The mixed ESS also occurs if the different strategies refer to asexual clones, albeit at different equilibrium frequencies, so it is not simply an artifact of this specific genetic system.

It is interesting that in the stable system ($K_1 = K_2 = 2$), foragers with 'sloppy' decisions fare slightly better than 'precise' foragers (Fig. 5b). This is a byproduct of my genetic model. Sloppy genotypes are heterozygous, whereas precise genotypes are homozygous. Random assortment dictates that heterozygotes would therefore predominate relative to homozygotes, provided there

+ **OPPORTUNIST**
□ **SLOPPY SELECTIVE 2**
○ **SLOPPY FACULTATIVE**
△ **SLOPPY SELECTIVE 1**
■ **PRECISE SELECTIVE 2**
● **PRECISE FACULTATIVE**
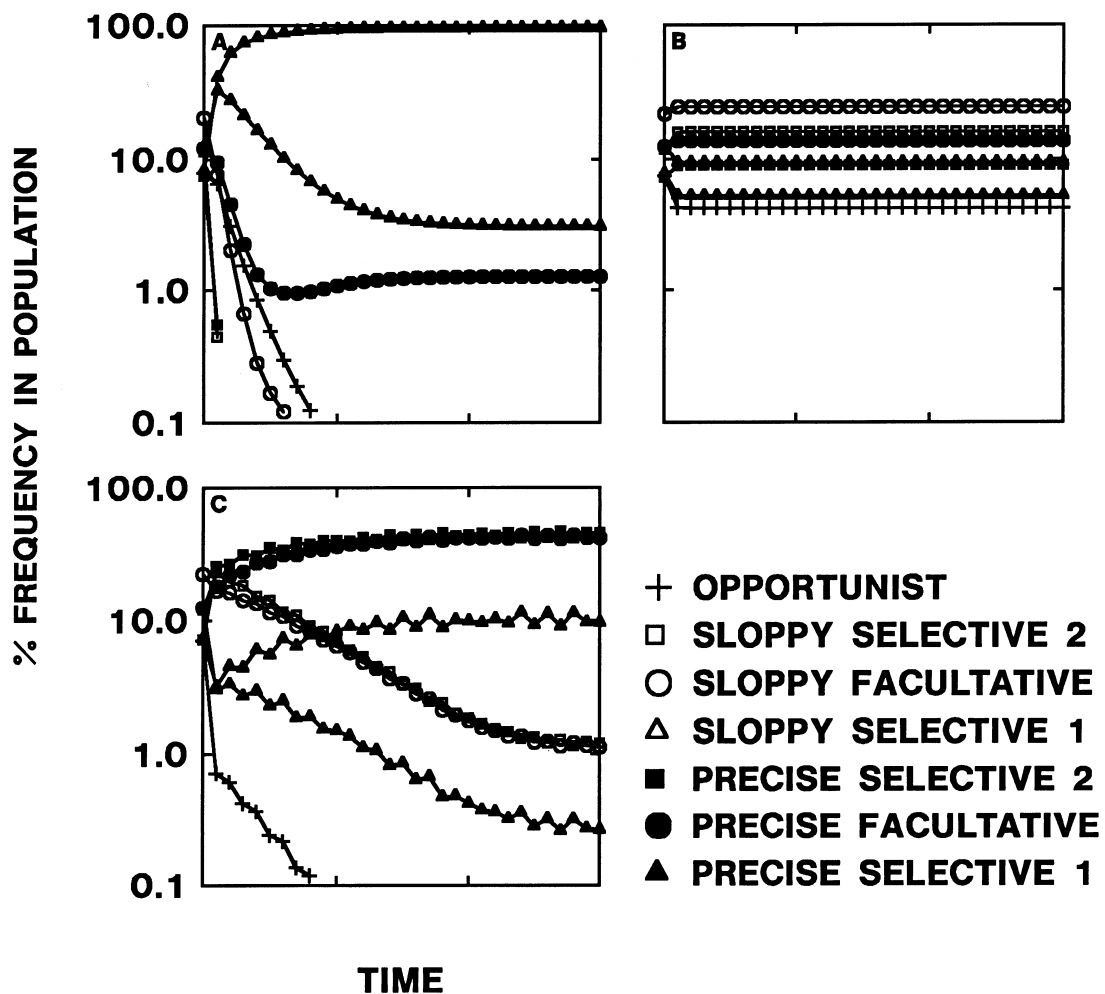▲ **PRECISE SELECTIVE 1**

