

# Alternative forms of competition and predation dramatically affect habitat selection under foraging–predation-risk trade-offs

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Habitat selection under foraging–predation-risk trade-offs has been a frequent topic of interest to theoretical behavioral and evolutionary ecologists. However, most habitat selection models assume that individuals compete exploitatively for resources and that predation is either density independent or diluted completely by competitor number, despite empirical evidence that other forms of competition and predation also occur in nature. I developed an individual-based model for studying the effects of alternative forms of competition and predation on the process of habitat selection under foraging–predation-risk trade-offs. To make the model more relevant to natural populations, I assumed that individuals vary continuously in traits related to competitive ability and vulnerability to predation and allowed resources and predators to be distributed across more than two habitats. The results of my investigation demonstrate that the predicted pattern of habitat selection can be affected dramatically by the form predation is assumed to take. When predation is density dependent or frequency dependent, individuals will tend to be distributed across habitats according to their absolute vulnerability to predation. In contrast, when predation is density dependent or vulnerability dependent, individuals will tend to segregate by competitive ability. Whether one assumes that individuals compete for resources via exploitation or interference also influences the predicted pattern of habitat selection. In general, interference competition results in a more even distribution of competitors across habitats. *Key words:* competition, foraging, habitat selection, predation, predation risk, trade-offs. [*Behav Ecol* 13:280–290 (2002)]

The process of habitat selection frequently requires individuals to choose among habitats that differ in growth potential and mortality risk due to predation. When the habitat that provides the highest rate of energetic gain is also the most dangerous, habitat selection will reflect a compromise between the conflicting demands of growth and survival (see Lima and Dill, 1990, on the ubiquity of this trade-off). In many cases, an individual's best resolution to this conflict will be influenced by the presence of conspecifics, who may, for example, reduce the growth potential in a habitat via competition for resources (Abrahams and Dill, 1989; Grand and Dill, 1997). Habitat selection under foraging–predation-risk trade-offs has been a frequent topic of investigation for behavioral and evolutionary ecologists (for reviews, see Brown, 1998; Lima, 1998; Lima and Dill, 1990). Much of this work, however, is limited in its applicability to natural populations, as only a single, common form of competition or predation is considered, and individual variation in competitive ability and vulnerability to predation is ignored.

Most theoretical studies of habitat selection under foraging–predation-risk trade-offs assume that individuals compete exploitatively (or “scramble”; Milinski and Parker, 1991) for resources (Brown, 1998; Grand and Dill, 1999; Moody et al., 1996; but see Hugie and Dill, 1994) and that predation is either density independent (Abrahams and Dill, 1989) or diluted completely by competitor number (Hugie and Dill, 1994; Moody et al., 1996; but see Grand and Dill, 1999, for a treatment of variation in the strength of risk dilution). Em-

pirical evidence, however, suggests that other forms of competition and predation are more common in nature (see Sutherland, 1996; Endler, 1991, respectively, for reviews). For example, pairs of competitors might engage in contest competition over individual prey items or defend territories against all others (see Milinski and Parker, 1991). Predators might behave as optimal foragers (Stephens and Krebs, 1986), preferentially attacking common prey phenotypes or those whose morphology renders them particularly vulnerable to capture. Furthermore, in contrast to the continuous variation that is typically observed in traits related to competitive ability and vulnerability to predation (e.g., body size; Grand and Dill, 1997; antipredator armor; Grand, 2000), most models of habitat selection under foraging–predation-risk trade-offs assume that competitors are identical (Moody et al., 1996) or belong to one of two discrete classes of phenotypes (Brown, 1998; Grand and Dill, 1999).

I developed a framework for studying the effects of alternative forms of competition and predation on the process of habitat selection under foraging–predation-risk trade-offs. As done for many other models of this sort, I based this framework on Fretwell and Lucas's (1970) theory of ideal free distributions. To incorporate continuous variation in traits related to competitive ability and vulnerability to predation, I used an individual-based simulation approach. I considered two forms of competition, exploitative and interference, and four forms of predation, density independent, density dependent (i.e., risk is diluted by competitor number), vulnerability dependent (more vulnerable phenotypes experience an increased risk of predation), and frequency dependent (rare phenotypes experience a reduced risk of predation). For simplicity, I focused primarily on an environment containing two habitats. However, the framework allows for consideration of multiple habitats and thus exploration of habitat selection patterns across gradients of resource availability and predation

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**Table 1**  
**Summary of all constants and variables used in the model**

Parameter	Definition	Units	Values investigated
$N_T$	Total population size	—	50–500
$i = 1$ to $N_T$	Individual	—	—
$H_T$	Number of habitats	—	2–5
$j = 1$ to $H_T$	Habitat	—	—
$R_j$	Resource availability in habitat $j$	Energy/time	Gradient = 2–10 (see text)
$B_j$	Background predation risk in habitat $j$	Probability of attack/time	Gradient = 2–10 (see text)
$k_i$	Relative competitive ability of individual $i$	—	1–10
$v_i$	Vulnerability of individual $i$	Probability of capture given attack	Values ranged from 0 to 1.0
$m$	Interference coefficient	—	2–5
$p_{ij}^{att}$	Probability of individual $i$ being attacked in habitat $j$	Probability of attack/time text for details)	min = 0, max = 1.0 (but see
$N_j$	No. of individuals in habitat $j$	Number	—
$\phi_i$	Attack probability reduction coefficient	—	1 to 0.1 (1 to 10 predation bins; see text)
$\theta_i$	Predation bin rank of individual $i$	—	See text
$w_{ij}$	Expected fitness of individual $i$ in habitat $j$	Offspring	—
$e_{ij}$	Expected energy intake of individual $i$ in habitat $j$	Energy/time	—
$s_{ij}$	Expected survival of individual $i$ in habitat $j$	Probability of survival/time	—
$\psi$	Energetic cost per offspring	Energy/offspring	—

Also included is the range of values for each parameter that result in qualitatively similar patterns of habitat selection.

risk (see Shenbrot and Krasnov, 2000, for further discussion of habitat selection across environmental gradients).

I begin by describing the general pattern of habitat selection predicted under each of the eight competition-predation scenarios modeled, demonstrating that the assumed forms of competition and predation result in substantially different predicted patterns of habitat selection. I then consider the effects of the number of habitats available and the steepness of the resource and predation gradients on the predicted patterns of habitat selection. Where possible, I compare the predictions of this model to those of existing models, demonstrating the utility of using a single modeling framework to address the same question under different ecological scenarios.

### The model

I modeled the distribution of a relatively large number of individuals ( $i = 1$  to  $N_T$ , the total population size) differing in traits related to competitive ability,  $k_i$  (i.e., their ability to compete for and acquire the resources required for growth) and vulnerability to predation,  $v_i$  (probability of capture given attack). Individuals of high vulnerability are more likely to be captured when attacked by a predator than are individuals of low vulnerability. For simplicity, I assumed that  $k_i$  and  $v_i$  are independent of habitat, competitor density (see below), and one another and that both remain constant over an individual's lifetime.

