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Fish and game: a game theoretic approach to habitat selection by predators and prey*

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Given a choice between habitats differing only in food availability, prey are known to select the habitat providing the highest energetic return. They do so in a frequency-dependent manner, accounting for the reduction in food availability caused by the presence of other individuals; this results in the well-known 'Ideal Free Distribution', an equilibrium solution to a spatial game. When habitats also differ in predation risk due, for example, to different predator densities, prey also appear able to take this into account. However, in most theory (and most experiments) the predation risk levels in the available habitats are assumed to be fixed. Here we ask what will happen if predators are able to adjust their distribution in response to the habitat choice decisions of their prey, i.e. we model a generalized habitat selection game between predators and prey. We first develop a basic model which captures the essence of the problem, and then expand it to include risk dilution and interference among predators. The model produces several new insights, notably that, in the absence of interference effects, the density of prey in a habitat is determined solely by the inherent 'riskiness' of that habitat (a habitat measure independent of predator density, which might reflect cover or light levels, for example) and is unaffected by habitat productivity (a measure of the food resource available to the prey). When interference exists between predators, prey density is also determined by habitat productivity but to a lesser extent than by riskiness. Consequently, prey may not respond significantly to changes in relative food resource availability among habitats if their predators are also free to choose the habitat which maximizes their expected fitness. We consider briefly the potential applications of game theory to diel vertical migration and other fish predator–prey scenarios.

Key words: game theory; habitat choice; foraging; predation risk; ideal free distribution.

INTRODUCTION

Optimality reasoning has been a powerful tool in understanding the behaviour of fish (and other animals) when the preferred outcome of a situation depends solely on the interests of a single party. In such cases an individual's best decision is simply the one which yields the highest expected fitness. However, the outcomes of many situations are under the partial control of more than one individual, each with a self interest which may conflict with the interests of the others. Standard optimization techniques are inappropriate for these situations, since an individual's best strategy will depend on the decisions made by the other individuals. Instead, a game theoretic approach is required. We illustrate this approach by developing a habitat selection game for predators and their prey. We hope to convince the reader of the value of looking at predator–prey interactions in this framework by emphasizing the novel insights provided by this approach.

Game theory was introduced into evolutionary biology and behavioural ecology by John Maynard Smith (for useful summaries see Maynard Smith,

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1982; Parker, 1984). Every game involves at least two ' players ', each with a ' strategy set ' consisting of alternative courses of action or ' pure ' strategies, such as ' fight ', ' flee ', etc. A ' mixed ' strategy is a probability distribution over pure strategies, for example, ' fight with probability 0·6, flee with probability 0·4 '. Every strategy, pure or mixed, is associated with a payoff which depends on the frequency distribution of opponent strategies in the population. Thus, games exhibit the quality of frequency-dependence.

The usual goal of evolutionary game theory is to find an equilibrium strategy, pure or mixed, which can persist in a population. The most familiar example of such a strategy is the Evolutionarily Stable Strategy (ESS), introduced by Maynard Smith (1974), but more general notions of dynamic evolutionary stability exist (Taylor & Jonker, 1978; Hofbauer & Sigmund, 1988; Friedman, 1991). An evolutionary equilibrium may be pure or mixed. In the case of a pure strategy equilibrium, all individuals in the population adopt the same pure strategy. In a mixed strategy equilibrium, the frequency distribution of pure strategies at equilibrium in many cases may be interpreted in two ways (see Maynard Smith, 1982). It may represent the proportions of pure strategists in a polymorphic population or, alternatively, the probability distribution of pure strategies used by all individuals in a monomorphic population. At equilibrium all individuals within a population must receive identical payoffs. The concept of a simple optimum no longer has meaning since, even though all players are assumed to be maximizing their respective payoffs, the game equilibrium need not produce the globally maximal payoff to any player.

Game theory has already been used widely to address various questions in behavioural ecology, including those involving fish. It has been applied, for example, to studies of aggressive behaviour (e.g. Enquist *et al.*, 1990), sex allocation (e.g. Petersen, 1991), alternative mating tactics (e.g. Gross, 1984), egg trading in simultaneous hermaphrodites (e.g. Fischer, 1988), and parental care (e.g. Dawkins & Carlisle, 1976). It has also been applied previously to the study of habitat selection, since the ' Ideal Free Distribution ' of competitors (e.g. Milinski, 1979; Godin & Keenleyside, 1984; Abrahams & Dill, 1989; see below) is really just a mixed ESS to a spatial game between foragers. Other games between fish as prey include predator inspection (Milinski, 1987; Dugatkin, 1990; Dugatkin & Godin, 1992), school joining (Turner & Pitcher, 1986), and perhaps synchronized aerial respiration (Kramer & Graham, 1976).

We are concerned here primarily with games between predators and their prey. The very nature of the behavioural interaction between the hunter and the hunted ensures that the two usually have different preferred outcomes, but only partial control over them, and that the best thing for one player to do will depend on the behaviour of the other; thus, game theory is the appropriate modelling approach. Curiously, despite its apparent relevance, attempts to apply game theory to predator–prey interactions have been extremely scarce, in any system (but see Stewart, 1971; Auslander *et al.*, 1978; Iwasa, 1982; Vega-Redondo & Hasson, 1993; van Baalen & Sabelis, 1993; Bouskila, 1993). In this paper we describe in some detail a habitat selection game between predators and prey to illustrate the basic concepts and the sorts of new insights that can be obtained by using a game theoretic approach.