Figure 5. Changes in relative frequency of nine foraging genotypes (three identical opportunistic genotypes are lumped together) over time (A: $K = 1$; B: $K = 2$; C: $K = 4$; in all cases $r = h = d = 1, a_1 = 1.5$, $a_2 = 1, e = 2$). Assumes foragers have perfect information regarding prey densities in the two habitats.

are no differences in fitness *per se*. Genotypes with precise behaviour (sharp behavioural functions) perform better than sloppy genotypes under unstable conditions, presumably because fitness differences are enough to supersede the inherent genetic predisposition for heterozygosity. Under unstable conditions ($K_1 = K_2 = 4$), precise foragers always outperform sloppy foragers, regardless of whether they use habitats selectively or facultatively (Fig. 5c).

I now consider the same range of parameter values for the system with uncertain habitat assessment. Uncertainty has little profound effect on evolutionary dynamics under highly stable conditions ($K_1 = K_2 = 1$), with the same sets of winners and losers emerging over time (Fig. 6a). In moderately productive environments ($K_1 = K_2 = 2$), all genotypes persist, although the rank order prevalence among genotypes is slightly altered. Opportunists do somewhat better than before, whereas open habitat selectors and facultative predators do somewhat worse than before. In highly
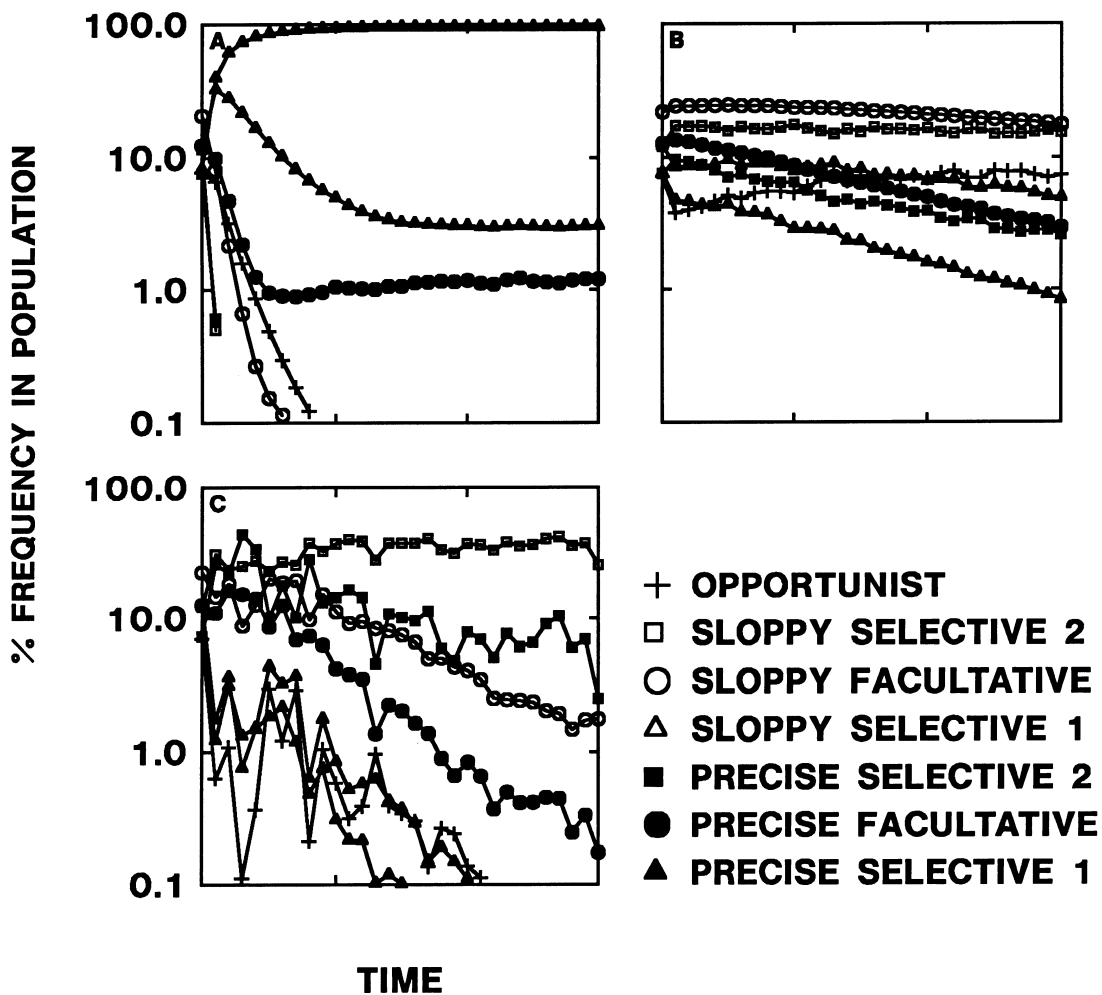

