

PREDATOR AND PREY HABITAT SELECTION GAMES: THE EFFECTS OF HOW PREY BALANCE FORAGING AND PREDATION RISK

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ABSTRACT

The spatial distributions of predators and prey can be shaped by both intra- and interspecific games. Most predator–prey studies, however, have ignored the interspecific game by focusing on how either predators or prey distribute themselves while holding the distribution of the other species fixed. We use genetic algorithms to examine how the distributional outcome of the game between predators and prey depends on how prey balance the costs of predation risk and the benefits of foraging success. We construct two prey fitness functions. The first prey fitness function has prey reproducing when they reach a threshold mass, which leads to prey choosing patches by minimizing the ratio of predation and foraging rates (μ/f). The second prey fitness function has prey reproducing at the end of a season with mass-dependent reproductive success, which leads to prey choosing patches by maximizing their increase in reproductive value over time. When prey minimize μ/f , predator and prey distributions are unaffected by the overall level of predation risk. In contrast, when prey maximize their increase in reproductive value, under conditions with low predation risk the distributions of prey and predators are shaped mainly by prey competition and the distribution of resources, and as the overall level of predation risk increases the distribution of prey is increasingly shaped by the distribution of predators. Thus, the dynamics of how predators and prey distribute themselves and interact may depend on factors that affect the overall level of predation risk, such as per predator capture rates, predator densities, and shelter from predation.

INTRODUCTION

The interactions of prey and predators are a key component in community dynamics. The rates and outcomes of their interactions directly and indirectly affect abundances at various trophic levels. However, very little is known about how predators and prey behave concurrently, in response to one another (Lima, 2002). There is extensive literature on how prey balance the benefits of foraging and the risks of predation (Lima and Dill, 1990; Lima, 1998) and how predators optimally forage for prey (Fretwell and

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Lucas, 1970; Stephens and Krebs, 1986), but surprisingly few studies have examined the two processes concurrently.

One fundamental issue is how predators and prey use space. The spatial overlap of predators and prey affects their interaction rates and thus the strength of predator effects on prey and community dynamics (Murdoch and Steward-Oaten, 1989; Krivan, 1997; van Baalen and Sabelis, 1999). Predators should use space in a manner that maximizes their foraging success, which is a function of prey densities and, often, predator interference. Thus, predators are expected to be more abundant in patches where prey are more abundant. Prey space use must balance the risk of predation and the benefits of foraging. How this balance is achieved depends on how predation and foraging success affects prey reproduction (Gilliam and Fraser, 1987; Ludwig and Rowe, 1990; Houston and McNamara, 1999), but in general prey should favor areas with higher resources and avoid areas with higher predation risk. Thus, predators should try to aggregate in areas with more prey and prey should try to avoid areas where predators have aggregated. This conflict between the habitat selection of predators and prey makes it critical to study predator and prey space use concurrently, rather than studying either in isolation.

A recent review by Lima (2002) suggested that there have only been a few experimental studies on how predators and prey use space when both are allowed to move freely (Sih, 1984; Formanowicz and Bobka, 1989; Bouskila, 2001). These studies have demonstrated that the spatial distributions of predators and prey are very different when both species are allowed to alter their spatial distribution, as opposed to when one species is experimentally fixed at a set distribution.

A few theoretical studies have examined how predators and prey should distribute themselves in space when both are free to choose their locations. Predominantly these models have focused on a system where a single predator species attacks a single prey species (see Bouskila, 2001, and Heithaus, 2001, for the inclusion of multiple predators and intraguild predation, respectively), prey compete for a resource, and both predators and prey are choosing between two patches with fixed levels of resources for prey (r) and shelter from predators ($1/k$). Using a game theory approach, Sih (1998) found the evolutionary stable strategy (ESS) distributions of predators and prey where neither could improve their fitness by moving to another patch. When patches varied in resources but offered equal levels of shelter, the proportion of predators in the patches matched the ratio of resources in the patches and prey were uniformly distributed if prey-dependent predation (i.e., predators do not interfere with each other) and ideal prey competition were assumed. This surprising result says that predators should distribute themselves to match the resource that their prey consumes, but that prey should apparently ignore the distribution of their resource. When predation risk was ratio-dependent (i.e., predators have ideal competition for prey), predators and prey both matched the ratio of resources in the patches. Finally, when patches offered equal levels of resources but varied in the levels of shelter from predation, and predation was prey-dependent, predators were uniformly distributed and the proportion of prey in the patches matched the ratio of shelter offered by the patches.

Hugie and Dill (1994) examined a similar situation, but included metabolic costs for

predators and prey and varied predator competition between the extremes of prey- and ratio-dependent predation. Their results were more complicated, but generally similar to those reported by Sih (1998). The primary difference is that predators or prey sometimes under-matched resource ratios because of metabolic and foraging costs. Unlike Sih (1998), they examined a situation where patches offered equal levels of resources but varied in their levels of shelter from predation and there was predator interference, and found a higher proportion of predators in the patch with less shelter and the distribution of the prey matching the ratio of shelter from predation.

Alonzo (2002) used dynamic state variable models to examine how predator and prey distributions are affected by whether individuals are maximizing survival or instantaneous reproduction, and by the risk of starvation and inclusion of state-dependent behavior. When predators and prey were assumed to be maximizing their instantaneous reproduction (the situation most comparable to the previous models), predators and prey exhibited ideal competition, and patches varied in resources (variable shelter in the patches was not included in the model), the proportion of predators and prey roughly matched the resource ratios of the patches, but not perfectly because prey near starvation disproportionately favored the patch with more resources (Alonzo, 2002). Thus, where the three models overlapped there is general agreement about how predators and prey are expected to distribute themselves, but state-dependent prey behavior may significantly affect the distributions and dynamics of predator and prey populations.

In the above models, prey must balance the costs of predation risk and the benefits of foraging success. How prey trade-off predation risk and foraging success has been a major topic in ecology and behavioral ecology, with two main modeling approaches being advocated for finding optimal prey behavior. One approach says that prey should minimize the ratio of the rate of predation risk (μ) and the rate of foraging gains (f) (Gilliam and Fraser, 1987). This approach produces optimal prey behavior if prey are growing to a threshold size at which reproduction occurs and prey have unlimited time to reach the threshold (Houston and McNamara, 1999). However, the approach does not produce optimal prey behavior if: (1) time is limited, (2) prey reproductive success is affected by how quickly they reach the threshold or by their size or mass beyond the threshold, or (3) the benefits of foraging vary with an individual's state (Ludwig and Rowe, 1990; Houston and McNamara, 1999). In those cases, the optimal prey behavior is the behavior that maximizes the individual's net rate of increase in reproductive value over time, which may change with an individual's state (Houston and McNamara 1999). In the latter scenario, optimal solutions are typically found using dynamic state variable models (Houston and McNamara, 1999; Clark and Mangel, 2000). Empirical data suggests that the second approach with state-dependent behavior describes prey behavior better than models that minimize μ/f (Skalski and Gilliam, 2002).