A HABITAT SELECTION GAME

Consider the situation in which individual prey have a choice between habitats which differ only in their level of some divisible resource. In such situations a spatial game exists between prey individuals: the best habitat to occupy depends not only on each habitat's resource level but also on the current distribution of other individuals competing for that same resource. Prey should switch to the habitat with the highest payoff until the payoffs in all habitats are equal. Fretwell & Lucas (1970) have shown that the solution to this game, termed the 'Ideal Free Distribution' (IFD), is a matching of the prey distribution to the distribution of resources across habitats. However, in nature the fitness of prey individuals is not determined solely by the availability of resources, but also by the risks of mortality associated with each habitat. Many studies have demonstrated that animals consider both foraging and mortality components of fitness when choosing a resource patch or habitat (see Lima & Dill, 1990 for many examples). Indeed, Abrahams & Dill (1989) showed that guppy (*Poecilia reticulata* Peters) distributions may still correspond to the IFD prediction, if individual prey are assumed to be maximizing (and equalizing) some combined function of energy intake and risk of mortality. However, that study, and others examining trade-offs between risk and food, assumed a fixed difference in predation risk between habitats.

Inherent in the assumption of a fixed distribution of predation risk is the assumption that predators do not move between habitats based on the consequences of such movement for their own fitness. This will not usually be the case in nature; predators, being foragers themselves, should redistribute themselves across habitats until their fitness (based on food intake through predation) is equalized. However, as predators move, corresponding changes in predation risk for the prey will result in changes in prey distribution. This will in turn feed back on the foraging success of predators, causing further adjustments in their distribution. Clearly, a game exists, not only between prey with respect to resource competition, but also between predator and prey with respect to predation mortality. In addition, predators are gaming amongst themselves, both indirectly through their effect on the prey's distribution and possibly directly due to interference competition. Although others have recognized the interactive nature of such a problem (e.g. Sih, 1984; Formanowicz & Bobka, 1989), there have been few previous attempts to use game theory to find a solution, i.e., the equilibrium distributions of prey and predators among habitats. One exception is the model of van Baalen & Sabelis (1993); however, they did not allow for frequency–dependent prey intake rates. In an approach similar to ours, Bouskila (1993) modelled the habitat choice of desert rodents and their rattlesnake predators. Here we present a more generalized game.

Our model (Fig. 1) considers habitats which differ in both their rate of production of a food resource for the prey and in habitat 'riskiness' (defined below). Like most models of the 'ideal free' sort, we assume that both predators and prey have 'ideal' information regarding the habitat parameters and each other's current distribution. Unlike previous models, we allow both predators and prey to switch between habitats, and assume that both are 'free' to do so, whenever the payoffs in the available habitats are unequal. As in other IFD

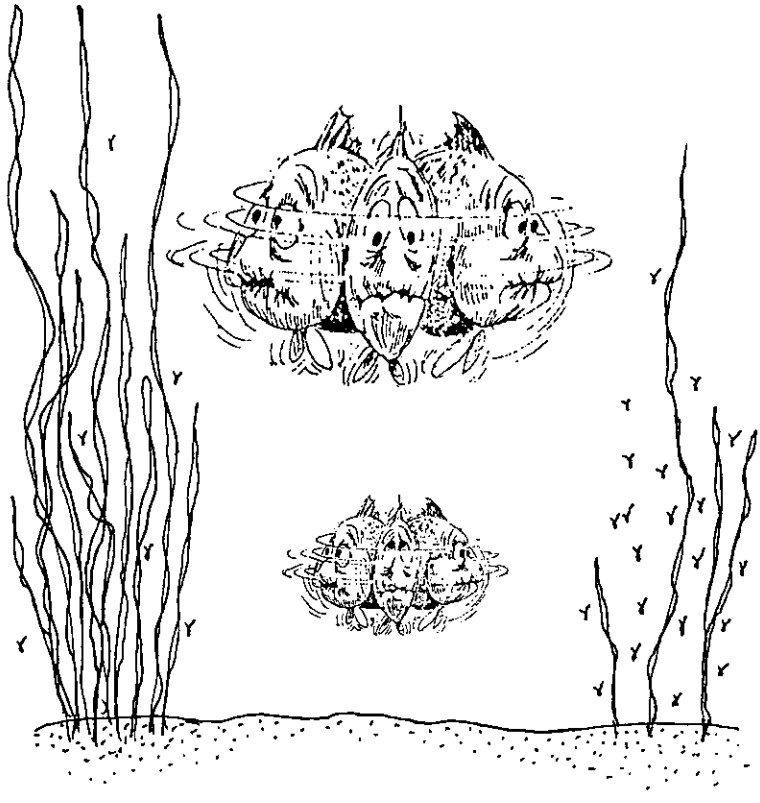

FIG. 1. An idealized habitat selection game between predators and their prey. The two habitats differ in productivity of the prey's food resource and in inherent ' riskiness ' due, in this case, to differences in available cover. Individual prey (lower) are free to choose the habitat which maximizes their expected fitness but the predators (upper) are free to do the same.

models, prey compete for energy within a habitat by dividing the available resource productivity equally amongst themselves. Predators gain energy by encountering and capturing prey randomly. We assume that predator mortality is constant across all habitats which would be the case, for instance, if they were top carnivores. Thus, our model spans three trophic levels, i.e., the prey's food resource base, the prey and the predators, with two trophic levels involved in gaming, i.e., the prey and the predators.