Figure 6. Changes in relative frequency of nine foraging genotypes (three identical opportunistic genotypes are lumped together) over time (A: $K = 1$; B: $K = 2$; C: $K = 4$; in all cases $r = h = d = 1, a_1 = 1.5$, $a_2 = 1, e = 2$). Assumes that the foragers' assessment of the prey ratio in the two habitats is a random normal deviate centred around the true prey ratio.

productive environments ($K_1 = K_2 = 4$), uncertain habitat assessment considerably changes the evolutionary outcomes. Genotypes that facultatively switch between habitats ($j = 1$) or genotypes that select the open habitat ($j = 0$) do much worse in the face of uncertainty than they do in the model with perfect habitat assessment, whereas selectors of the dense habitat ($j = 2$) do better than before. In all cases, the sloppy genotypes do better than their more precise brethren, whereas the opposite is true in the model with perfect habitat assessment.

I tested the robustness of these conclusions by iterating the habitat choice model for 1000 random combinations of parameters. Each parameter value was selected from a random uniform deviate with the following ranges: 1.0–2.0 for e, a_1 and a_2; 0.0–1.0 for r_1, r_2, d and h; 0.0–4.0 for K_1 and K_2. Note that in the Monte-Carlo simulations, both r and K vary independently across habitats. I discarded simulations in which predators went extinct. I also ensured that search rates were always highest in habitat 1, by simply swapping a_i parameters whenever necessary. Each simulation was conducted for 1000 time steps, by which point evolutionary changes in genotypic frequency are usually well established (Figs 5, 6). As in the previous examples, I set a lower limit of 10^{-5} for population density of each genotype, to ensure ample opportunity for reinvasion of rare genotypes with higher-than-average fitnesses. I used Shannon's diversity index ($-\sum_i x_i \ln[x_i]$, where $x_i =$ the relative proportion of genotype i in the predator population) as an estimator of genetic variability in the predator population. If vanishingly small frequencies remain at the end of a simulation for all but one genotype, then genotypic diversity would be 0. In contrast, if all nine genotypes have equal fitness and therefore differ in frequency only because of the Mendelian genetic structure, then genotypic diversity would be approximately 2.08.

Results of the Monte-Carlo simulations confirm that there tend to be three types of outcomes, as shown by three peaks in the multimodal frequency distribution (Fig. 7). The most common outcome is for dominance by a single genotype, as shown by the left-hand peak in the diversity frequency distribution (Fig. 7). This corresponds to the stable dynamic model shown in Fig. 5a, in which a single genotype has a selective advantage. The second most common outcome is for relatively equal proportions of all nine genotypes (right-hand peak in Fig. 7), such as seen in the simulation shown in Fig. 5b. The third most common outcome is domination by three or four genotypes (middle peak in Fig. 7), such as that shown in Fig. 5a. Monte-Carlo simulations with
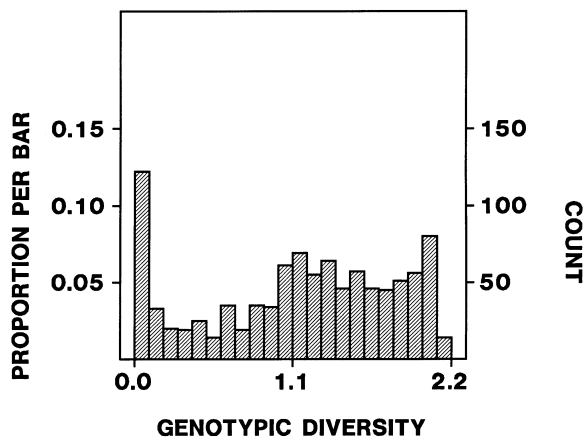

Figure 7. Genotypic diversity at the end of 1000 time steps of 1000 Monte-Carlo simulations of the habitat-use model. Parameter values were selected as uniform random deviates within the following ranges: e, a_1 and $a_2 = 1.0$–2.0; r_1, r_2, d and $h = 0.0$–1.0; K_1 and $K_2 = 0.0$–4.0.

uncertain habitat assessment yielded a very similar pattern. The Monte-Carlo simulations suggest that most paramater combinations yield substantial levels of genetic diversity – mixed ESS's tend to be the norm rather than a single ESS in systems with even the simplest habitat structure.