I considered an environment containing a number of habitats ( $j = 1, 2, \dots$ ) differing in resource availability,  $R_j$  (energy/time), and inherent riskiness (Hugie and Dill, 1994),  $B_j$  (probability of attack/time). Riskiness might be expected to differ between habitats due to differences in predator abun-

dance, structural complexity, or the availability of refuge sites (see Lima and Dill, 1990). Throughout, I assumed that resources are continually renewing, and therefore nondepleting, and that the rate of energy gain per unit of competitive ability is inversely related to the sum of the competitive abilities in a habitat (see below).

I used minimum and maximum values of  $R_j$  and  $B_j$  to create a gradient of resource availability and riskiness across habitats and assumed both gradients to be linear and inversely correlated. Thus, during habitat selection, individuals face a trade-off between energy intake (which increases reproductive output) and survival. For simplicity, I also assumed that  $R_j$  and  $B_j$  remain constant over time. Thus, I did not consider the dynamics of either the resources or the predator population. For a summary of all constants and variables used in the model, see Table 1.

To compare the effects of different forms of competition and predation on patterns of habitat selection, I used an individual-based simulation approach (see Huston et al., 1988). Each simulation begins by (1) specifying the form that competition and predation will take (see below), (2) choosing minimum and maximum values of resource availability and riskiness in the environment, (3) specifying the population size and the number of habitats present, and (4) specifying the minimum and maximum competitive abilities and vulnerabilities to predation present in the population.  $R_j$  and  $B_j$  are then calculated for all habitats (see above) and competitive abilities and vulnerabilities are randomly assigned to all individuals (within the ranges specified), resulting in a uniform distribution of the two continuous traits. Individuals are randomly assigned to a habitat and fitness of all individuals in their chosen habitat calculated (see details below). The fitness

of each individual in all other habitats is then determined in turn (i.e., assuming all other individuals remain in their original habitat), and the individual that can increase its fitness most by switching habitats is moved to the habitat where its fitness is greatest. The simulation continues to move individuals between habitats according to the above rule until no individual can increase its fitness further. By definition, the resultant distribution is the equilibrium distribution of individuals across habitats. This distribution is always stable to small, local perturbations.

Individuals compete for resources via (1) exploitative or (2) interference competition and are subject to predation which is (1) density independent, (2) density dependent, (3) vulnerability dependent (more vulnerable phenotypes experience an increased probability of capture), or (4) frequency dependent (rare phenotypes experience a reduced probability of capture).

Expected fitness,  $w_{ij}$ , of the  $i$ th individual in the  $j$ th habitat is the product of expected energy intake,  $e_{ij}$ , and expected survival,  $s_{ij}$ , in that habitat divided by the energetic cost of producing a single offspring,  $\psi$ . For simplicity, I assume that all energy acquired is available to be translated directly into offspring (see also Grand and Dill, 1999), that there is no upper limit to the number of offspring that an individual can produce, and that  $\psi$  is identical for all individuals in all habitats. Thus,

$$w_{ij} = \frac{e_{ij} \cdot (s_{ij})}{\psi}. \quad (1)$$

Under exploitative competition, individuals do not interact directly with one another while acquiring resources, but scramble for as large a share as possible (see Grant, 1993; Milinski and Parker, 1991). Consequently, all resources are used and divided among all individuals within the habitat according to their relative competitive ability (see Parker and Sutherland, 1986; Sutherland and Parker, 1985). Thus,

$$e_{ij} = \frac{k_i}{\sum k_{ij}} R_j, \quad (2)$$

where  $k_i$  is the relative competitive ability of the  $i$ th competitor and  $\sum k_{ij}$  is the sum of competitive abilities of all individuals in the  $j$ th habitat.

In contrast, under interference competition, direct interactions between individuals during resource acquisition are common (Sutherland, 1996). In this case,

$$e_{ij} = \frac{k_i}{\left(\sum k_{ij}\right)^m} R_j \quad (3)$$

where  $m$  is a coefficient scaling the level of interference ( $m > 1$ ). Under interference competition, not all resources are available for growth. The larger the value of  $m$ , the greater the resource wastage (Sutherland, 1996).

An individual's probability of survival in habitat  $j$  depends on both its probability of being attacked by a predator in that habitat,  $p_{ij}^{att}$ , and its probability of being captured given an attack,  $v_i$ . Thus,

$$s_{ij} = 1 - [p_{ij}^{att}(v_i)]. \quad (4)$$

When prey forage solitarily or predators are capable of capturing entire foraging groups in a single attack, an individual's probability of being attacked may be density independent, and

$$p_{ij}^{att} = B_j. \quad (5)$$

In contrast, when predators are limited in their ability to capture or handle more than a single prey item per attack, perhaps because groups of prey are more likely to detect (Elgar,

1989) or confuse (Milinski and Heller, 1978) them, or because, after the first predatory attack, all surviving members escape, an individual's risk of being attacked will be density dependent:

$$p_{ij}^{att} = \frac{B_j}{N_j} \quad (6)$$

where  $N_j$  is the number of individuals in habitat  $j$  and assuming that such numerical dilution (e.g., Foster and Treherne, 1981) of predation risk is complete. Note that Equation 6 assumes that predators are equally likely to attack individuals in large and small groups (see Turner and Pitcher, 1986, for discussion of relationship between group size and predator attack rate).

In some cases, an individual's relative vulnerability may influence its probability of attack such that individuals whose morphology renders them particularly vulnerable are preferentially attacked (i.e., if predators are optimal foragers; Stephens and Krebs, 1986). Such vulnerability-dependent predation might be expected to occur if attacking less vulnerable prey imposes significant costs on the predator (e.g., damage caused by antipredator morphology such as spines or chemical repellents). When predation is vulnerability-dependent,

$$p_{ij}^{att} = \frac{v_i}{\sum v_{ij}} B_j. \quad (7)$$

Thus, an individual's probability of being attacked is weighted by its relative vulnerability to predation; the lower its vulnerability relative to the total vulnerability of individuals in the habitat ( $\sum v_{ij}$ ), the lower its probability of being attacked by the predator.