The reader should note the following convention. All constants in the model are represented by capital letters, while variables and functions are described by lower case or Greek letters. Subscripts refer to habitat and primes indicate values pertaining to predators. Nowhere does a prime indicate the derivative of a function.

MODEL CONSTANTS

All constants in the model are shown in Table I. N and N' are the sizes of the prey and predator populations. S_i is the size (area or volume) of each habitat. Habitat ' riskiness ' (R_i) is mathematically equivalent to Holling's (1963) ' rate of successful search ', and is the product of predator search rate and the conditional

TABLE I. Constants in the habitat selection game model

Constant (dimensions)	Symbol	Value
*Total number of prey	N	10 000
Total number of predators	N'	1000
Size of habitat i (area or volume)	S_i	1000 (sum)
*Habitat riskiness (size · time^{-1})	R_i	0·005 (mean)
*Habitat productivity (energy · size^{-1} · time^{-1})	P_i	1 (mean)
Energy value of prey (energy · prey^{-1})	V	2
*Foraging efficiency of prey (proportion)	F	0·9
Foraging efficiency of predators (proportion)	F'	0·9
*Metabolic rate of prey (energy · time^{-1})	M	0·04
Metabolic rate of predator (energy · time^{-1})	M'	0·04
Prey initial growth cost (energy)	G	1
Predator initial growth cost (energy)	G'	1
Energy cost of prey offspring (energy · offspring^{-1})	O	0·5
Energy cost of predator offspring (energy · offspring^{-1})	O'	0·5
Expected lifespan of predators (time)	L'	500
Dilution coefficient (time)	D	5
*Predator collision coefficient (area or volume · time^{-1})	C_i	0·05 (all habitats)
*Interference coefficient (time)	I	5

All values are assumed to be positive with the exception of the interference (I) and dilution (D) coefficients, and the initial growth costs (G and G'), which may be zero. The subscript i refers to the i th habitat. The right column shows the values used in the model or the sum or mean across all habitats. Only those constants indicated with an asterisk affect the game equilibrium. All other constants are irrelevant, given a valid ($w(i)$ and $w'(i)>0$) equilibrium.

probability of prey capture given encounter. In our model we assume that differences in R_i reflect differences in those habitat characteristics which influence predator search ability, or their ability to capture prey. These include such habitat features as light level and the amount of physical structure; several examples of the latter, many involving fishes, are reviewed by Gotceitas & Colgan (1989).

Productivity (P_i) refers to the rate at which the food resource becomes available to the prey in each habitat. P_i is assumed to be constant, with no depletion over time, and positive, since we are only interested in habitats with some food resource available to the prey. The energy value of the prey (V) is the gross energy content of a single prey individual.

F and F' are the proportions of gross energy intake available to the prey and predator, respectively, after accounting for all costs which are proportional to gross energy intake, such as searching, handling and processing costs. M and M' refer to all constant (i.e., intake independent) energy demands on individual prey or predators for baseline activity and maintenance. This may also include the cost of growth for indeterminately growing animals, but we assume no increased advantage for larger size in our model.

Growth may also be incorporated into the model as an initial energy requirement for somatic growth and maintenance to a threshold size before reproduction can taken place. G and G' represent this energy requirement for prey and predators, respectively. When considering games between adult

animals, G and G' may be set to zero without affecting the outcome of the game. The energy cost of individual offspring produced by the prey and predators is given by O and O', respectively. As explained previously we assume that the expected lifespan of the predators (L') is independent of the habitat chosen. The expected lifespan of the prey is variable, depending on their habitat choice, and is discussed below.

Thus, in our model, the gross energy intake of both predators and prey may be expended as 'foraging' costs (F and F') proportional to energy intake, as constant 'metabolic' costs (M and M'), on initial 'growth' (G and G'), or for the production of offspring (O and O').

Constants related to dilution and interference are described later.

BASIC MODEL

The strategy set for both predators and prey is the choice of which habitat to live in. The proportion of prey and predator individuals playing strategy i is given by p_i and p_i', respectively (the sums of p_i, and of p_i', across all habitats, both equal 1). However, the distribution of individuals across habitats is more ecologically, and practically, described by the density of each in the ith habitat.

Prey density
$$d_i = \frac{p_i N}{S_i} \tag{1}$$

Predator density
$$d_i' = \frac{p_i' N'}{S_i} \tag{2}$$

We model encounters between predators and prey as a random process, such that the overall rate of prey death in habitat i ($\gamma(i)$) is:

$$\gamma(i) = d_i d_i' R_i S_i \tag{3}$$

The *per capita* prey death rate, or the probability of death per unit time ($\beta(i)$), is described by the overall rate of prey death in the habitat divided by the number of prey present there:

$$\beta(i) = \frac{\gamma(i)}{d_i S_i} = R_i d_i' \tag{4}$$

Similarly, the *per capita* predator capture rate ($\theta(i)$) is the overall rate of prey death divided by the number of predators in that habitat:

$$\theta(i) = \frac{\gamma(i)}{d_i' S_i} = R_i d_i. \tag{5}$$

Note that the predator's capture rate in this basic model is unaffected by either risk dilution or interference effects; each of these points are addressed in subsequent additions to the model described below.