Discussion

It has long been recognized that functional and numerical responses by predators to changes in prey density have critical importance to the stability of predator–prey interactions. Under the most typical ecological circumstances in which a predator has a finite handling time for each prey item attacked, the functional response curve is monotonically decelerating and therefore the per capita risk of predation declines with prey density. Such inverse density-dependence implies that predation is usually destabilizing (Rosenzweig, 1971; Gilpin, 1972; May, 1972; Murdoch and Oaten, 1975; Tanner, 1975; Caughley, 1976). In principle, this unstable tendency imposed by finite handling times can be superseded when predators concentrate disproportionately on the most abundant prey species available (so-called switching behaviour; Murdoch and Oaten, 1975; Tansky, 1978).

All of this would be fine, if it were not for the fact that switching models are generally maladaptive – a switching predator would have lower fitness than a predator that did not switch (Holt, 1983). The exception to this case arises when predators must choose between adjacent habitats which differ with respect to search efficiency, as in my model of facultative habitat use (Lawlor and Maynard Smith, 1976; Murdoch, 1977; Rosenzweig, 1981; Holt, 1983). Under these conditions, energy-maximizing decisions lead to switching behaviour that would be selectively advantageous over a wide range of prey densities.

Numerous studies in both the field and laboratory suggest that predators preferentially use habitats yielding the highest rates of energy, expanding into poorer habitats only when predator densities in the preferred habitat are such that marginal gains are equivalent to those in alternate habitats (see Rosenzweig, 1991, for a useful introduction to this wide literature). Carefully controlled laboratory studies have also shown several clear cases of switching behaviour as a function of prey relative densities (reviewed by Murdoch and Oaten, 1975; Hubbard *et al.*, 1982). For example, Murdoch and co-workers' (1975) experiments with guppies presented with two types of prey either on the bottom of aquaria or floating on the surface, showed that guppies preferentially exploited the microhabitat with most abundant prey, resulting in a total response (functional multiplied by numerical response) identical to that used in my trophic model. Hence, there is a substantial body of empirical evidence consistent with the behavioural process incorporated into this trophic model.

Such switching behaviour between habitats can stabilize predator–prey dynamics, provided that at least one of the habitats can support stable populations of predators and prey in isolation. Alternative foraging strategies persist, however, in the conditions under which facultative habitat choice is most strongly stabilizing. This is because facultative switching yields equivalent fitness at equilibrium as selective habitat use or opportunistic habitat use. The fitness costs of deviation from optimal habitat choice are most extreme when prey ratios are far from the switch point (McNamara and Houston, 1987), as illustrated in Fig. 3. As a consequence, the selective advantage of facultative choice would also be most intense in highly variable systems. This relaxation in selection differential implies that at least some ecologically stable systems would neither favour, nor disfavour, predators with flexible behavioural strategies.

In unstable systems, opportunists and selectors of the open habitat cannot compete with facultative foragers or foragers that selectively concentrate on the dense habitat. Heterozygote advantage by the facultative genotype guarantees perpetuation of some habitat-selective

homozygotes, the proportion of which is then enhanced by imperfect habitat switching. The relative frequency of open habitat selectors compared to that of dense habitat selectors depends on the proportion of time the system exceeds the habitat switching point or falls below the habitat switching point (Fig. 3). For the parameter combinations shown in Fig. 4, mean fitness of dense habitat selectors is slightly higher than that of open habitat selectors. Other parameter combinations that we have examined generate cycles in abundance, yet genotypes that are selective for open habitats are more common than those in dense habitats. Invariably, however, instability favours facultative genotypes.

Perfect switching behaviour is unlikely in real organisms, because of uncertainty in habitat assessment, variation in perceptual ability, physiological state or motivation among individual foragers, or simply statistical variability around any expected value (Stephens, 1985; McNamara and Houston, 1987). Hence, any biologically reasonable approximation to facultative habitat selection implies a fitness cost which is likely to be most apparent when prey densities are in the neighbourhood of the switch point, because that is when the biological sources of behavioural variability would be most profound. Accordingly, even in unstable systems one might expect multiple behavioural strategies to persist among foragers, as demonstrated in Fig. 5c.