Alternatively, if prey detection relies on the formation of a search image (e.g., Endler, 1988) or the skills required to capture prey of different phenotype interfere with one another (e.g., cruising vs. ambush predation; see also Endler, 1991), predators might be expected to preferentially attack common phenotypes. Under frequency-dependent predation (or "apostatic selection"; see Endler, 1991):

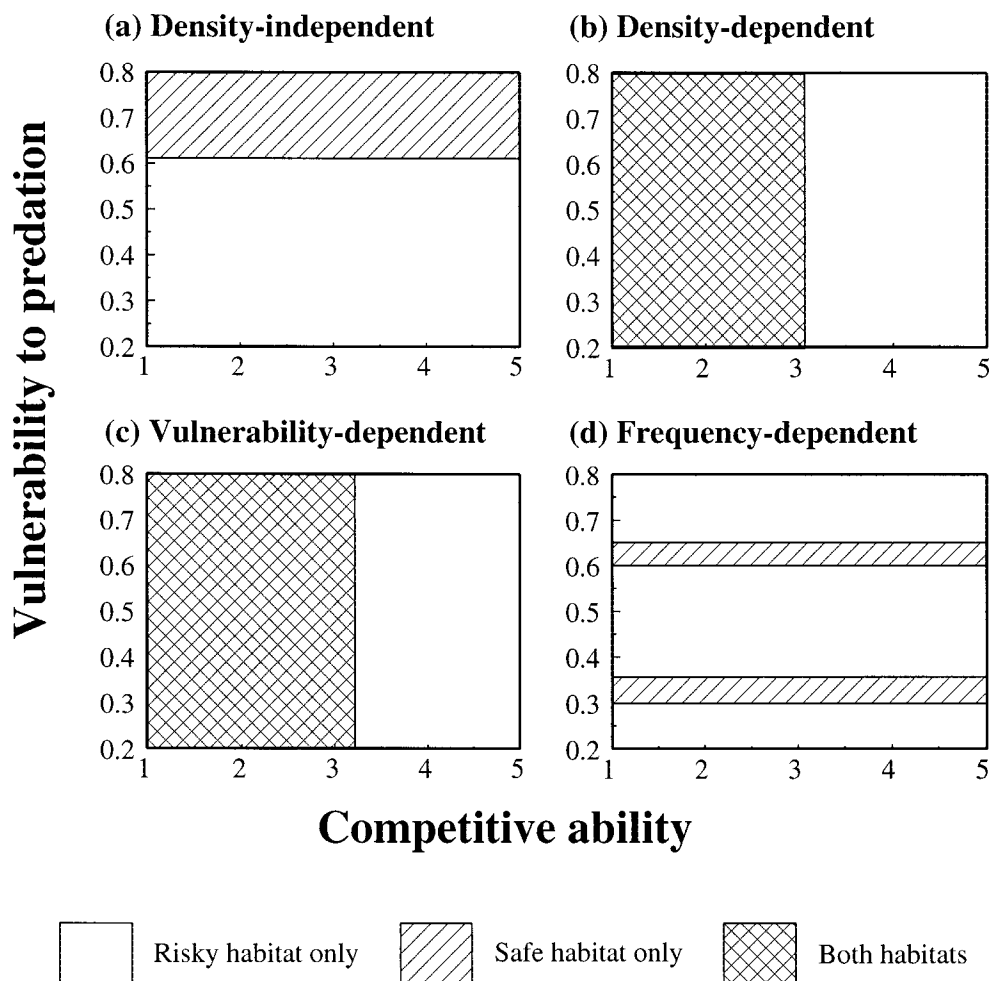
$$p_{ij}^{att} = \phi_i B_j \quad (8)$$

where  $\phi_i$  is a coefficient that scales the reduction in attack probability of the  $i$ th individual.  $\phi_i$  depends on the discrimination abilities of the predator and the number of other individuals who are perceived by the predator as being of similar vulnerability. Individuals are grouped into bins, with individuals of similar vulnerability. Each bin represents an equal proportion of the complete range of vulnerability values in the population. When predator discriminations abilities are good, many bins exist. When predator discrimination abilities are poor, only a few bins exist. Bins are ranked according to frequency; the bin with the highest frequency of individuals receives a rank of 1. Thus,

$$\phi_i = \frac{1}{\theta_i} \quad (9)$$

where  $\theta_i$  is the rank of the bin in which individual  $i$  has been grouped. When discrimination abilities are poor (i.e., the predator sees only one category of prey), all individuals are perceived as being equally vulnerable to predation and  $\phi_i = 1$  for  $i = 1$  to  $N_j$ . When predator discrimination abilities are good (i.e., the predator sees 10 categories of prey), individuals of the most common phenotype will not experience any reduction in attack probability (i.e.,  $\phi_i = 1$ ), while individuals of the least common phenotype will have their probability of attack reduced, in this example, by 90% (i.e.,  $\phi_i = 0.1$ ).

Below, I describe the general patterns of habitat selection predicted by the model under the eight competition-preda-



**Figure 1**  
General patterns of habitat selection predicted by the model when competition is exploitative and predation is (a) density independent, (b) density dependent, (c) vulnerability dependent, and (d) frequency dependent. The habitat(s) occupied by individuals of each trait-value combination are indicated by shading. In all cases  $R_{\min} = 1$ ,  $R_{\max} = 5$ ,  $B_{\min} = 0.1$ ,  $B_{\max} = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ . In panel (d), predators divide prey into five categories.

tion scenarios outlined above. Although the model has been formulated to allow for multiple habitats, for clarity of presentation, I focus primarily on the results for a two-habitat environment (but see Figure 4). Unless otherwise noted, general patterns of habitat selection in multihabitat environments do not differ qualitatively from the simple results presented (see “Habitat Number”). I then explore the effects of steepness of the resource and predation gradients on the predicted patterns of habitat selection.

I conducted sensitivity analyses on each of the model’s parameters by systematically varying the value of one parameter while holding all others constant. As suggested by Gladstein et al. (1991) and Houston et al. (1992) (for dynamic programming models, specifically, but also simulation models in general), I report the range of values over which qualitatively similar results were obtained (see Table 1).

## RESULTS

### General patterns

#### *Exploitative competition*

When individuals compete exploitatively for resources and predation is independent of the density of competitors in a habitat, individuals tend to segregate across habitats according to their relative vulnerability to predation (Figure 1a). Individuals whose morphology renders them least susceptible to capture given an attack occupy the more productive but riskier habitat. This is because the increased risk of predation associated with that habitat is offset by increased growth for

them, but not for their more vulnerable conspecifics. Such segregation by vulnerability is a common prediction of habitat selection models that consider both competition and predation, although here the pattern is generated by absolute differences in vulnerability (which are independent of habitat), rather than differences in the ratio of vulnerabilities across habitats (Grand and Dill, 1999) or interphenotypic trade-offs between competitive ability and vulnerability to predation (Brown, 1998). As in Grand and Dill (1999), the predicted pattern of habitat selection is independent of competitive ability (but see “Predation Gradient” below).

In contrast, when predation is density dependent (i.e., predation is completely diluted by competitor number), the pattern of habitat selection is independent of relative vulnerability to predation. Instead, individuals tend to be distributed according to competitive ability (Figure 1b). However, rather than being strictly segregated across habitats, as in the case of density-independent predation described above, some phenotypes are predicted to use a mix of habitats. Individuals of the highest competitive ability are found only in the risky, more productive habitat (i.e., they behave selectively; Rosenzweig, 1981), whereas individuals of lower competitive ability are found in both risky and safe habitats (i.e., they behave opportunistically; Rosenzweig, 1981). Density-dependent predation also tends to result in a slight increase in the number of individuals using the risky habitat (see Table 2). These results are similar to that predicted by the model of Grand and Dill (1999), who found that the tendency of competitors to aggregate in the risky, more productive habitat depended on the strength of risk dilution (among other things).