Payoff for prey

In order to incorporate both energy and mortality components of fitness the payoff for strategy i, for both prey and predators, was calculated in terms of net reproductive output (R_o). Other theoretical studies of animal distributions (e.g. Werner & Gilliam, 1984; Aksnes & Giske, 1990) have also used net reproductive output as a measure of fitness. While mathematically tractable, R_o is an appropriate measure of fitness only when population size is constant over time (Stearns, 1992). Therefore, we assume that both prey (N) and predator (N') populations are held constant globally due to density-dependent factors, such as parasitism or disease, which affect mortality or reproduction independent of habitat. Fitness is first calculated assuming no such population regulation and is then corrected for zero population growth. In our model, this correction has no effect on the equilibrium solution.

Although we calculate fitness in terms of net reproductive output over an individual's life, our model is valid for games of any duration played between individuals which are maximizing their future fitness. This is because population size is held constant in the model, we impose no maximum lifespan on individuals, and reproductive rate is independent of age. Under these conditions net reproductive output is identical to an individual's residual reproductive value at any age.

The prey's expected lifespan in habitat i ($l(i)$) is simply:

$$l(i) = \frac{1}{\beta(i)} \tag{6}$$

while its expected net energy intake rate ($e(i)$) is given by

$$e(i) = \frac{P_i}{d_i} F - M \tag{7}$$

Thus, the prey's uncorrected fitness ($\omega(i)$), in habitat i, is

$$\omega(i) = \frac{l(i)\, e(i) - G}{O}. \tag{8}$$

Since we assume that the prey population is constant in size the prey's fitness must be corrected so that the mean fitness of the population is 1. The corrected fitness ($w(i)$) is obtained by dividing the uncorrected fitness in each habitat by the mean uncorrected prey fitness in the population ($\overline{\omega}$), thus

$$w(i) = \frac{\omega(i)}{\overline{\omega}} \tag{9}$$

where $$\overline{\omega} = \sum_i p_i\, \omega(i).$$

It is worth noting that maximizing $w(i)$ is equivalent to maximizing $e(i)/\beta(i)$, the ratio of net energy intake and the probability of death unit time. In Gilliam & Fraser's (1988) terminology this ratio is expressed as f/μ. In either case, it follows directly from the assumption that prey are maximizing net reproductive output.

Payoff for predators

The predator's payoff is also calculated in terms of net reproductive output. A predator's net energy intake rate in habitat i ($e'(i)$) is given by

$$e'(i) = \theta(i)\, V F' - M'. \tag{10}$$

A predator's uncorrected fitness in i ($\omega'(i)$) is therefore

$$\omega'(i) = \frac{L'\, e'(i) - G'}{O'}. \tag{11}$$

Correcting for zero population growth (as before) by dividing $\omega'(i)$ by the mean uncorrected predator fitness in the population ($\overline{\omega}'$) gives:

$$w'(i) = \frac{\omega'(i)}{\overline{\omega}'} \tag{12}$$

where $$\overline{\omega}' = \sum_i p_i'\, \omega'(i).$$

Again, it is worth noting that maximizing $w'(i)$ is equivalent to maximizing the predator's capture rate $\theta(i)$.

We only accept equilibria with positive fitness for both predators and prey. Therefore, for a valid equilibrium, $\omega(i)$ and $w(i) > 0$ and $\omega'(i)$ and $w'(i) > 0$ for all component pure strategies.

Equilibrium

It can be shown that any equilibrium, for this basic game, and for both subsequent modifications, must be a mixed equilibrium with support from all pure prey and predator strategies (see Appendix I), and is dynamically stable (see Appendix II). In other words, at equilibrium all habitats will contain some proportion of the prey and predator populations. The equilibrium to this game is most efficiently described by the ratio of the prey or predator densities between any two habitats (i and j). For any mixed strategy equilibrium, the payoff to all pure strategies in support of the equilibrium must be equal. Setting $w(i) = w(j)$ and $w'(i) = w'(j)$ and solving for the equilibrium density ratio reveals:

$$\frac{d_i}{d_j} = \frac{R_j}{R_i} \tag{13}$$

and

$$\frac{d_i'}{d_j'} = \frac{P_i F - d_i M}{P_j F - d_j M}. \tag{14}$$

At equilibrium, the distribution of prey is determined solely by habitat riskiness. More specifically, the ratio of prey densities between any two habitats is given by the inverse of their habitat riskiness ratio [equation (13); Fig. 2(a)]; if one habitat is twice as risky as another it should have half the density of prey.

The predator's distribution is affected dramatically by both relative habitat riskiness and relative habitat productivity [Fig. 2(b); compare the scale of the ordinate to that of Fig. 2(a)]. More precisely, the ratio of predator densities is