The models by Hugie and Dill (1994) and Sih (1998) assumed that prey balance the benefit of foraging and the risk of predation associated with alternative patches by minimizing the ratio of predation and foraging rates (μ/f). Thus, they are modeling a situation where prey are growing to a threshold at which they reproduce. Their results were insensitive to the magnitude of predation risk (i.e., the predicted distributions of

prey and predators from these models were unaffected by the number of predators in the system or by how effectively the predators capture prey). When prey are minimizing μ/f , increasing predation risk in both patches by the same factor has no effect on the relative values of μ/f in the patches.

Here, we examine how the predicted distributions of predators and prey are affected by assumptions about prey reproduction, by the overall level of predation risk across patches, and by patches simultaneously varying in resources and shelter. We use genetic algorithms to construct predator and prey patch-switching rules, which then produce the expected distributions of predators and prey. We first confirm that the genetic algorithm produces equilibrium distributions of predators and prey by using the same assumptions as Sih (1998), particularly that prey reproduce when they reach a threshold mass and balance predation costs and foraging benefits by minimizing μ/f , and showing that the genetic algorithm produces the same results as Sih's game theory model. We then assume that prey reproduction occurs at the end of a season and depends on the prey's final mass, and find that this produces different predicted predator and prey distributions than the previous models. In particular, we find that the overall level of predation risk has a large effect on the distribution of predators and prey. Finally, we examine how differences in patch resources and shelter from predation interact by simultaneously varying the two factors.

METHODS

We model a simple tritrophic chain with predators, prey, and resource eaten by the prey. There are two patches, where each patch has a fixed level of the resource, and each patch offers prey a level of shelter from predation. Both predators and prey are free to move between the two patches without any costs or time delays. These assumptions match previous models (Hugie and Dill, 1994; Sih, 1998; Alonzo, 2002).

To find equilibrium distributions of predators and prey in the two patches, we use genetic algorithms. Genetic algorithms use the algorithm of natural selection to identify optimal solutions from a set of potential solutions, with the variance in proposed solutions maintained by mutations and crossing-over events (Holland, 1975). The primary strength of genetic algorithms is that they can solve optimality problems that are too complex for other modeling approaches, such as game theory and dynamic state variable models. They have been extensively used for finding optimal solutions in machine learning, constructing networks, and predicting dynamical systems (Goldberg, 1989; Mitchell, 1996). They have also been successfully used to investigate biological optimization problems (Sumida et al., 1990; Bouskila et al., 1998). We chose to use genetic algorithms for two reasons. First, genetic algorithms allowed us to locate equilibrium predator and prey distributions when prey reproduction was state-dependent and occurred at the end of season, a common natural scenario that previous models using a dynamic state variable game approach were not able to identify (Alonzo, 2002). Second, the genetic algorithm approach will allow us, in the future, to investigate how movement costs and imperfect information affect predator and prey distributions.

We assume that there are initially 500 predators and 500 prey each season. Using equal numbers of predators and prey minimizes differences in the level of selection and genetic variance for the two species. We assume that there are 60 time-steps in a season and during each time-step each individual (predator and prey) has the opportunity to leave its patch (below we give details about how that decision is made.) Before the first time-step (the beginning of a generation), we randomly place individuals in the two patches with equal probabilities. During each time-step, the order in which individuals are given the opportunity to move is randomly determined. After a prey’s decision to stay or switch patches, it forages and its foraging success is deterministic. We assume ‘Ideal’ competition among prey; i.e., prey mass (x) increases linearly with the level of resources in the patch (r_i), but is an inverse function of the number of prey in the patch (N_i). Prey are removed from the system by either predation or when they reach a threshold mass for reproduction (which depends on the prey fitness function). To avoid the situation where prey depletion results in increased per capita resources for prey, we scale the amount of resources to the fraction of the prey remaining in the system (with N_{max} being the initial number of prey and N_{total} being the total number of prey still in the system). This assumption had no qualitative effect on our results, but lowered the variance in predator and prey distributions given the threshold fitness function. The mass of prey j at time-step $t + 1$ is then

$$x_j(t + 1) = x_j(t) + \frac{r_i \frac{N_{total}}{N_{max}}}{N_i} \tag{1}$$

We assume that there are no metabolic costs, and thus prey do not starve.

After a predator decides to stay or leave a patch, it forages for prey. We consider two scenarios: (1) there is no interference between predators (prey-dependent predation risk) and (2) interference between predators is ideal (ratio-dependent predation risk). The expected rates of foraging success for a predator in patch i for these scenarios are

$$\begin{aligned} z(N_i, P_i, \text{patch}) &= a k_i N_i && \text{prey-dependent} \\ z(N_i, P_i, \text{patch}) &= a k_i \frac{N_i}{P_i} && \text{ratio-dependent} \end{aligned} \tag{2}$$

The overall level of predation risk is set by the predator capture rate (a), and the relative riskiness of the patches is set by ratio of k ’s for the patches. For either function, the expected rate of predator foraging success can exceed 1. Since partial prey mortality is impossible, the number of prey eaten by a predator is randomly truncated or rounded up based on the fraction of prey eaten. The cumulative number of prey a predator m has eaten is updated at each time-step:

$$E_m(t + 1) = E_m(t) + \text{predator success} \tag{3}$$

We determine which prey a predator kills by randomly selecting and removing prey from the patch occupied by the predator.

At the end of a season, predators and prey reproduce and die. Generations are non-overlapping. To reduce differences in inherent opportunities for evolution for the two species, we assumed that predator and prey generations were of equal lengths. To focus on behavior, and for simplicity, we did not consider population dynamics. Instead, we held predator and prey numbers constant across generations.

We examine how two different prey fitness functions affect the distributions of predators and prey. The first prey fitness function (threshold reproduction) assumes that prey reproduce when they reach a threshold mass ($x_c = 10$). To ensure that prey have enough time to reach the threshold, we raise the number of time-steps in generations of prey and predators to 120. Thus, the only way prey can fail to reach the threshold is to be killed by a predator before reaching x_c . There are no fitness advantages for reaching x_c quickly (other than reducing the number of time-steps the individual is exposed to predation risk) or for exceeding x_c . These assumptions match the conditions in which minimizing μ/f gives optimal prey behavior and thus match the assumptions in Hugie and Dill (1994) and Sih (1998). When prey reach x_c , their level of reproduction (w_N) is set equal to 1 and they are removed from the system.

The second prey fitness function (mass-dependent reproduction) assumes that prey that survive to the end of a season reproduce and their reproductive success is a linear function of their mass at the end of the season. Thus, the level of reproduction for prey j is

$$\begin{aligned} w_N(j) &= x_j(60) && \text{if alive at end of season} \\ w_N(j) &= 0 && \text{otherwise} \end{aligned} \tag{4}$$

This fitness function is appropriate for species with a relatively distinct foraging season followed by a breeding season, such as many amphibians and insects. The assumption of size-dependent reproductive success has commonly been observed. Larger females often produce more offspring and in some cases are preferred mates, and larger males in some cases provide better parental care and gain more copulations through female mate choice or male–male competition (reviewed in Andersson, 1994).