Table 2

Predicted mean (SE) density of individuals in each of two habitats (low risk-low growth and high risk-high growth) under the eight competition–predation scenarios depicted by the model

Competition	Predation	Riskiness of habitat	
		Low	High
Exploitative	Density independent	135.2 (0.36)	364.8 (0.36)
	Density dependent	124.5 (0.32)	375.5 (0.32)
	Vulnerability dependent	124.5 (0.31)	375.5 (0.31)
	Frequency dependent	107.3 (0.50)	392.7 (0.50)
Interference	Density independent	205.4 (0.41)	294.6 (0.41)
	Density dependent	207.7 (0.48)	292.3 (0.48)
	Vulnerability dependent	208.1 (0.52)	292.9 (0.52)
	Frequency dependent	194.6 (0.50)	305.4 (0.50)

Each value represents the mean of 100 simulations with  $R_L = 1$ ,  $R_H = 5$ ,  $B_L = 0.1$ ,  $B_H = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ . Predators were assumed to divide prey into five categories; 500 iterations of the model were run for each simulation.

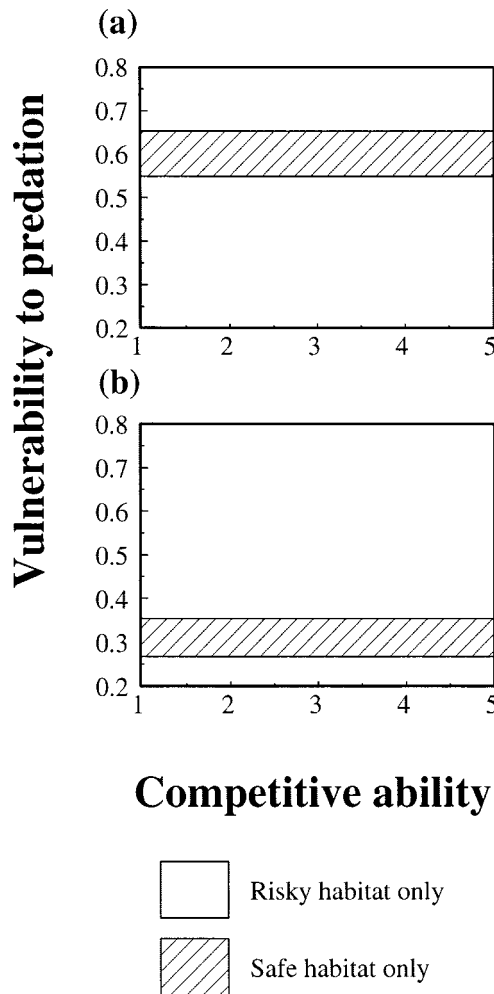


Figure 2

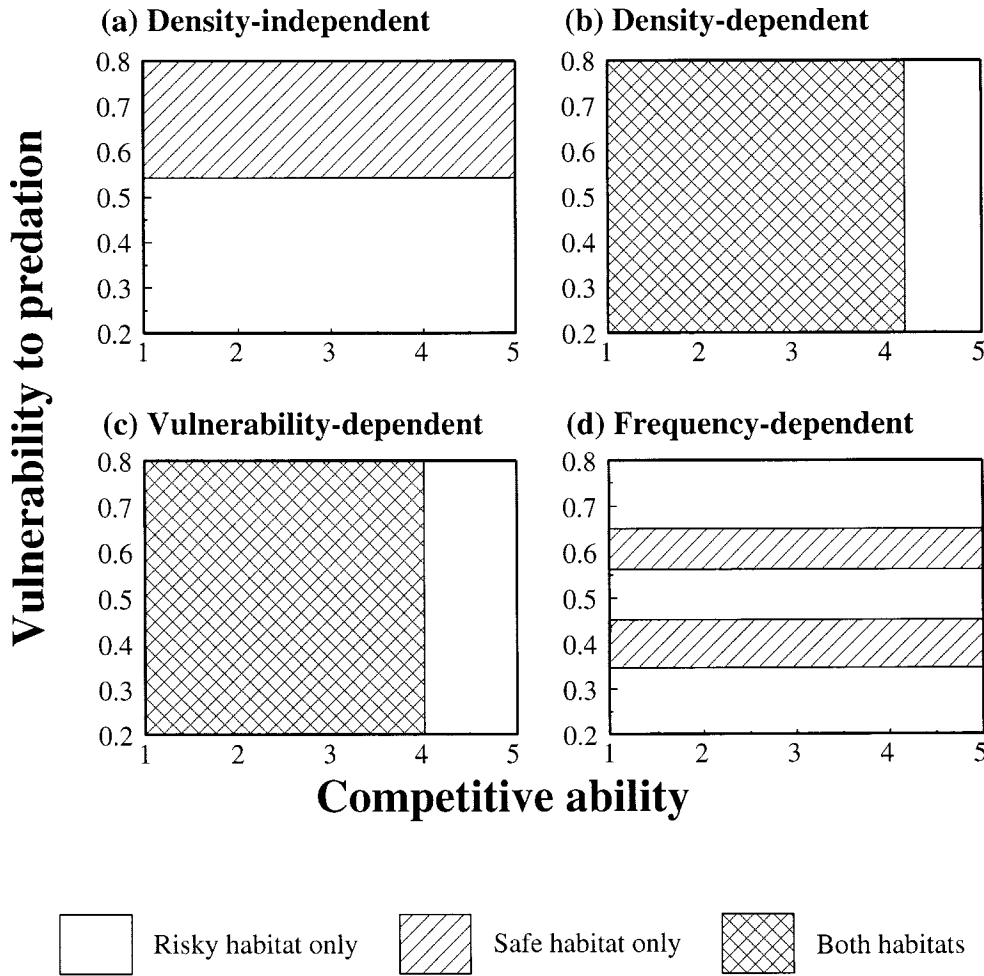
Alternative patterns of habitat selection predicted by the model under exploitative competition and frequency-dependent predation. Differences between the outcomes illustrated in panels (a) and (b) are due to differences in the initial distribution of traits among individuals and the initial distribution of individuals across habitats. In all cases  $R_{\min} = 1$ ,  $R_{\max} = 5$ ,  $B_{\min} = 0.1$ ,  $B_{\max} = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ .

When an individual's probability of attack depends not on its absolute vulnerability to predation (as above), but on its vulnerability relative to that of all other individuals in the habitat, individuals tend to be distributed according to competitive ability (Figure 1c). As in the case of density-dependent predation, vulnerability-dependent predation results in the best competitors using only the risky, most productive habitats, while all other phenotypes are found in both risky and safe habitats. The competitive ability of the poorest competitors using the selective strategy, however, is slightly higher than that predicted by the density-dependent scenario, although densities in the risky habitat are similar under the two scenarios (see Table 2).