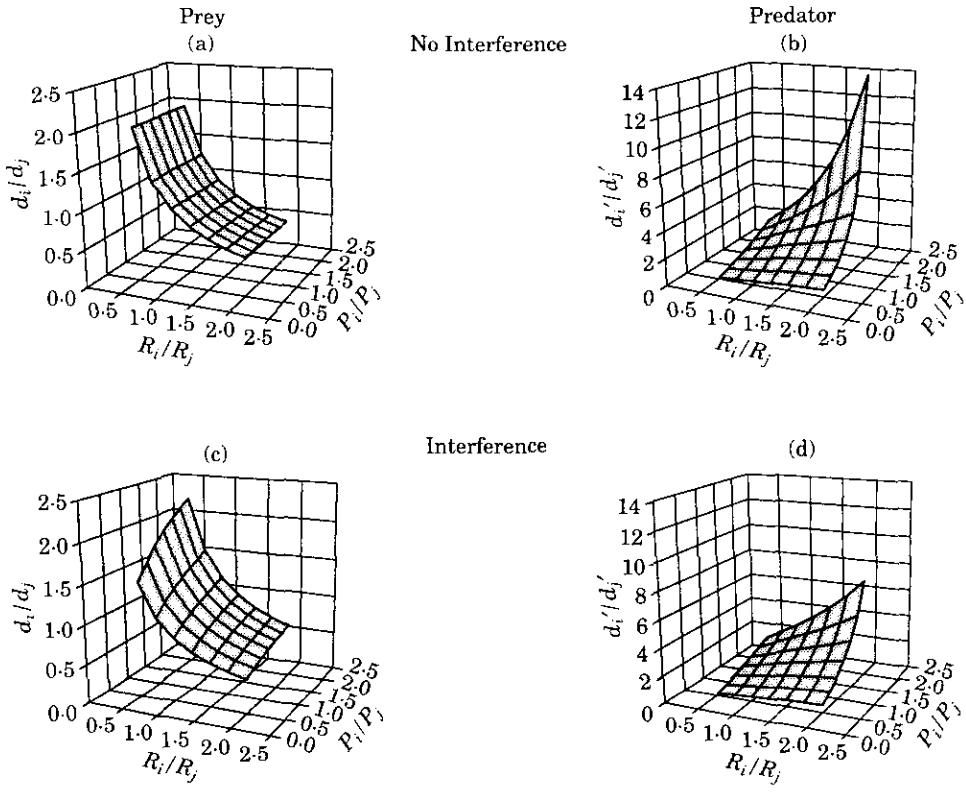

FIG. 2. Results of the habitat selection game for any two habitats i and j. All panels show the ratio of prey (d_i/d_j) or predator (d_i'/d_j') densities as a function of the ratios of habitat riskiness (R_i/R_j) and productivity of the prey's food resource (P_i/P_j). The value of other model constants are given in Table I and described in the text. Panels (a) and (b) are the results for the basic model; (c) and (d) are the results with interference between predators. Dilution has no effect on the equilibrium, with or without interference.

equal to the ratio of the productivity levels after they have been discounted by the ' foraging ' and ' metabolic ' costs of the prey in each habitat [equation (14)]. This ratio depends on prey abundances since the greater the prey density, the greater the amount of energy required for their maintenance. Since prey density depends on habitat riskiness (see above), predator density will also depend on the habitat riskiness ratio [Fig. 2(b)]. The magnitude of the effect will depend on the prey's foraging efficiency (F), metabolic rate (M), and population size (N). Figure 2 illustrates the results for values of M, F, and N (see Table I) chosen so that 10% of the total productivity of the system (all habitats combined) is used up by the prey as ' foraging ' costs, and 40% lost through fixed ' metabolic ' costs. While these values are arbitrary, the predator distribution is significantly affected by habitat riskiness as long as metabolic costs (expressed in M) exceed about 20% of the total energy available.

INCORPORATING DILUTION

To this point, we have effectively modelled a functional response without any saturation, i.e., the number of prey eaten by a predator (and by the predator population as a whole) rises linearly with prey density. This is clearly unrealistic,

since the *per capita* prey mortality rate most often decreases as prey density increases, an effect known as ' risk dilution '. To increase the model's realism, we now incorporate into the model the fact that predators must spend a certain proportion of their time handling and digesting already captured prey, and that they cannot use this time to search for additional prey. We do so by adding an additional term to the equations for $\theta(i)$ and $\beta(i)$, based on Holling's (1959) disc equation. By doing this we convert our functional response to a Holling Type II response and provide a functional model of the dilution effect. The prey's probability of death now declines asymptotically with prey density, while the predator capture rate increases at a decelerating rate with prey density:

$$\beta(i) = R_i\, d_i' \left[\frac{1}{1+R_i\, D\, d_i} \right] \tag{15}$$

$$\theta(i) = R_i\, d_i \left[\frac{1}{1+R_i\, D\, d_i} \right] \tag{16}$$

where D is the amount of time spent handling (catching, eating and digesting) a single prey item. Of course, this is only one possible behavioural mechanism which will produce a dilution effect, but the general form of the equation will be similar in the other cases.

Interestingly, the equilibrium prey and predator density ratios [equations (13) and (14)] are unaffected by the addition of dilution to the model. Thus, dilution has no effect on the equilibrium distributions of predator and prey.

INCORPORATING INTERFERENCE

Just as encounters with prey take up time that cannot be used for searching, so do encounters with other predators; this can be considered interference. The total amount of time spent on conspecific interactions depends on predator density (d_i'), the predator collision coefficient (C_i; equivalent to rate of successful search, but for contact between one predator and another), and the time cost of each encounter (I = the amount of time spent interacting with a single competitor). By analogy with the derivation of the disc equation (Holling, 1959), we end up with the following equations for the *per capita* prey death and predator capture rates:

$$\beta(i) = R_i d_i' \left[\frac{1}{1+R_i\, D\, d_i + C_i\, I\, d_i'} \right] \tag{17}$$

$$\theta(i) = R_i d_i \left[\frac{1}{1+R_i\, D\, d_i + C_i\, I\, d_i'} \right] \tag{18}$$

Again, there are other ways to imagine interference working, but all will have the same effect, namely a decrease in predator capture rate and a deceleration in the rate of increase in prey death rate with increasing predator density. Interference is often represented in population models using the mathematically more tractable equation of Hassell & Varley (1969). We avoided this equation due to

its undesirable characteristic of increasing predator capture rate with increasing interference when predator densities are less than 1.