One might argue that natural selection should serve to reduce this behavioural variability around the optimal step function over time. Indeed, sloppy foragers fare more poorly than precise foragers under conditions of perfect habitat assessment when inherent instability of the system causes wide variation in prey densities over time. This pattern was reversed, however, in the presence of uncertainty in habitat assessment (i.e. assessment of prey ratios in the two habitats). This implies that partial habitat preferences may improve fitness when organisms make mistakes in judgement about habitat quality. The reason for this would seem to be due to a fundamental asymmetry in fitness gains versus costs (Fig. 3). The cost of staying in the wrong habitat when gains are higher elsewhere exceed the potential gains obtained by moving at the right time, because the type II functional response yields diminishing returns with incremental increases in prey density. Sloppy foragers suffer reduced costs relative to precise foragers whenever they misjudge habitat quality, so they tend to prosper when habitat quality is uncertain.

At the beginning of this paper, I asked whether ecological dynamics of the community might influence the evolution of alternative foraging strategies. My results argue that community dynamics have a sizeable impact on natural selection for traits affecting habitat use. Ecological stability arising from facultative habitat use by at least one genotype enhances behavioural diversity, because the fitness landscape for all genotypes is flat at ecological equilibrium. In contrast, ecological instability favours the evolution of genotypes with behavioural flexibility to avoid being in the wrong place at the wrong time. Uncertain information about habitat quality erodes the adaptive advantage of otherwise 'optimal' behaviours. These could be potent forces maintaining behavioural heterogeneity within forager populations.

It is also interesting to consider whether inclusion of genetics substantially changes evolutionary dynamics. Fryxell and Lundberg (1997) examine a predator–prey system with an identical behavioural submodel in which morphs do not not interbreed, the classic method of analysing ESS in an ecological context. The non-genetic model yields many results similar to that of the genetic model: open habitat selectors predominate in unproductive systems (Fig. 5a), all morphs co-exist at intermediate levels of productivity (Fig. 5b), and facultative foragers and dense habitat selectors predominate in highly productive systems (Fig. 5c). In all systems, however, the genetic model predicts persistence of a much wider range of genotypes than does the phenotypic model. This suggests that explicit genetic mechanisms may have important implications for behavioural ecology (Mangel and Roitberg, 1994), particularly *vis-à-vis* the maintenance of behavioural variability within populations because of heterozygote advantage (Clark and Yoshimura, 1993b).

There have been numerous previous models of predator evolution within multi-habitat communities (e.g. Lawlor and Maynard Smith, 1976; Rosenzweig, 1981, 1986; Matsuda and Namba, 1989; Brown, 1990, 1996; Clark and Yoshimura, 1993a,b). Despite differences in model structure, a common finding of these previous models has been that the ESS cannot exceed the number of different resources (species or habitats) available, although there are often different combinations of ESS depending on system parameter values. For quite a substantial number of parameter combinations, however, my habitat model predicts a multitude of co-existing behavioural phenotypes in a single population. This may be due to several differences between my model and previous habitat-based models: (1) ecological instability for many parameter combinations, (2) partial habitat preferences due to my behavioural submodel, and (3) heterozygote advantage leading to the perpetuation of less-fit homozygotes (see also Clark and Yoshimura, 1993b). I would argue that these biological features should be relevant in at least some ecological systems.

Some of my conclusions reinforce findings from density-dependent habitat-use models (Wilson and Yoshimura, 1994), particularly the importance of variability in population density favouring flexible behavioural genotypes. In Wilson and Yoshimura's (1994) model, population variability was generated through stochastic environmental effects, whereas in my model, variability is a direct consequence of dynamical instability or errors in habitat assessment. Wilson and Yoshimura (1994) also found that co-existence of alternate genotypes is made possible largely through the modulating effects of generalists, analogous in some sense to facultative foragers in my model.

My findings also echo an important theme outlined by Mangel (1991), regarding the evolution of behavioural traits in convoluted fitness landscapes. Often there are minor fitness differences between individuals with different behavioural traits, even those as fundamental as foraging strategies. My results suggest that the topology of this landscape is likely to change according to local ecological parameters, particularly those factors influencing ecological productivity. In the face of uncertain information, 'optimal' traits may not be entirely obvious. From an evolutionary point of view, there may even be times when it pays to be sloppy.

Acknowledgements

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