We use a single predator fitness function that assumes that their level of reproduction is a linear function of the number of prey they have eaten by the end of the season,

$$w_p(j) = E_m(60) \tag{5}$$

We calculate the relative fitness of each individual (j) of each species

$$\begin{aligned} \Phi_N(j) &= \frac{w_{N(j)}}{\sum_{i=1}^{500} w_{N(i)}} \\ \Phi_p(j) &= \frac{w_{P(j)}}{\sum_{i=1}^{500} w_{P(i)}} \end{aligned} \tag{6}$$

The parentage of offspring in the subsequent generation is determined by roulette sampling, where offspring are randomly assigned a parent based on the relative fitness of each adult (Mitchell, 1996).

PATCH-SWITCHING RULES

For each patch, each individual (predator or prey) has a patch-switching rule that sets the probability of leaving its current patch. The rules are similarly constructed for the two species, and we will describe the rule for an individual prey in patch 1. A prey individual's decision to stay or leave a patch should depend on: (1) foraging success in the current versus the alternative patch, which is a function of resources and the number prey in the two patches, and (2) predation risk in the current versus the alternative patch, which is a function of shelter and the number of predators in the two patches. Thus, a prey patch-switching rule should account for many factors and could be quite complicated.

As noted earlier, genetic algorithms can be a powerful tool for solving complicated optimality problems. To emphasize, although genetic algorithms use the metaphor of genes, selection, and evolution to solve optimality problems, they are not meant to mirror the actual genetics of any specific biological system. Instead, a key to a successful genetic algorithm is keeping the number of 'genes' shaping behavior as low as possible, since too many genes leads to weakened selection and a lowered probability of the genetic algorithm finding optimal solutions. Therefore, we designed a prey behavioral rule that incorporates the above factors while only using a small number of 'genes'.

We first defined a set of 4 genes per patch (8 total, see Appendix) that determine a prey individual's indifference surface—the set of conditions when a prey individual has an equal probability of staying versus leaving the current patch (Fig. 1). If $N_1 < N_1^*$ (where N_1^* is the number of prey present in patch 1 when probability of leaving the patch is 0.5), then the probability of the prey leaving patch 1 is less than 0.5, whereas if $N_1 > N_1^*$, it has a probability greater than 0.5 of leaving patch 1. A lower value of N_1^* means that prey have a greater tendency to leave patch 1 (not as much competition is needed to drive prey out of patch 1). An additional parameter, Δ , determines the rate at which the probability of a prey individual leaving patch 1 changes as N_1 varies from N_1^* (see Appendix). If Δ is small, then small changes in N_1 cause a steep change in the probability of leaving patch 1. Very small values of Δ correspond to a 'yes-no', threshold behavioral rule. If $N_1 < N_1^*$, then prey stay in patch 1, whereas if $N_1 > N_1^*$, prey leave the patch. In contrast, larger values of Δ mean that changes in N_1 cause smaller changes in the probability of leaving patch 1.

The predator patch-switching rules follow the same basic form, except that increasing prey numbers in the current patch increases rather than decreases the probability that the predator will stay in the patch. For a given resource and shelter regime, the genetic algorithm solves for the ESS—the best prey and predator patch-switching rules, accounting for the rules followed by other individuals of both species.

The predator and prey decision rules are not state-dependent. The rules do not incorporate the current mass of the individual or the current time period. This was done

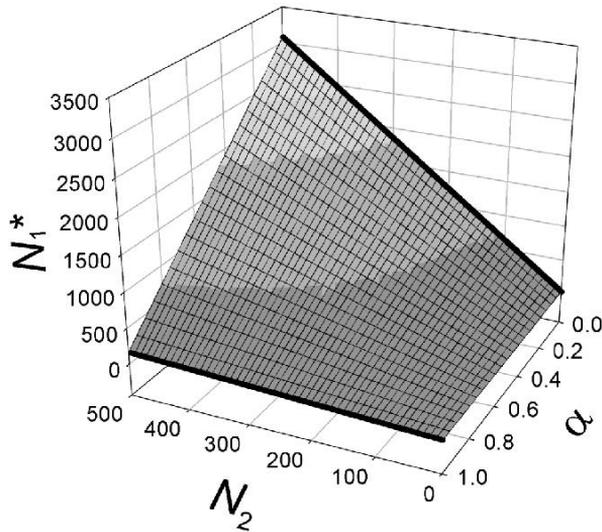


Fig. 1. Indifference surface for a prey individual in patch 1. For every combination of N_2 and α (proportion of the predators in the prey individual's current patch), there is an associated N_1^* , which is the number of prey present in patch 1 that cause the individual prey to have a 0.5 probability of leaving patch 1. The two lines at $\alpha = 0$ and 1 are each set by a pair of genes (a slope and an intercept at $N_2 = 0$, see Appendix), and points between the two lines are linear interpolations along the corresponding N_2 value. The probability of prey leaving patch 1 decreases (i.e., N_1^* increases), when N_2 increases, presumably because competition in patch 2 is increased, and when α decreases, presumably because predation risk in patch 1 is decreased.

to keep the genomes smaller. We reduced the need for state-dependent rules by assuming there are no metabolic costs and therefore no risk of starvation, and by assuming the predator and prey fitness functions are linear.

SOURCES OF GENETIC VARIANCE

Each run of the model is 1000 generations. At the beginning of each run we randomly draw the genotypes of each individual. For predators and prey, the 8 indifference surface parameters ('genes') are drawn from a uniform distribution from -5 to 5 , and Δ is drawn from a uniform distribution from 0 to 500 . The distributions from which the gene values are drawn have little effect on the results. All of the gene values are continuous and, as described later, are subject to mutation. Values of the indifference surface parameters are unconstrained, while $\Delta > 0$.

Offspring imperfectly inherit their parent's genes. For each offspring there is a probability (0.05) of exchanging genes with another offspring. When this occurs, another offspring of the same species and starting and stopping points are randomly chosen. Genes at these points and in between are exchanged between the offspring.

These crossing-over events create new gene combinations and have been shown to significantly affect the performance of genetic algorithms (Mitchell, 1996).

Each gene for each offspring has a probability of mutating (0.1). When a mutation occurs a deviation is added to the original value at the gene. The deviations are drawn from a normal distribution (mean of 0 and a variance of 0.2) for each of the genes. Mutations maintain the genetic variance needed for the genetic algorithm to search for the optimal solution. Finally, we further enhance genetic variance by randomly selecting one predator and one prey every 100 generations and replacing those individuals with individuals with randomly drawn genotypes, using gene value distributions described earlier.

ANALYSIS

We present the average proportion of prey and predators in patch 1 for the final 500 generations of each 1000-generation run, excluding the first 10 time periods of the 60 time period season during which predators and prey are moving away from their initially random distributions. We only present results from parameter values that typically resulted in between 100 and 400 prey being consumed by predators per generation. This was done to avoid bottlenecks where either too few prey survive a generation or too few predators successfully forage and reproduce.

We vary the predator capture rate (a) to examine how the overall level of predation risk affects predator and prey distributions. Intuitively, it seems reasonable that when predator capture rates are low, prey should begin to ignore them. In that case, prey distributions should be largely set by their resources (i.e., prey should aggregate where there are more resources) and predators should presumably aggregate where there are more prey. Interestingly, in previous models, a drops out and does not affect predator and prey distributions.