Due to the mathematical complexity introduced by adding interference, the equilibrium for this version of the game cannot be solved analytically. However, setting $w(i)=w(j)$ and $w'(i)=w'(j)$ and solving for the equilibrium ratios of prey (d_i) and predator (d_i') densities between any two habitats (i and j), gives the following pair of equations:

$$\frac{d_i}{d_j}=\frac{R_j(1+C_i d_i' I)}{R_i(1+C_j d_j' I)} \tag{19}$$

$$\frac{d_i'}{d_j'}=\frac{P_i F-d_i M}{P_j F-d_j M}. \tag{20}$$

The prey ratio now includes terms for predator density (d_i'), the predator collision coefficient (C_i) and the interference coefficient (I) as well as habitat riskiness (R_i). The predator's density ratio, expressed in equation (20), is similar in form to equation (14) given for the basic model, and is interpreted similarly. However, because the addition of interference to the model changes the prey distribution, equation (20) is not strictly identical to equation (14) and yields different results [cf. Figs 2(b) and (d)]. Again, dilution does not appear in either equation and has no effect on the equilibrium.

To determine the actual equilibrium density ratios, we simulated the game (for two identical sized habitats) on a computer using the constant values given in Table I and the evolutionary difference equations described in Appendix II. For simplicity, the values in Table I were chosen assuming that predators and prey are similar in size but prey are 10 times as abundant. Although many of the values in Table I were chosen arbitrarily, most are irrelevant to the equilibrium anyway. The choice of the prey's 'foraging efficiency' (F), 'metabolic' rate (M) and population size (N) has already been discussed. The interference (I) and predator collision coefficient values (C_i) were chosen so that the predator's capture rate ($\theta(i)$) at the mean predator density was reduced by 20% due to interference. The results of the simulations are given in Figs 2(c) and (d). Both the prey and predator density ratios are affected by the addition of interference. The prey's density ratio is now partially determined by the habitat productivity ratio, although the habitat riskiness ratio remains the most important determinant. The predator's density ratio is qualitatively unchanged but the magnitude of both the riskiness and productivity effects are reduced by interference; not surprisingly, with interference the predators are more evenly distributed between habitats.

DISCUSSION

Ecological implications

In all versions of our model prey distribution is determined by habitat riskiness (the inherent riskiness of the habitat independent of predator density). Prey should prefer habitats where predator search rate or capture efficiency are

compromised. This prediction is not surprising and is supported by the many observations of prey preferring habitats with more cover provided by physical structure. For example, Schmitt & Holbrook (1985) showed that juvenile black surfperch, *Embiotoca jacksoni* Agassiz, prefer structurally-complex substrates in the presence of predators. Several other examples are reviewed by Lima & Dill (1990). More specifically, our model predicts that prey density should be inversely related to habitat riskiness (' safety matching '); we know of no data to test this prediction.

More surprising is the prediction that prey distributions are not affected (with no interference between predators) or may be only marginally affected (with interference) by differences in productivity (the availability of food resources) between habitats. Therefore, prey distributions will not respond, or will respond only slightly, to experimental changes in food abundance. This prediction is quite different than that of the Ideal Free Distribution (prey should respond to productivity) or the IFD incorporating predation risk (prey should respond to both productivity and the overall predation risk—due to the combined effects of habitat ' riskiness ' and predator density). Our model makes no prediction about the influence of predator density on prey habitat use. Indeed, it is meaningless now to talk about experimental manipulation of predator distribution, since they will re-assort themselves anyway.

It is important to emphasize that even though habitat productivity does not influence their equilibrium distribution, prey are explicitly considering both foraging and risk when choosing a habitat, since both affect fitness. Food availability and predator densities influence patterns of prey distribution, but do so through circuitous and unobvious routes when the predators and prey are able to respond to one another's habitat choices. We might think about these effects as ' the ghosts of competition and predation present '.

Furthermore, although the prey distribution is unaffected by habitat productivity, the prey turnover rates will be. Animals will lead shorter but more productive lives in the richer environment, and this will have consequences for population age structure.

Our habitat game predicts that predators should be more numerous in inherently ' risky ' habitats [Figs 2(b) and (d)]. This prediction is not surprising though we can find no data to support it. What is more interesting is the prediction that predators should also be more numerous in habitats with higher productivities. Predators will appear to distribute themselves in an ideal free manner, but with respect to a trophic level two steps removed, rather than to their own prey abundances. Gilliam & Fraser (1988) made the same prediction concerning the relationship of predator and food density, but only for the case of stationary predators. van Baalen & Sabelis (1993) predicted a similar result from their ESS model of patch distribution. They observed (p. 660) that ' it is striking that patch quality distribution is more conspicuously reflected in the ESS predator patch selection strategy than in the prey patch selection strategy ', but did not consider further the observation or its ultimate cause. Again our predictions are different from the IFD; predators will not necessarily be distributed according to their prey's distribution.

Dilution has no effects on the distribution of either predators or prey in our model. Interference, however, affects both distributions; with interference the

prey's distribution is affected by productivity and the predator distribution is more homogeneous.