When rare phenotypes experience a reduced risk of predation, segregation by vulnerability to predation once again occurs (Figure 1d). However, unlike the single segregation boundary which characterized the density-independent scenario (Figure 1a), multiple segregation boundaries are predicted. That is, although groups of similarly vulnerable individuals will tend to occur in the same habitat, the risky and safe habitats will not be populated by the least and most vulnerable individuals, respectively. Typically, individuals of the most rare phenotype will experience a sufficient reduction in attack probability as to make the risky, more productive habitat profitable. When this occurs, groups of individuals with similarly high vulnerability will join their less vulnerable counterparts in the high-risk–high-growth habitat. Unlike the three previous forms of predation, under frequency-dependent predation, the predicted pattern of habitat selection is highly dependent on starting conditions (for alternative outcomes, see Figure 2), in particular, the distribution of vulnerability phenotypes in the population and the habitat to which they were initially (and randomly) assigned. At least for the parameter values illustrated in Figures 1 and 2, frequency-dependent predation tends to result in a substantial increase in the number of individuals using the risky, more productive habitat (see Table 2), although the outcome appears to be more variable than those for the other predation scenarios considered (compare SEs in Table 2). For an ecologist collecting data on associations between habitat and phenotype, it may appear that individuals of different vulnerability are distributed randomly across habitats, when, in fact, according to the predictions of this model, frequency-dependent predation is structuring the spatial distribution of the population.

#### Interference competition

In general, the patterns of habitat selection predicted by the model under interference competition do not differ substan-



**Figure 3**  
 General patterns of habitat selection predicted by the model under interference competition and (a) density-independent, (b) density-dependent, (c) vulnerability-dependent, and (d) frequency-dependent predation. In all cases  $R_{\min} = 1$ ,  $R_{\max} = 5$ ,  $B_{\min} = 0.1$ ,  $B_{\max} = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ .

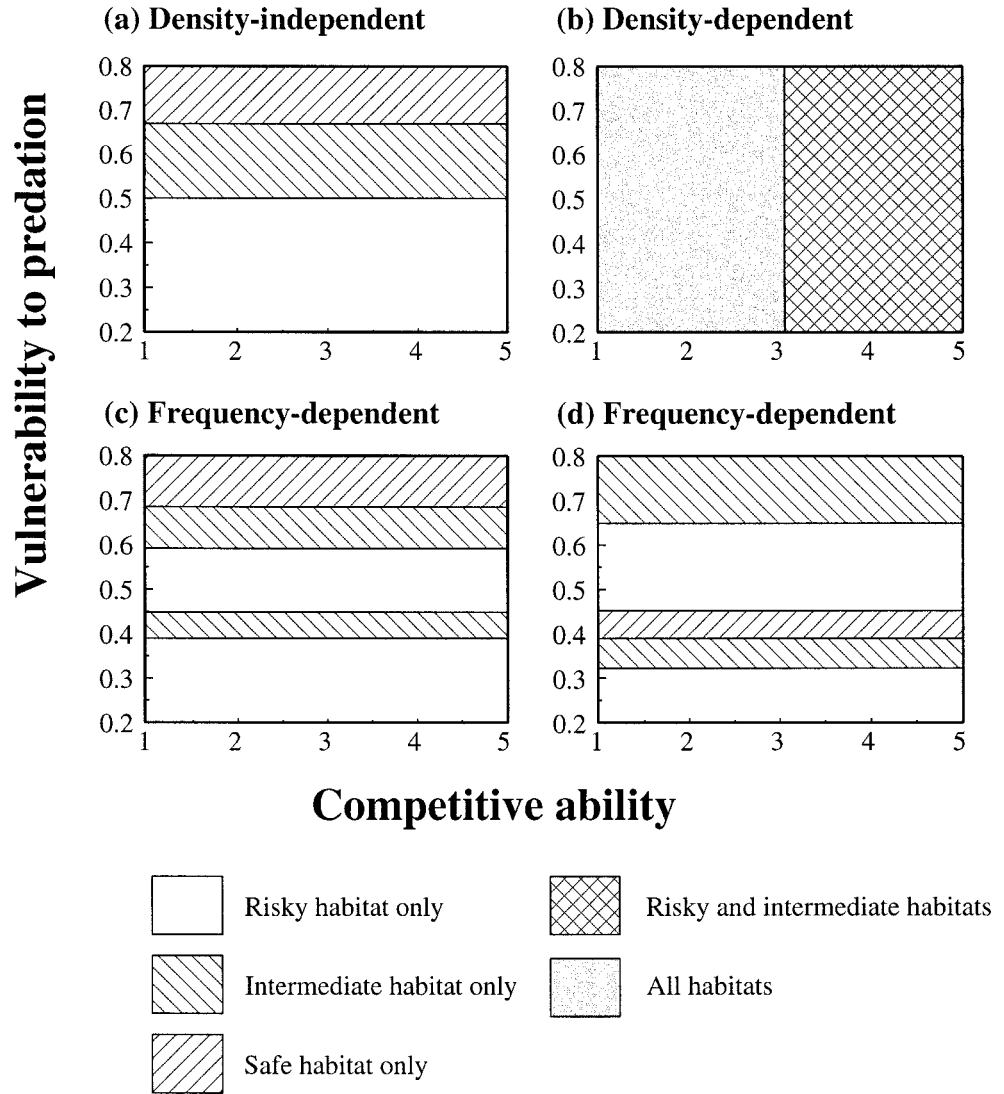
tially from those predicted when competition is exploitative (Figure 3). In all cases, the principal effect of interference competition is to reduce the number of individuals using the risky, more productive habitat (Table 2), making the distribution of individuals across habitats more even. A similar effect has been reported by Hugie and Dill (1994) for predators in a tri-trophic habitat selection game. The effect of interference competition is most pronounced when individuals are distributed across habitats according to competitive ability (e.g., under density- and vulnerability-dependent predation; Figure 3b,c), and it results in an increase in the competitive ability of the poorest competitors using only the risky habitat. This is because the effects of interference competition vary with competitive ability (i.e., poor competitors suffer a proportionally greater reduction in energy acquisition) and only for the best competitors is the substantial predation risk associated with that habitat offset by high rates of energy gain.

When individuals are distributed across habitats according to vulnerability to predation (e.g., under density-independent and frequency-dependent predation; Figures 3a,d), interference competition results in a reduction in the vulnerability of the least vulnerable individuals using the risky, more productive habitat. Again, this occurs because reduced growth in the risky habitat no longer balances the risk of predation experienced there by the individuals most susceptible to predation. Once again, specifics of the pattern of habitat selection expected under frequency-dependent predation depend on the distribution of phenotypes within the population and the habitat to which those individuals were assigned at the start of the simulation (see Figure 2).

**Habitat number**

The general patterns of habitat selection described above remain qualitatively similar (within the range of parameter values described in Table 1) for environments characterized by three, four, or five habitats. That is, individuals remain distributed according to vulnerability to predation under density-independent and frequency-dependent predation (Figure 4a,c,d) and according to competitive ability under density- (Figure 4b) and vulnerability-dependent predation. When the number of habitats exceeds five, however, patterns become less clear, in particular, for scenarios in which habitat selection is characterized by segregation by competitive ability. Only by increasing population size significantly (more than 1000 individuals) and essentially removing the variation in competitive ability and vulnerability to predation do patterns once again emerge. These results suggest that in order for patterns like those described above to be evident along the environmental gradients typical of many natural environments, population sizes will need to be relatively large.