RESULTS

THRESHOLD PREY FITNESS FUNCTION WITH PREY-DEPENDENT PREDATION RISK

To confirm that the genetic algorithm and the assumed form of the patch-switching rules produce equilibrium predator and prey distributions, we use the same assumptions as those in Sih (1998) and compare our results to ESS solutions that came from that game theory model. When predation risk is prey-dependent (i.e., no predator interference) and patch 1 has four times more resources than patch 2 ($r_1 = 160, r_2 = 40$), we find that prey are uniformly distributed and predators match the resource ratio (Fig. 2a). When predators match resources, a uniform distribution of prey produces equal ratios of predation rates and foraging rates in the two patches, because in patch 1 prey are gaining four times more resources but suffering four times greater predation risk than in patch 2. When prey are uniformly distributed, predators achieve equal predator foraging rates in either patch, but only when predators match the resource ratio do the prey distribute themselves uniformly (Table 1). When resources are equal in the patches, but patch 1

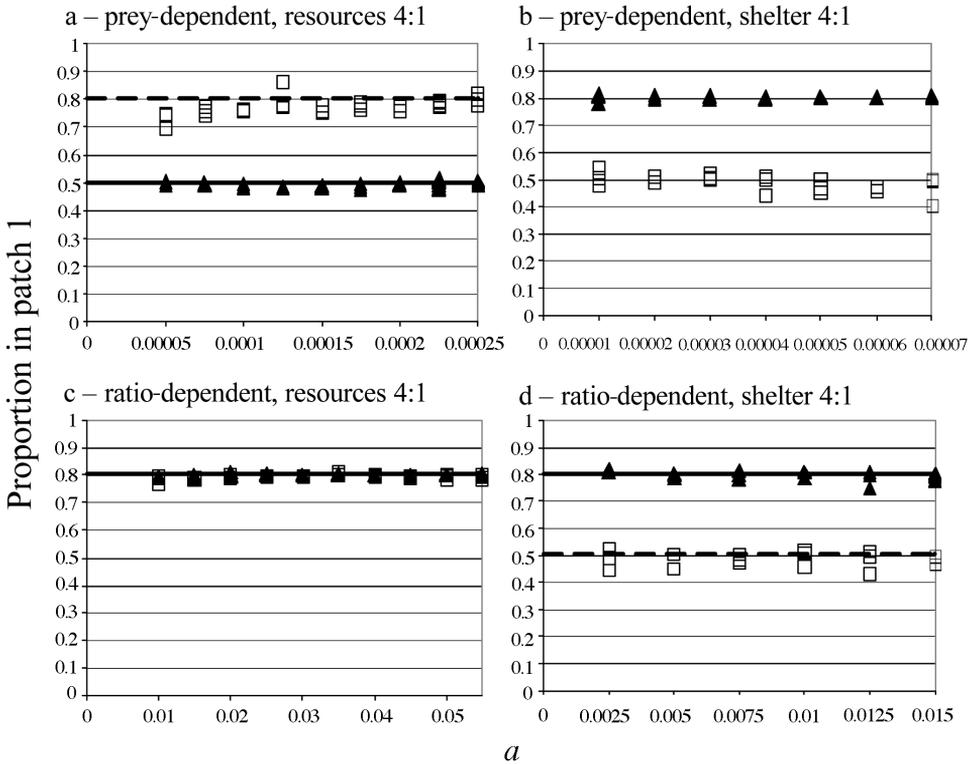


Fig. 2. Distribution of predators and prey given a threshold prey fitness function and patches varying in resources or shelter. Proportion of prey (filled triangles) and predators (open squares) in patch 1 as the capture rate (a) varies for prey-dependent predation with (a) 4:1 resources ($r_1 = 160$, $r_2 = 40$, $k_1 = 1$, $k_2 = 1$), (b) 4:1 shelter ($r_1 = 40$, $r_2 = 40$, $k_1 = 1$, $k_2 = 4$), and ratio-dependent predation with (c) 4:1 resources ($r_1 = 160$, $r_2 = 40$, $k_1 = 1$, $k_2 = 1$), (d) 4:1 shelter ($r_1 = 40$, $r_2 = 40$, $k_1 = 1$, $k_2 = 4$). The heavy solid line is the predicted distribution of prey and the heavy dashed line is the predicted distribution of predators from Sih (1998).

offers four times more shelter from predators than patch 2 ($k_1 = 1$, $k_2 = 4$), prey match the shelter ratio and predators are uniformly distributed (Fig. 2b). When prey match the shelter ratio, predators achieve equal predator foraging rates in either patch because patch 1 has four times more prey than patch 2 but the prey are four times harder to catch in patch 1 than in patch 2. However, only when predators are uniformly distributed are prey forced to match the shelter ratio (Table 1). Thus, the predators are uniformly distributed to maintain the equilibrium. Notably, predator and prey distributions are unaffected by the predator capture rate (a).

Table 1

Factors that shape the distributions of prey and predators. The same factors potentially shape prey and predator distributions for the prey threshold and mass-dependent fitness functions. However, with the threshold fitness function, the effects of predators and shelter on prey distributions dominate the effects of resources and competition on prey distributions. With the mass-dependent fitness function, the relative effects of predators and shelter on prey distributions increase as the capture rates of predators increase. With the threshold fitness function and prey-dependent predation risk, predators receive equal payoffs in either patch when prey are at their equilibrium distributions, with patches differing either in resources or shelter. In those cases, the resulting predator distribution is the one that holds prey at their equilibrium distribution

Predation risk	Patches differ in resources	Patches differ in shelter
Prey-dependent	Prey patch use: \uparrow resources, \downarrow competition (prey), \downarrow predators	Prey patch use: \uparrow shelter, \downarrow competition (prey), \downarrow predators
	Predator patch use: \uparrow prey	Predator patch use: \uparrow prey, \downarrow shelter
Ratio-dependent	Prey patch use: \uparrow resources, \downarrow competition (prey)	Prey patch use: \uparrow shelter, \downarrow competition (prey)
	Predator patch use: \uparrow prey, \downarrow competition (predators)	Predator patch use: \uparrow prey, \downarrow competition (predators) \downarrow shelter

THRESHOLD PREY FITNESS FUNCTION WITH RATIO-DEPENDENT PREDATION RISK

When patch 1 has four times more resources than patch 2 ($r_1 = 160$, $r_2 = 40$), predators and prey both match the resource ratio (Fig. 2c). With ratio-dependent predation risk, the risk of predation experienced by a prey is unaffected by the number of predators present in a patch, assuming that at least one predator is present. Any increase in the number of predators in a patch is perfectly balanced by predator interference reducing per capita foraging success for predators. Thus, when predators are present in both patches, prey can ignore the distribution of predators. The risk of predation experienced by a prey is also unaffected by the number of prey in the patch, because changes in prey densities cause complimentary changes in dilution effects and predation rates. Thus, the prey distribute themselves to match the distribution of the resources. Since prey are ignoring the distribution of predators, predators can distribute themselves to maximize their foraging rates, which with ratio-dependent predation risk means matching the distribution of the prey. When resources are uniformly distributed, but patch 1 offers four times more shelter from predators than patch 2 ($k_1 = 1$, $k_2 = 4$), prey match the shelter ratio and predators are uniformly distributed (Fig. 2d). Since distributions of the predators and the

prey have no effect on the predation rate experienced by prey, prey predation risk is always 4 times lower in the patch with 4 times more shelter than in the other patch. However, prey competition lowers prey foraging rates as prey numbers increase in a patch. When prey match the shelter ratio, μ/f is equal in patches because in patch 1 the predation and foraging rates are both 4 times less than in patch 2. Predators achieve equal foraging rates in the two patches by being uniformly distributed.