In the ecological literature, particularly the aquatic ecology component, there has been considerable interest in the issue of top-down *v.* bottom-up control (see, e.g. Matson & Hunter, 1992). According to the top-down scenario, a population's characteristics (especially its size, but other characteristics as well) are determined by the trophic level above itself (i.e. effects cascade downward from the top carnivore level); by contrast, according to the notion of bottom-up control, populations are influenced most by the trophic level directly below themselves, and ultimately by the primary producers. What does a game-theoretic approach to habitat selection have to say about such a dichotomy? When the opportunity for gaming exists between and within trophic levels the equilibrium cannot be predicted simply by either ' top-down ' or ' bottom-up ' logic. For example, in our model prey distributions are not predictable solely from the distribution of their food resource (from below) or their predators' distribution (from above). Similarly, the predator's distribution cannot be predicted solely on the basis of the prey's distribution (from below). Clearly, the 'top-down *vs* bottom-up ' dichotomy is far too simplistic to handle the complex interactions introduced by habitat games, which surely are characteristic of real communities (cf. DeMelo *et al.*, 1992).

As with any model, it is important to consider the assumptions of our model. We assume, as do many IFD models, that prey divide all of the habitat productivity equally amongst themselves. Other models of resource utilization by prey exist and could change the outcome of the game. We assume that the prey's food resources are relatively immobile and unable to ' game ' for themselves. Similarly, we assume that predator mortality (and hence lifespan) is constant across habitats as would be the case if they were top carnivores. Different results would be expected if additional trophic levels were added to the game. Finally, we assume that both the prey and predator populations are constant in size.

Application of habitat games to fish predator–prey interactions

Game theory may be applied to any situation in which prey fish must choose between feeding habitats (or patches) varying in both food availability and the risk of predation. Some such situations are dynamic, whereby the optimal habitat choice depends on forager size (an example of state dependence), leading to the well-known ontogenetic niche shifts of fish as they grow (e.g. Werner & Gilliam, 1984).

There are other sorts of dynamic situations where a game theoretic approach may be a worthwhile addition to the fish biologist's toolbox. For example, many planktivorous fish migrate vertically in the water column on a daily basis, being closer to the surface at night than during the day. Functional explanations of this phenomenon are exceedingly diverse, but its role in reducing predation risk is widely accepted (see, e.g. Clark & Levy, 1988). Frequently, the zooplanktonic prey of these fishes exhibit diel vertical migrations as well, and this is usually interpreted as a predator avoidance tactic (Zaret & Suffern, 1976). It is apparent that diel vertical migration has all the elements of a habitat selection game, since both zooplankton and fish are free to distribute themselves among depth strata,

and temporal changes in habitat characteristics (food availability and riskiness, the latter dependent on light level) may produce corresponding changes in the equilibrium distributions, resulting in diel migrations of both parties. There have been two previous attempts to model vertical migration as a game, but they have both been incomplete. Iwasa (1982) failed to include a self-interaction term for either the predator or the prey. In his model, the fitness of either party depends only on the spatial distribution of the other, but not of themselves; thus, his equilibrium distribution cannot be stable (see Gabriel & Thomas, 1988). Although they claimed to be dealing with the same problem, Gabriel & Thomas (1988) actually modelled a game between the prey, rather than between predators and prey (the predatory fish were assumed not to migrate vertically).

To apply a game theoretic model to diel vertical migration it will first be necessary to add a fourth trophic level, since the presence (and behavioural decisions) of predatory fish undoubtedly modifies the migratory behaviour of the planktivores. As Eggers (1978) puts it: 'The pattern of mutual diel vertical migration of zooplankton and planktivorous fish is a complex equilibrium of the processes of resource exploitation and predator avoidance affecting four trophic levels'. We are currently working on this problem, and will report the results elsewhere.

There are other fish habitat selection games involving migration. For example, some small fishes show diel horizontal migrations in lakes [e.g. golden shiners, *Notemigonus crysoleucas* (Mitchill), Hall *et al.*, 1979; silversides, *Menidia beryllina* (Cope), Wurtsbaugh & Li, 1985; northern redbelly dace, *Phoxinus eos* (Cope), Naud & Magnan, 1988]. The day–night faunal changeover in coral reef fishes (Hobson 1972; Helfman, 1986) provides a rich source of other examples of fish migration which might be studied profitably from a game theoretic perspective.

CONCLUDING REMARKS

Perhaps the single most important new insight arising from our modelling of habitat selection as a game is the prediction that prey distributions may not respond to experimental changes in food abundance, whenever their predators are also free to respond in a dynamic way. This is a particularly novel and interesting result, because it is both non-intuitive and subject to experimental test.

We have become increasingly convinced of the value of applying a game theoretic perspective to studies of predator–prey interactions. Not only can it be useful in thinking about broad scale problems like habitat selection, but also in considering the details of the actual behavioural interactions between predator and prey. For example, in our laboratory we are currently using the approach to study the evolutionary stability of the apparent pursuit deterrence signal ('bobbing'; Smith & Smith, 1989) given to predatory lizardfish (*Saurida* sp.) by the Hawaiian goby *Asterropteryx semipunctatus* Rüppell.

We have also applied game theory to a quite different sort of behavioural interaction, the 'hiding–waiting game' between a hiding prey and the predator waiting for it to re-emerge. For example, the polychaete worm *Serpula vermicularis* L., when frightened by vibration or water movement caused by an attacking

gunnel or blenny, withdraws into its calcareous tube. Within its tube the worm is safe, but it cannot feed or respire. Consequently, it must emerge eventually, and the fish can choose to wait for it or pursue other prey. This is quite obviously a game, since the best hiding time of the worm depends on the waiting time chosen by the fish, and *vice versa*.