In environments with few habitats, however, the trait values of boundary phenotypes (e.g., the vulnerability value which separates risky and safe habitat occupants in Figure 1a) and the strategy (i.e., opportunistic or selective) of a particular phenotype may vary with habitat number. This occurs primarily as a consequence of changes in the densities of individuals in the riskiest and safest habitats with the addition of habitats of intermediate riskiness (cf. Tables 2 and 3). For example, when competition is exploitative and predation is density independent, the vulnerability of the least vulnerable



**Figure 4**  
 General patterns of habitat selection predicted by the model for a three-habitat environment under exploitative competition and (a) density-independent, (b) density-dependent, and (c) and (d) frequency-dependent predation. In all cases  $R_{\min} = 1$ ,  $R_{\max} = 5$ ,  $B_{\min} = 0.1$ ,  $B_{\max} = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ .

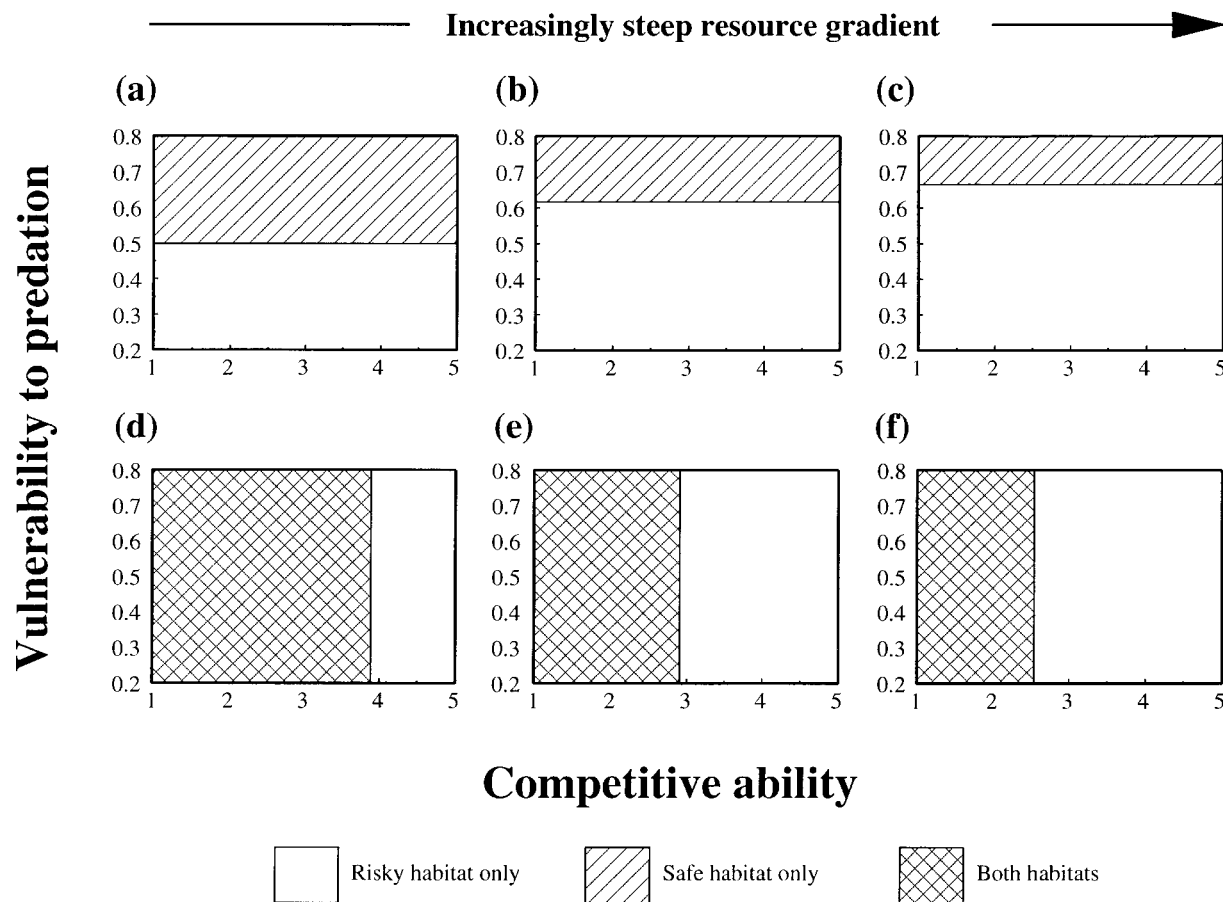
individuals using the safest habitat increases with habitat number (cf. Figures 1a and 4a). When competition is exploitative and predation is density dependent, the best competitors switch from using only the riskier of two habitats (Figure 1b) to the two riskiest of three habitats (Figure 4b). Poorer com-

petitors continue to be opportunistic, using all habitats, regardless of habitat number. When predation is frequency dependent, the most vulnerable members of the population tend to avoid the riskiest habitat (see Figure 4c,d), although which of the safer habitats is chosen depends once again on

**Table 3**  
 Predicted mean (SE) density of individuals in each of three habitats (low risk-low growth, intermediate risk-intermediate growth, high risk-high growth) under the eight competition-predation scenarios depicted by the model

Competition	Predation	Riskiness of habitat		
		Low	Intermediate	High
Exploitative	Density independent	82.3 (0.29)	180.5 (0.36)	237.2 (0.41)
	Density dependent	82.8 (0.29)	168.9 (0.41)	248.3 (0.42)
	Vulnerability dependent	83.3 (0.28)	168.4 (0.38)	248.4 (0.40)
	Frequency dependent	71.9 (0.43)	168.2 (0.46)	259.9 (0.47)
Interference	Density independent	134.8 (0.34)	172.7 (0.42)	192.5 (0.44)
	Density dependent	136.8 (0.39)	171.8 (0.42)	191.4 (0.44)
	Vulnerability dependent	140.0 (0.42)	171.8 (0.44)	191.3 (0.44)
	Frequency dependent	129.1 (0.49)	173.7 (0.59)	197.2 (0.53)

Each value represents the mean of 100 simulations with  $R_L = 1$ ,  $R_I = 3$ ,  $R_H = 5$ ,  $B_L = 0.1$ ,  $B_I = 0.45$ ,  $B_H = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ . Predators were assumed to divide prey into five categories; 500 iterations of the model were run for each simulation.



**Figure 5** Effects of increasing the steepness of the resource availability gradient on patterns of habitat selection predicted by the model under exploitative competition and (a–c) density-independent and (d–f) density-dependent predation. In all cases,  $R_{\min} = 1$ ,  $B_{\min} = 0.1$ ,  $B_{\max} = 0.8$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ . (a, d)  $R_{\max} = 2$ ; (b, e)  $R_{\max} = 5$ ; (c, f)  $R_{\max} = 9$ .

initial conditions (see above). As for the two-habitat scenario (Figures 1d and 2), the least vulnerable individuals are always found in the riskiest habitat.