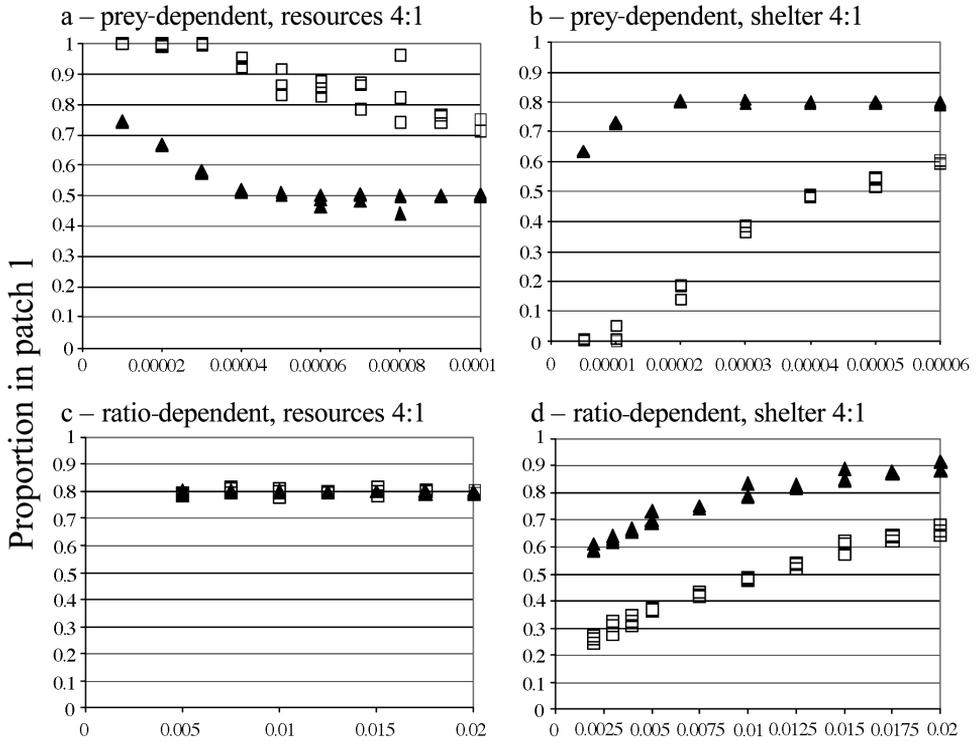
Our genetic algorithm produced consistent and reliable results. Replicate runs of the genetic algorithm typically produced very similar results and the results varied very little across values of a . The results match previous results from ESS models by Sih (1998). Hugie and Dill (1994) incorporated prey metabolism into their models, thus they found that prey slightly undermatch resources ratios. They also modeled competition between predators as interference, rather than as ratio-dependent predation risk as we and Sih (1998) have done. Despite these differences, our results are also very similar to Hugie and Dill's. In particular, our results match their result for when predation risk is prey-dependent and patches vary in their levels of shelter (a scenario not modeled in Sih (1998)).

MASS-DEPENDENT PREY FITNESS FUNCTION WITH PREY-DEPENDENT PREDATION RISK

With mass-dependent prey reproduction, predator and prey distributions vary with the overall level of predation risk. When patch 1 has four times more resources than patch 2 ($r_1 = 160$, $r_2 = 40$), if predator capture rates (a) are low predators exclusively occupy patch 1 (the patch with more resources) and prey are also more common in patch 1. As a increases and thus the overall risk of predation increases, the proportion of prey in patch 1 declines until they are uniformly distributed and the proportion of predators in patch 1 also declines.

When the overall risk of predation is low (a small a), the benefit of foraging in the patch with more resources (patch 1) outweighs the associated predation risk of occupying the patch with all of the predators present. Thus, more prey are found in patch 1 than in patch 2. Not all of the prey move into the patch with more resources because of prey competition for resources (Table 1). When the overall risk of predation is high (a large a), the higher predation risk in patch 1 outweighs the foraging benefit of patch 1 and prey are uniformly distributed. When prey are uniformly distributed, predators achieve the same foraging rate in either patch, but as a increases it takes a smaller skew in the distribution of predators to force the prey to a uniform distribution. Predators continue to use patch 1 more often than patch 2, because a greater predation risk in patch 1 than in patch 2 is still needed to keep prey uniformly distributed and the system at equilibrium.

When patch 1 offers prey four times more shelter from predators than patch 2 ($k_1 = 1$, $k_2 = 4$) and a is low, prey favor patch 1 but undermatch the shelter ratio and predators exclusively occupy patch 2 (Fig. 3b). Prey undermatch the shelter ratio because predators are not creating a high risk of predation and prey competition is pushing prey towards a uniform distribution (Table 1). As a increases, prey match the shelter ratio and predators increasingly move into patch 1. When prey match the shelter ratio, predators



a

Fig. 3. Distribution of predators and prey given a mass-dependent prey fitness function and patches varying in resources or shelter. Proportion of prey (filled triangles) and predators (open squares) in patch 1 as the capture rate (a) varies for prey-dependent predation with (a) 4:1 resources ($r_1 = 160, r_2 = 40, k_1 = 1, k_2 = 1$), (b) 4:1 shelter ($r_1 = 40, r_2 = 40, k_1 = 1, k_2 = 4$), and ratio-dependent predation with (c) 4:1 resources ($r_1 = 160, r_2 = 40, k_1 = 1, k_2 = 1$), (d) 4:1 shelter ($r_1 = 40, r_2 = 40, k_1 = 1, k_2 = 4$).

receive equal payoffs in either patch. With a higher capture rate it takes a smaller skew in the number of predators in patch 1 to counterbalance prey competition and force prey to match the shelter ratio. Another way of viewing this is that when predators are more dangerous prey are less inclined to venture into the patch with less shelter, and thus predators must increasingly move into the patch with more shelter.

Why do these results differ from the results using the threshold prey fitness function? With the threshold fitness function, optimal prey behavior minimizes the ratio of predation risk and foraging success. Since the prey are assumed to have unlimited time to reach their threshold, they can adopt a strategy that produces small foraging gains with small levels of predation risk. They are insensitive to the absolute magnitudes of predation risk in the two patches. Even when predation risk is low and the difference

in predation risk between patches is small, the ratio of predation risks affects their behavior. With the mass-dependent fitness function, prey have limited time and gain potentially unlimited benefits from increasing their mass. Thus, they favor the behavioral option that maximizes their net rate of increase in reproductive value with time (Houston and McNamara, 1999). The rate of change in their reproductive value depends on how their expected reproductive success is determined by their mass and their probability of being killed by a predator. How much reproductive value an individual loses when killed by a predator depends on its current mass and the length of time left till it would have reproduced (Clark, 1994). Thus, prey behavior is shaped by the magnitude of predation risk, rather than by a ratio of predation and foraging rates.