Our point is that games are to be seen everywhere in predator–prey interactions—when you know what to look for. We believe that thinking of fish predator–prey interactions in this framework will enrich our understanding of the predation process, and provide a novel and useful guide for future observation and experiment.

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APPENDIX I: ALL HABITATS ARE OCCUPIED

We show that any evolutionary equilibrium must be a mixed equilibrium with support from all pure prey and predator strategies. Any pure strategy which is played with a non-zero probability in a mixed equilibrium is said to be in ' support ' of that equilibrium (see Maynard Smith, 1982). A stable evolutionary equilibrium, not supported by prey strategy i (i.e. $p_i=0$) cannot exist if:

$$w(i) > w(j) \tag{A1.1}$$

where j is any prey strategy in support of the equilibrium. Substituting in the appropriate terms and simplifying (knowing that $\overline{\omega} > 0$ for any valid equilibrium) yields:

$$\left[\frac{1}{\beta_i}\left(\frac{P_i}{d_i}F - M\right) - G\right]/\mathrm{O} > \omega(j) \tag{A1.2}$$

As p_i (and hence d_i) approaches zero, equation (A1.2) must become true since $0 < \omega(j) < \infty$ and $0 \leq \beta_i < \infty$ (n.b. equation (A1.2) will also become true as d_i', and therefore β_i, approaches zero). Intuitively, this proof merely states that as the density of prey (or predators) in habitat i approaches zero, the prey's payoff in habitat i becomes very large. Thus, any evolutionary equilibrium must be supported by all pure prey strategies.

For a mixed equilibrium supported by all pure prey strategies, the payoffs for any two pure prey strategies (i and j) must be the same:

$$w(i) = w(j) \tag{A2.1}$$

Let i correspond to a predator strategy not in support of the equilibrium (i.e. $p_i' = 0$) and j a strategy in support (i.e. $p_j' > 0$) of the equilibrium. Again, after substituting in the appropriate terms and simplifying (knowing that $\overline{\omega} > 0$ for any valid equilibrium), equation (A2.1) becomes:

$$\frac{1}{\beta_i}\left[\frac{P_i}{d_i}F - M\right] = \frac{1}{\beta_j}\left[\frac{P_j}{d_j}F - M\right]. \tag{A2.2}$$

Clearly, as p_i' (and hence β_i) approaches zero, equation (A2.2) must become false since d_i, d_j and $\beta_j > 0$. Again this proof merely states that as the density of predators in i approaches zero, the prey's payoff in i becomes very large. Therefore, we conclude any evolutionary equilibrium must also be supported by all pure predator strategies.

APPENDIX II: EVOLUTIONARY STABILITY

We examined the evolutionary stability of all equilibria produced by our model in terms of dynamic evolutionary stability (Taylor & Jonker, 1978; Hofbauer & Sigmund, 1988; Friedman, 1991). We did this by simulating the game using the finite evolutionary dynamics described by equations (A5) and (A6), which are based on the evolutionary difference equation described by several authors (see Maynard Smith, 1982, equation D.1; Hofbauer & Sigmund, 1988, equation 27.3). This equation assumes that fitness represents the multiplication 'rate' (R_o) defined over the generation time. However, because the generation times (i.e. lifespans) of the predators and prey vary in our model, the finite multiplication 'rates' must be re-defined over the same time units (see Giske *et al.*, 1993). The appropriate multiplication 'rates', defined over a single time unit, for the prey ($\lambda(i)$) and predators ($\lambda'(i)$) in each habitat are given by:

$$\lambda(i) = w(i)^{1/l(i)} \tag{A3}$$

$$\lambda'(i) = w'(i)^{1/L'} \tag{A4}$$

Substituting equations (A3) and (A4) into Maynard Smith's (1982) evolutionary difference equation produces the following equations for the finite changes in p_i (Δp_i) and p_i' ($\Delta p_i'$) over one time unit:

$$\Delta p_i = p_i \frac{\lambda(i) - \overline{\lambda}}{\overline{\lambda}} \tag{A5}$$

$$\Delta p_i' = p_i' \frac{\lambda'(i) - \overline{\lambda}'}{\overline{\lambda}'} \tag{A6}$$

where $\overline{\lambda}$ and $\overline{\lambda}'$ are the mean lambda values for the prey and predators, respectively, given by:

$$\overline{\lambda} = \sum_i p_i \lambda(i)$$

$$\overline{\lambda}' = \sum_i p_i' \lambda'(i).$$

We simulated all equilibria (for the basic model, the model with dilution, and the model with interference, with and without dilution) using the constant values given in Table I (plus many other sets) for two, three and four habitat scenarios. In all cases the simulations quickly converged on the equilibrium as long as the equilibrium fitness values were valid ($w(i)$ and $w'(i) > 0$). We thus conclude that our game is evolutionarily stable.

It is worth noting that while equations (A5) and (A6) represent the dynamics of an evolving polymorphic population, they could also reasonably model the dynamics of individuals switching between habitats during their life in order to maximize their residual reproductive value. In either case, an increase in p_i or p_i' will result when the expected residual reproductive value in habitat i is greater than the population mean. Thus, we interpret the mixed equilibrium as either the proportions of pure strategists in a polymorphic population, or a probability distribution of pure strategies in a monomorphic population, with individuals switching between habitats according to equations (A5) and (A6).