#### Steepness of environmental gradients

The general patterns of habitat selection outlined above are independent of the steepness of both resource availability and predation risk gradients (or, in the two-habitat case, the absolute difference in resource availability and predation risk between them). Environmental gradients do, however, tend to influence the trait values of boundary phenotypes.

#### Resource gradient

When predation risk is density independent, the principle effect of increasing the steepness of the resource gradient is an increase in the maximum vulnerability of individuals using the risky, more productive habitat (Figure 5a–c). This is because, as the steepness of the resource gradient increases, there is relatively more food available in the risky habitat; food which now offsets the risk of predation experienced by individuals of higher vulnerability. Similarly, when predation risk is density dependent, increasing the availability of resources in the riskier habitat results in a decrease in the mean competitive ability of individuals there (Figure 5d–f). Increasing the steepness of the resource gradient simply increases the carrying capacity of the riskier habitat (and less risky habitats, in multiple-habitat environments). In both cases, increasing the

steepness of the resource gradient results in an increase in the density of competitors using the risky, more productive habitat.

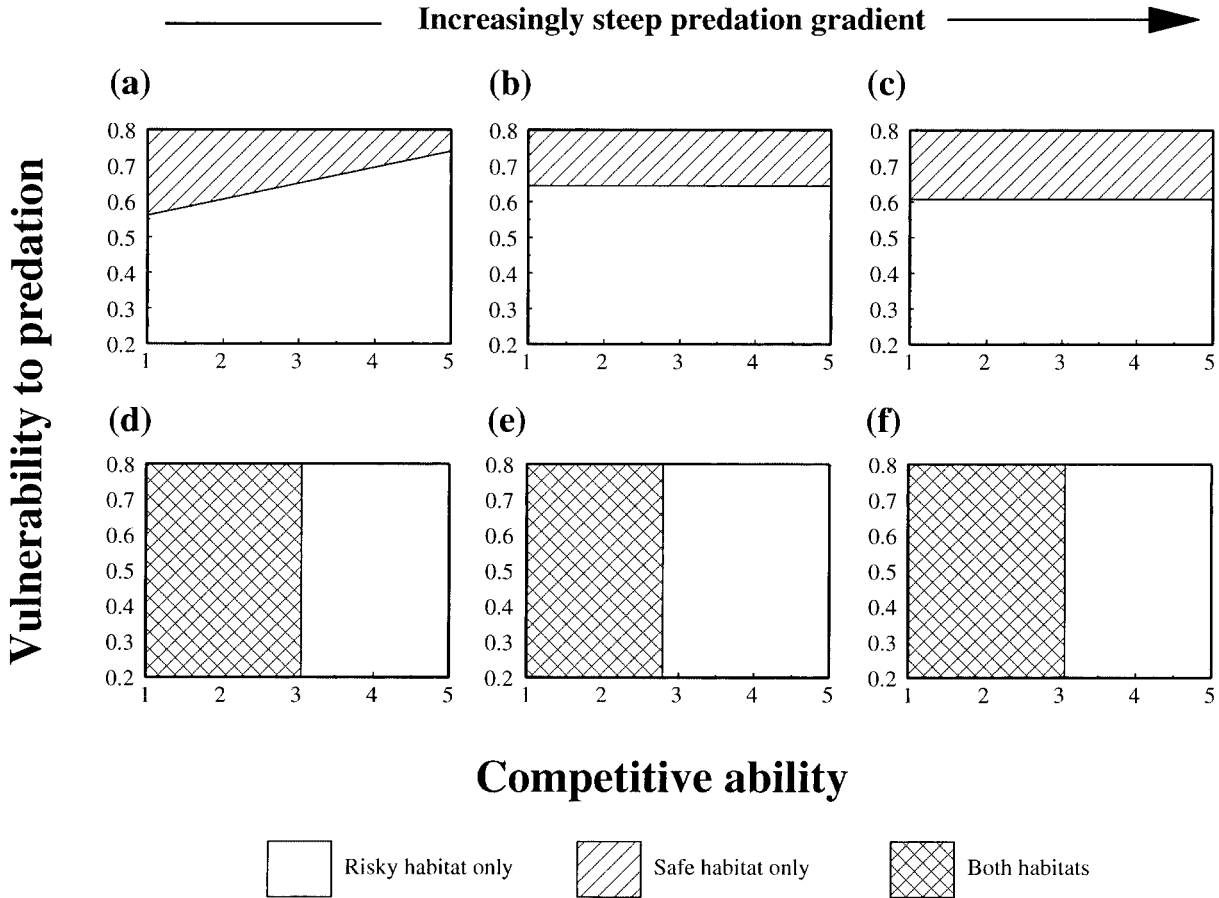
#### Predation gradient

When competition is exploitative and predation is density independent, increasing the predation gradient primarily results in a decrease in the mean vulnerability of individuals using the risky, more productive habitat (Figure 6a–c). This is because, as predation risk increases in the riskier habitat, only individuals of relatively low vulnerability can continue to accept this risk. When the predation gradient is extremely shallow (i.e., habitat differences in riskiness are only slight), both vulnerability and competitive ability interact to produce the pattern of habitat selection (Figure 6a). Highly vulnerable individuals are predicted to occur in the risky habitat if they also possess traits rendering them highly competitive. In contrast, when predation is density dependent, increasing the predation gradient has no apparent effect on the predicted pattern of habitat selection.

#### DISCUSSION

In generating a framework for studying habitat selection under foraging–predation-risk trade-offs by individuals differing in traits related to competitive ability and vulnerability to predation, I have demonstrated that the predicted pattern of habitat selection can be affected dramatically by the form that



**Figure 6**

Effects of increasing the steepness of the predation risk gradient on patterns of habitat selection predicted by the model under exploitative competition and (a–c) density-independent and (d–f) density-dependent predation. In all cases,  $B_{\min} = 0.1$ ,  $R_{\min} = 1$ ,  $R_{\max} = 5$ ,  $k_{\min} = 1$ ,  $k_{\max} = 5$ ,  $v_{\min} = 0.25$ ,  $v_{\max} = 0.75$ ,  $m = 3$ , and  $N_T = 500$ . (a, d)  $B_{\max} = 0.2$ ; (b, e)  $B_{\max} = 0.5$ ; (c, f)  $B_{\max} = 0.9$ .

predation is assumed to take. When predation is density independent (as is frequently assumed) or frequency dependent, individuals will tend to segregate across habitats according to vulnerability to predation. In contrast, when predation is density dependent or vulnerability dependent, segregation by competitive ability will tend to occur. Thus, when competitive ability and vulnerability to predation are determined by different traits, the trait that appears to structure the spatial distribution of a population will depend on the form that predation takes. Whether one assumes that individuals compete for resources via exploitation or interference also influences the predicted pattern of habitat selection, albeit less dramatically than does the form of predation. In general, interference competition results in a more even distribution of competitors across habitats and a simple dampening of the patterns predicted under exploitative competition.