MASS-DEPENDENT PREY FITNESS FUNCTION WITH RATIO-DEPENDENT PREDATION RISK

When predation risk is ratio-dependent and patch 1 has four times more resources than patch 2 ($r_1 = 160$, $r_2 = 40$), prey and predators both match the resource ratio and are insensitive to the overall risk of predation (Fig. 3c). This matches the result for the threshold prey fitness function. Like with the threshold fitness function, when predation risk is ratio-dependent prey ignore the distribution of predators and maximize their foraging rate (Table 1). Predators match the distribution of the prey.

When patch 1 offers four times more shelter from predation than patch 2 ($k_1 = 1$, $k_2 = 4$), the proportion of prey and predators in patch 1 depends on the overall risk of predation (Fig. 3d). Given ratio-dependent predation risk, predation risk for prey is 4 times lower than in patch 2 for all predator and prey distributions. The magnitude of the difference in predation risk for prey in the two patches increases as a increases. As a increases, a larger difference in prey competition is needed to counterbalance the increasing difference in predation rates. Thus, we see that as a increases a larger proportion of the prey use patch 1, even to the point of exceeding the shelter ratio. Predators distribute themselves in response to the distribution of the prey, but they do not match the prey distribution because prey are easier to catch in patch 2 than in patch 1.

VARYING r AND k

We next examine how predator and prey distributions vary when the levels of resources and shelter in the two patches vary simultaneously. We focus on two situations: (1) a trade-off scenario where patch 1 offers 4 times more resources than patch 2 ($r_1 = 160$, $r_2 = 40$), but patch 2 offers four times more shelter from predators than patch 1 ($k_1 = 4$, $k_2 = 1$), and (2) a superior patch scenario where patch 1 has four times more resources ($r_1 = 160$, $r_2 = 40$) and four times more shelter than patch 2 ($k_1 = 1$, $k_2 = 4$).

THRESHOLD FITNESS FUNCTION

With prey-dependent predation risk, given a trade-off between a safer patch and a richer patch, prey prefer the safer patch and predators prefer the richer patch (Fig. 4a). This matches the previous result that predators match resource ratios and prey match shelter ratios (Figs. 2b and 4a, note that in Fig. 2b patch 1 is the safer patch and in Fig. 4a

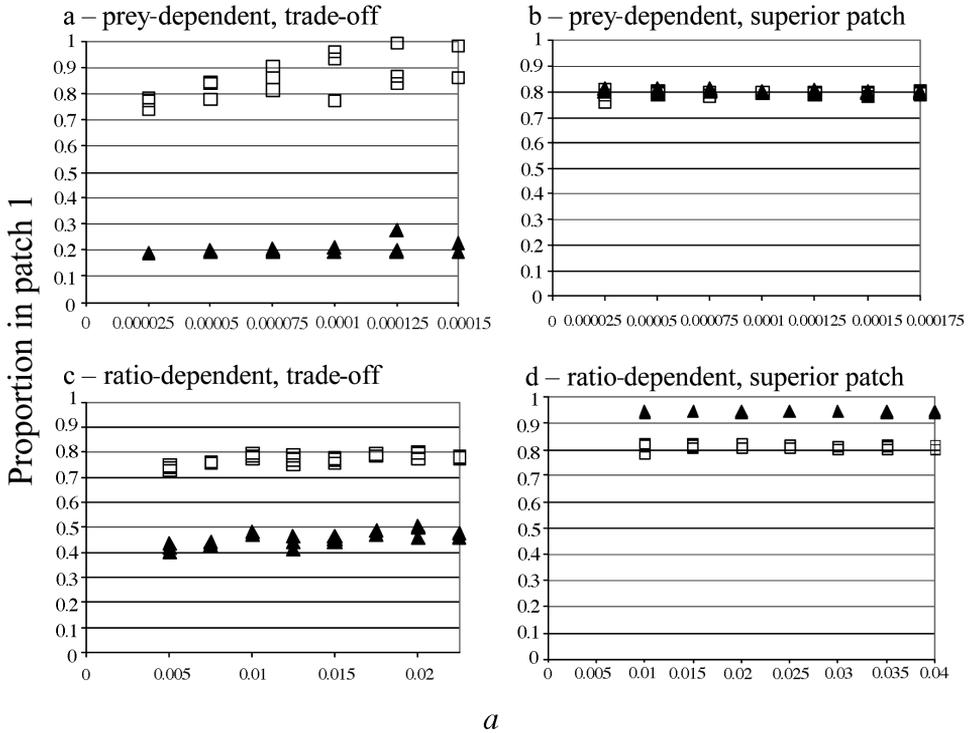


Fig. 4. Distribution of predators and prey given a threshold prey fitness function and patches varying in both resources and shelter. Proportion of prey (filled triangles) and predators (open squares) in patch 1 as the capture rate (a) varies for prey-dependent predation with (a) a trade-off scenario ($r_1 = 160, r_2 = 40, k_1 = 4, k_2 = 1$), (b) a superior patch scenario ($r_1 = 160, r_2 = 40, k_1 = 1, k_2 = 4$), and ratio-dependent predation with (c) a trade-off scenario, (d) a superior patch scenario.

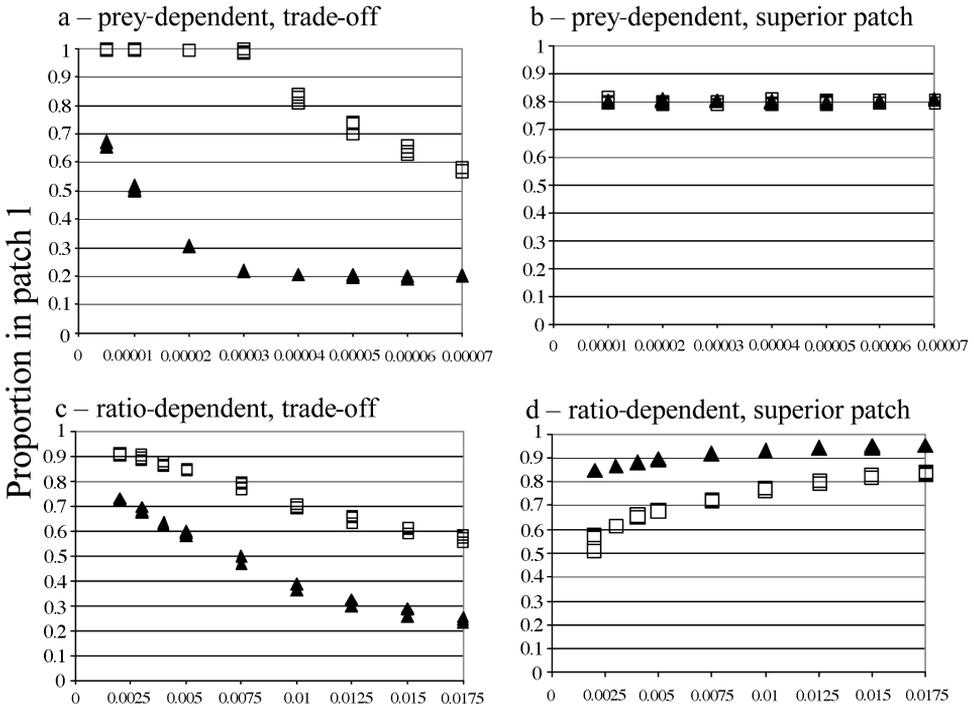
patch 2 is the safer patch). This scenario leads to the smallest observed spatial overlap between predators and prey. Given the superior patch scenario, both predators and prey prefer the superior patch and match the resource and shelter ratios (Fig. 4b). One way of viewing this result is that prey prefer the patch with more resources, and predators are unable to drive them out of the patch because the patch offers prey more shelter. With prey matching the shelter ratio, predators do equally well at any distribution. However, predators must match the shelter ratio to keep predation rates equal in the two patches and prey at the equilibrium distribution.

With ratio-dependent predation, given a trade-off between a safer patch and a richer patch, prey show no strong preference and predators prefer the richer patch (Fig. 4c). For prey the predation rate in patch 1 is 4 times greater than in patch 2 for all predator and prey distributions. Thus, the two patches will only produce equal μ/f ratios if patch 1 has

a 4 times higher foraging rate than patch 2, which occurs when prey are uniformly distributed. Predators then achieve equal predation rates in patches by matching the shelter ratio. Given the superior patch scenario, most of the prey are found in the superior patch (patch 1) and the predators prefer the superior patch, nearly matching the resource and shelter ratios (Fig. 4d). For prey, patch 1 is 4 times safer than patch 2. The only force preventing all of the prey from occupying patch 1 is prey competition for resources. Again, predators distribute themselves in response to the distribution of the prey, but slightly undermatch the prey distribution because prey are easier to catch in patch 2 than in patch 1.

MASS-DEPENDENT FITNESS FUNCTION

With prey-dependent predation, given a trade-off between a safer patch and a richer patch, prey prefer the richer patch when a is low and the safer patch when a is high, and



a

Fig. 5. Distribution of predators and prey given a mass-dependent prey fitness function and patches varying in both resources and shelter. Proportion of prey (filled triangles) and predators (open squares) in patch 1 as the capture rate (a) varies for prey-dependent predation with (a) a trade-off scenario ($r_1 = 160, r_2 = 40, k_1 = 4, k_2 = 1$), (b) a superior patch scenario ($r_1 = 160, r_2 = 40, k_1 = 1, k_2 = 4$), and ratio-dependent predation with (c) a trade-off scenario, (d) a superior patch scenario.

predators prefer the richer patch in both cases but more strongly when a is low (Fig. 5a). We have seen that when a is low predators prefer patches with either more resources or less shelter (Fig. 3a,b) and thus predators prefer patch 1. Prey are more abundant in patch 1 when a is low, but are driven out of patch 1 as a increases. Compared to the case where the patches have the same amount of resources but different levels of shelter (Fig. 3b), prey match the shelter ratio at a higher a when the more dangerous patch has more resources (Fig. 5a). Also, predators maintain a higher proportion in the patch with less shelter (patch 1) than seen when resources were equal. However, when a is high the distribution of prey is unaffected by the distribution of resources. Thus, resources and shelter combine to affect the distributions of predators and prey, but their relative contributions depend on the level of a . Given the superior patch scenario, predators and prey prefer the superior patch and match the resource and the shelter ratios (Fig. 5b). This matches the result for the same scenario with the threshold prey fitness function (Fig. 4b). When predators and prey both match the shelter and resource ratio, foraging and predation rates for prey are equal in the two patches. Thus, their distribution is unaffected by how they balance foraging gains and predation risk.

When predation risk is ratio-dependent, for the trade-off scenario, the change in the distribution of predators and prey as the predator capture rate (a) increases is similar to what is found with prey-dependent predation risk. Predators and prey are found more often in the richer patch (patch 1) if a is low, and they are found increasingly more often in the safer patch as a increases (Fig. 5c). For the superior patch scenario, prey favor the superior patch and predators are nearly uniformly distributed when predators are less effective (Fig. 5d). As a increases prey favor the superior patch even beyond the resource ratio. They are accepting a lower foraging rate in the superior patch caused by high prey competition in exchange for higher shelter from predation. Predators also increase their use of the superior patch as a increases, but the proportion of predators in patch 1 is lower than the proportion of prey because prey are easier to catch in patch 2 than in patch 1.

DISCUSSION

The complexity of the mix of intra- and interspecific games that form the predator-prey habitat selection game has limited our understanding of how predators and prey interact and distribute themselves over space. Game theory models have been used to frame the structure of the problem and have produced some intriguing and testable predictions about the distributions of predators and prey (Hugie and Dill, 1994; Sih, 1998). However, solving the models has required simplifying assumptions, such as no state-dependent behavior and simple prey fitness functions. Using state-dependent games, Alonzo (2002) showed that state-dependent behavior can significantly affect predator and prey distributions. However, with some naturally relevant predator and prey fitness functions, including mass-dependent reproduction at the end of a season, the state-dependent game approach did not produce equilibrium solutions. Here, using genetic algorithms, we were able to examine how mass-dependent prey reproduction affects predator and prey

distributions. We confirmed that our genetic algorithm produced equilibrium solutions by first showing that when we adopted the same assumptions as the previous game theory models, the genetic algorithm produced the same results as those models. We also replicated our runs of the genetic algorithm and showed that the results generally varied very little.

Our model shows that factors that affect prey reproductive success, and thus how prey trade off predation risk and foraging benefits, can significantly affect the predicted spatial distributions of prey and predators. Changing the prey fitness function from being a threshold to being mass-dependent had three important effects on the distributions of predators and prey. First, it caused predator and prey distributions to become sensitive to the overall level of predation risk. If prey reproduce when they reach a threshold size or mass and their time to reach the threshold is unlimited, then their distribution among alternative patches should be based on the ratios of predation and foraging rates in those patches, but insensitive to the overall magnitude of predation risk. When time is unlimited, prey should avoid patches that offer an increased foraging rate, but with a proportionally greater increase in the predation rate, even if the magnitude of the increase in the predation rate is very small. Since predators set their spatial distribution based on the spatial distribution of prey and the forces that set the prey distribution, when the prey distribution is insensitive to the magnitude of predation risk the predator distribution is as well. In contrast, if prey reproduction is dependent on their mass or size at a particular time point or on how quickly they accumulate mass or size, then the distribution of prey is usually sensitive to the absolute magnitude of predation risk. When predator capture rates are low, the distribution of prey is primarily determined by prey competition and the distribution of resources, and not by the distribution of predators. However, as predator capture rates increase the distribution of predators has a larger effect on the distribution of prey.

One of the most striking predictions from previous game theory models is that when predation risk is prey-dependent and prey competition is ideal, prey should distribute themselves uniformly, ignoring the distribution of the resource they consume, while predators should match the distribution of the resource that they do not consume (Hugie and Dill, 1994; Sih, 1998). This result, however, is weakened if prey reproduction is mass-dependent. With mass-dependent reproduction, prey should favor the patch with more resources when overall predation risk is low. When overall predation risk is higher, predators should undermatch the resource ratio. We believe that in most systems the reproductive success of prey will be affected either by how large or how quickly they grow and mature, and therefore it is reasonable to expect that how much predators affect the distribution of prey will depend on the magnitude of predation risk.