According to the predictions of the model, segregation by vulnerability to predation can take two forms. When predation is density independent, each habitat will house a single group of similarly vulnerable individuals, with the most vulnerable individuals occurring in the safest habitat and the least vulnerable individuals occurring in the riskiest habitat. Thus, the phenotypic gradient will mirror the environmental gradient (see Figures 1a and 4a). In contrast, when predation is frequency dependent, each habitat may house multiple groups of individuals who differ in their vulnerability to predation, such that the riskiest habitat may contain individuals of both low and high vulnerability (see Figures 1d, 2, and 4d).

This is because some highly vulnerable phenotypes, by virtue of their rarity, will experience a reduced probability of capture by the predator, making the riskier, more productive habitat the habitat in which fitness is maximized. Thus, under frequency-dependent predation, the phenotypic gradient will no longer mirror the environmental gradient. Consequently, depending on the scale at which data are collected and analyzed, an ecologist studying associations between habitat and morphology in a population subject to frequency-dependent predation might conclude that individuals are distributed randomly with respect to phenotype and that the population's spatial distribution is independent of predation risk. I know of no other habitat selection models that incorporate such frequency-dependent predation, despite its presumed importance in the maintenance of variation in natural populations (see Endler, 1991). Regardless of which of the above two forms the pattern of segregation takes, individuals of similar phenotype will tend to be strict habitat selectors (Rosenzweig, 1981). That is, they will all occur in the same habitat type.

In contrast to the effects of frequency-dependent predation, when predation depends on the density of individuals in a habitat or their relative vulnerability to predation, individuals will be distributed according to competitive ability, with only the best competitors occurring in a single habitat (the riskiest, most productive habitat; see Figures 1b,c and 3b,c). Poorer competitors will occur in multiple habitats, using an opportunistic strategy (Rosenzweig, 1981). Taken together, these results suggest that simply determining whether phenotype-

habitat associations are based on resource acquisition or antipredator traits and whether phenotypes in a particular population behave as habitat selectors or habitat opportunists may provide insight into the form of predation involved in habitat-related foraging–predation-risk trade-offs.

Empirical studies of habitat selection under foraging–predation-risk trade-offs often report correlations between phenotype and habitat use. Frequently, the phenotypic trait of interest is body size. For example, Sillett and Foster (2000) observed that small juvenile stickleback (*Gasterosteus aculeatus*) tend to spend more time in vegetated habitats than their larger counterparts. These authors (and authors of similar studies) argue that such data support the hypothesis that individual differences in antipredator morphology lead to differences in habitat use, and hence, that individuals are segregated across habitats according to vulnerability to predation. However, because body size is sometimes positively correlated with competitive ability (see Grand, 1997), size-related habitat selection could also be interpreted as evidence for segregation by competitive ability. Ideally, researchers interested in determining the form that competition and predation might take in a particular system would be wise to choose traits whose ecological function is clear. The three-spined sticklebacks studied by Sillett and Foster (2000) would seem to be an appropriate species in which to test the ideas introduced here. In addition to differing in body size, individuals also differ in the length of their dorsal spines and in the number of lateral plates and pelvic girdle components they possess (Grand, 2000), traits known to influence susceptibility to vertebrate predators (Hoogland et al., 1957; Reimchen, 1994). Simply quantifying the relationship between antipredator armor and habitat choice would provide information about whether predation was likely to be density dependent, density independent, vulnerability dependent, or frequency dependent.

As is true of most models, my model makes a number of assumptions that may have influenced the predicted patterns of habitat selection. For example, in an effort to limit the complexity of the model, I assumed that predation risk was spatially fixed and that neither the predator populations nor the population of resources consumed by competitors varied in size over time. Allowing predators to redistribute themselves according to the distribution of their prey (i.e., making the model a game between predators and prey; see Hugie and Dill, 1994; Sih 1998, for a discussion of such habitat selection games) might be expected to reduce the tendency of competitors to aggregate in the risky, more productive habitat when predation is density dependent (see Hugie and Dill, 1994), although it is unclear how the relationship between phenotype and habitat choice might change. For simplicity, I also assumed that neither predators nor competitors satiate and, thus, that the general patterns of habitat selection predicted by the model are independent of population size. In reality, there is an upper limit to the rate at which most animals can process resources, presumably resulting in proportionally greater use of the risky, more productive habitat when population size is small (see Brown, 1998; Morris, 1988, 1992). However, changes in population size will also affect the predation risk experienced by individuals, in particular, when predation is density, vulnerability, or frequency dependent, making it difficult to predict how population size might influence the association between phenotype and habitat. I have also assumed that the fitness value of energy remains constant over time and is the same for all competitors, regardless of phenotype. As demonstrated by McNamara and Houston (1990) and Moody et al. (1996), however, relaxation of these assumptions can lead to competitor distributions that reflect neither the distributions of resources nor the distribution of predation risk. Finally, I have assumed that individuals have

perfect information about the distributions of resources, competitors, and predators and that movement between habitats incurs no cost (see Fretwell and Lucas, 1970). Incorporating less than perfect information and time or energy costs of habitat selection would presumably result in a more even distribution of individuals across habitats (see Abrahams, 1986; Brown, 1998).

To allow for multiple habitats and continuous variation in traits related to competitive ability and vulnerability to predation, I used an individual-based simulation approach. Individual-based models (IBMs) are being used more frequently in ecological studies, in particular for studying the outcomes of complex, spatially explicit interactions between individuals that differ phenotypically from one another (Grimm, 1999; Huston et al., 1988). Although IBMs are relatively straightforward to program, they are often more difficult to interpret than their analytic counterparts, in part because they tend to have more parameters (which may interact with one another in complex ways), but also because their predictions are often sensitive to initial conditions and stochastic events. Typically, one must conduct many experiments, in which parameter values are changed one at a time, to ensure an understanding of the results produced (Grimm, 1999). Although I investigated a relatively large range of values for most parameters (see Table 1), I did not exhaustively investigate the entire parameter space of the model (with its 10 parameters). Thus, it is possible that beyond the range of values investigated, other patterns of habitat selection may emerge.

Unlike previous models of habitat selection under foraging–predation-risk trade-offs, which typically consider only a single form of competition (exploitative; but see Hugie and Dill, 1994; Sih, 1998) and one or two forms of predation (density independent and density dependent; Brown, 1998; Grand and Dill, 1999; Hugie and Dill, 1994; Moody et al., 1996), the model described here allows for simultaneous consideration of two forms of competition and four forms of predation, resulting in eight ecological scenarios available for study. In addition to allowing for the consideration of ecological interactions not previously studied in this context (e.g., vulnerability- or frequency-dependent predation), the common framework generated makes it relatively easy to compare the patterns of habitat selection predicted under the various competition–predation scenarios. Using this framework, it would be relatively straightforward to explore additional forms of predation (e.g., cannibalism) and competition (e.g., kleptoparasitism; see Parker and Sutherland, 1986) and even other types of ecological interactions (e.g., intraguild predation; see Holt and Polis, 1997). Such a framework should be particularly useful for guiding empirical studies of habitat selection under foraging–predation-risk trade-offs, as it provides not just a single hypothesis for testing, but multiple, alternative hypotheses to which data can be compared.

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