The second effect of changing the prey fitness function from being a threshold to being mass-dependent is on how predators distribute themselves in relation to the shelter from predation that alternative patches offer. Given a prey threshold fitness function, the distribution of predators was unaffected by patches offering prey different levels of shelter, but was affected given a mass-dependent prey fitness function. When predator capture rates were relatively low, predators favored the patch that offered prey less

shelter from predation. But, as capture rates increased prey increasingly favored the patch offering more shelter and in response predators were increasingly found in that inherently safer patch. As predators become more effective at catching prey, prey retreat to the patch with more shelter and predators are forced to more often occupy that patch despite the inherent difficulty in capturing prey in that patch. Thus, the spatial overlap of prey and predators increases in this situation as the capture rate increases.

The third effect of changing the prey fitness function from being a threshold to being mass-dependent is how prey distribute themselves when given a choice between a safer patch and a richer patch. With the threshold fitness function, prey always favored the safer patch. However, with the mass-dependent fitness function, the relative contributions of resources and shelter in determining prey distributions depended on the overall level of predation risk. For example, as a increases prey are expected to effectively ignore increasingly larger differences in resources between patches.

The importance of the interspecific predator-prey game in determining the spatial distributions of predators and prey depends on the intensity of predator competition. When predator competition was ideal and thus predation risk was ratio-dependent, the distribution of predators had no effect on the distribution of prey. In this case, from the prey's perspective there is no interspecific game and their distribution is set by relative resource levels, competition for resources, and relative levels of shelter (Table 1). The distribution of predators is also unaffected by the interspecific game. Since prey are not responding to their distribution, predators are free to match a combination of the prey distribution and the relative shelter of the alternative patches.

We chose to model predation risk as either prey-dependent or ratio-dependent. Predation risk is likely to be intermediate between these two extremes (Abrams and Ginzburg, 2000). Skalski and Gilliam (2001) found that 19 data sets of predator feeding rates provided little support for predator feeding rates being either independent of predator density (i.e., prey-dependent predation risk) or ratio-dependent. Thus, further investigation is needed to see how handling times and interference among predators affect predator and prey spatial distributions.

We have presented how the distributions of predators and prey vary as the predator capture rates (a) vary. Our manipulations of a changed the overall level of predation risk, and in the case of the mass-dependent prey fitness functions, changed the relative importance of predation risk and resources in governing the patch choice decisions of prey. However, the overall level of predation risk is also a function of the levels of shelter in the patches and predator density. Raising or lowering the level of shelter in both patches by an identical factor is the same as raising or lowering a (eq 2). Manipulating the level of shelter throughout an experimental arena may be an effective approach for testing whether predator and prey distributions vary with the overall level of predation risk, as we have predicted. Varying predator densities generally has the same effect on the distributions of predators and prey as varying a , when predation risk is prey-dependent. However, results from varying predator densities can deviate from our presented results because the number of predators not only affects the overall risk of predation, but also the relative strengths of selection and genetic variation for predators

and prey. Manipulating predator densities in ecological experiments may be an effective test of our model, since the strength of selection and genetic variance are not likely to be significant factors in short experiments, but the predicted results would depend on the functional form of predator interference. When predation risk is ratio-dependent or predator inference is high, the number of predators should have no or little effect on the distributions of predators and prey, because changing the density of predators has little or no effect on predation risk for prey.

How predators and prey distribute themselves across space is a complex problem and the resulting distributions are often contingent on the state of the environment and factors that affect the success of predators and prey. For example, Alonzo (2002) showed that the distributions of predators and prey are predicted to depend on the risk of starvation and, therefore, the state-dependent behavior of predators and prey. Thus, the predicted distributions of predators and prey are contingent on how current resource levels in the environment affect the risk of starvation for prey and predators. We showed that when prey reproduction is mass-dependent the predicted distributions of predators and prey are contingent on the overall magnitude of predation risk for prey. Many simplifying assumptions have been made in our model and in previous models. These include: (1) that prey and predators having perfect knowledge of the current distributions of predators and prey, and of the characteristics of alternative patches; (2) no movement costs between patches, and (3) equal abilities and opportunities for predators and prey to move between patches. Varying these simplifying assumptions will likely produce more complicated predictions, that should further enhance our understanding of predator-prey games.

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see Appendix next page

APPENDIX

We assume that the probability of a prey individual leaving a patch is

$$\text{Pr}(\text{prey leaves patch 1}) = \frac{N_1 - \left[(Y_{1,0} + b_{1,0}N_2) + \alpha((Y_{1,1} + b_{1,1}N_2) - (Y_{1,0} + b_{1,0}N_2)) \right]}{2\Delta} + 0.5 \tag{7}$$

where N_1 and N_2 are the number of prey in patch 1 and patch 2, respectively, α is the proportion of the predators in the prey's current patch, and the Y 's and b 's are indifference surface parameters (that set how N_2 and α affect the probability of leaving the patch). For example, $Y_{1,0}$ corresponds to the rule in patch 1 when $\alpha = 0$, while $Y_{1,1}$ corresponds to the rule in patch 1 when $\alpha = 1$. The term in brackets is N_1^* (the threshold of indifference), where the prey has a 0.5 probability of leaving its current patch. The first term in parentheses is the N_1^* for when no predators are present in the prey's current patch ($\alpha = 0$). The second term in parentheses is the slope associated with interpolating N_1^* between $\alpha = 0$ and $\alpha = 1$, which is multiplied by α .

The rate at which the probability of the prey leaving the patch increases or decreases as N_1 varies from N_1^* is set by Δ . When Δ is close to 0, there is a sharp threshold where the individual stays in its current patch if $N_1 < N_1^*$ and leaves the patch if $N_1 > N_1^*$. With a sharp threshold, mutations that change the threshold will only affect an individual's behavior if the threshold is near N_1 . As Δ increases, the threshold is broadened and thus the range over which mutations affect an individual's behavior is increased. In a sense, a broader threshold leads to a more constant selection on genotypes. We allow the genetic algorithm to find the optimal threshold type, with Δ typically being much greater than 0 for both predators and prey. The approach allowing the threshold to broaden reduced fluctuations in prey and predator distributions in comparison to a sharp threshold.

The formulation of the predator patch-switching rule is the same, except that the probability of the predator leaving its patch is greater than 0.5 when $N_1 > N_1^*$, and less than 0.5 when $N_1 < N_1^*$,

$$\text{Pr}(\text{predator leaves patch 1}) = \frac{\left[(Y_{1,0} + b_{1,0}N_2) + \alpha((Y_{1,1} + b_{1,1}N_2) - (Y_{1,0} + b_{1,0}N_2)) \right] - N_1}{2\Delta} + 0.5 \tag{8}$$

Each individual for each patch has two pairs of Y and b that set their indifference surface. We assume that Δ is the same for each patch. Thus, each individual (predator or prey) has a genotype composed of nine genes ($Y_{1,0}, b_{1,0}, Y_{1,1}, b_{1,1}, Y_{2,0}, b_{2,0}, Y_{2,1}, b_{2,1}, \Delta$).

In the rules, we use the proportion of predator in each patch, rather than the number of predators in each patch, to reduce the number of parameters. However, we use the number of prey in the current and the alternative patch, rather than the proportion of prey, because the density of prey is reduced by predation over the season and competition for resources and predation risk depend on the densities of prey.