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HABITAT SELECTION UNDER PREDATION HAZARD: TEST OF A MODEL WITH FORAGING MINNOWS¹

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Abstract. Animals commonly choose among habitats that differ both in foraging return and mortality hazard. However, no experimental study has attempted to predict the level of increase in resources, or the decrease in mortality hazard, which will induce a forager to shift from a safer to a more hazardous (but richer) foraging area. Here we present and test a model that specifies the choice of foraging areas (“habitats”) that would minimize total mortality risk while allowing collection of some arbitrary net energy gain.

We tested the model with juvenile creek chubs (*Semotilus atromaculatus*) in an experimental field stream in which the foragers could utilize a foodless refuge and choose between two foraging areas that differed in experimentally manipulated resource densities (*Tubifex* spp. worms in sediments) and mortality hazard (adult creek chubs). For the case tested, the model specified a simple rule: “use the refuge plus the site with the lowest ratio of mortality rate (μ) to gross foraging rate (f),” i.e., “minimize μ/f .” Independent prior measurements of mortality hazard (as a function of predator density) and gross foraging rate (as a function of resource density) allowed us to predict the resource level in the more hazardous foraging site that should induce a shift from the safer to the more hazardous site. The chubs’ preferences in subsequent choice experiments agreed well with the theoretical predictions.

The “minimize μ/f ” rule (deaths per unit energy), perhaps in modified form, provides a simple alternative to the “maximize f ” (energy per unit time) criterion that applies to long-term rate maximization when predation hazard does not differ among choices.

Key words: Cyprinidae; experimental streams; fish; foraging; habitat selection; headwater streams; mortality hazard; optimization model; predator-prey; *Semotilus atromaculatus*; trade-off.

INTRODUCTION

In the course of foraging, many mobile animals routinely choose among habitats or foraging sites that differ in both their net energetic return rate and the risk of death to the forager. Numerous experimental studies have shown that foragers shift habitats or exhibit other behavioral changes in the presence of predators, at the cost of obtaining a lower foraging rate (e.g., Stein and Magnuson 1976, Milinski and Heller 1978, Caraco et al. 1980, Grubb and Greenwald 1982, Sih 1982, Dill and Fraser 1984, Holmes 1984, Kotler 1984, Lima 1985, Lima et al. 1985, Schmitt and Holbrook 1985, Fraser and Huntingford 1986, Holomuzki 1986, Fraser and Gilliam 1987).

Collectively, these studies emphasize that the effect of predators on populations and communities commonly transcends simple removal of individuals, since intimidation by predators shapes patterns of habitat use and hence resource exploitation and species interactions. For example, Power et al. (1985) showed that

intimidation by piscivorous stream fish can prevent minnows from grazing attached algae in some sections of streams, thereby dramatically altering algal distributions. Werner et al. (1983), following Mittelbach (1981), showed that intimidation by largemouth bass induced size class habitat segregation in bluegill sunfish; this segregation resulted in increased individual growth rates for large, invulnerable bluegills that selected open areas of a pond, and decreased growth rates for smaller individuals that remained in safer but energetically poorer vegetated areas.

Fraser and Cerri (1982), Cerri and Fraser (1983), and Fraser et al. (1987) have shown that juvenile creek chubs (*Semotilus atromaculatus*, Cyprinidae) inhabiting headwater streams make choices among locations that may differ widely in food resources and predators (Fraser and Sise 1980), and that these choices can be influenced by the density of predators in pools. However, these studies, like the others cited above, did not attempt to predict the resource enrichment necessary to produce a switch to a more hazardous site. Here we test whether a simple optimality model can be useful in making such predictions. In the present experiment,

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these minnows were given a refuge and a choice between two foraging areas in an experimental field stream in which the level of mortality hazard (=number of piscivorous adult creek chubs) and the resource levels (=density of *Tubifex* spp. worms in natural sediments) were experimentally varied. For this case a simple rule, "when foraging, minimize the ratio of mortality rate to gross foraging rate (i.e., minimize μ/f)," follows from the more general model developed below. Independent prior estimates of mortality and foraging rates, together with the rule, specified predicted choices.

A MODEL

Given an array of sites ("habitats"), each with an associated foraging rate and mortality rate for a forager, what choice(s) would maximize fitness? This model specifies the habitat(s) to be used if an animal is to minimize the total probability of predatory death over a foraging bout, while achieving some arbitrary net foraging rate for the period.

Assume an animal can allocate time among n habitats, and represent the net foraging rates (e.g., joules per second) in the n habitats as an n vector $\mathbf{h} = [h_1, \dots, h_n]$. Similarly, represent the mortality rate (e.g., probability of death per second) as $\mu = [\mu_1, \dots, \mu_n]$. A forager can allocate time among the habitats; let the vector $\mathbf{p} = [p_1, \dots, p_n]$ denote the proportion of time spent in each habitat, where $\sum p_i = 1$ and $p_i \geq 0$ for all i . The overall net foraging rate for the period (e.g., a day) is taken to be $H = \mathbf{p} \cdot \mathbf{h}$ (i.e., the inner product, $\sum p_i h_i$), and the mortality rate to be $U = \mathbf{p} \cdot \mu$. We wish to determine the vector \mathbf{p}^* that minimizes the objective function U , subject to a constraint $H \geq H'$, where H' is a "target" overall net foraging rate to be met over the period. In this paper, we are not concerned with the value of H' an animal should adopt, but only how it would go about minimizing U while meeting some arbitrary H' . In some cases H' might be reasonably specified as a constant "requirement" (e.g., the maintenance ration of an endotherm in the non-breeding season). In other cases, we would expect the target foraging rate to change as the options (the vectors μ and \mathbf{h}) change; in fact our experiments provide evidence against a constant target "requirement." In these cases, the determination of an optimal H' requires an integration of foraging and life history theory (see Discussion). For present purposes, however, we will show that habitat choice can often be predicted if H' is known only to lie within some interval.

This problem has a straightforward linear programming structure: $\min U = \mathbf{p} \cdot \mu$ subject to $\mathbf{p} \cdot \mathbf{h} \geq H'$ and

$p_i \geq 0$ for all i . The solution is easily and intuitively obtained by inspection. Graphical and algebraic solutions are both instructive.

The graphical solution is found by plotting the points (h_i, μ_i) on a plane. The linear combinations of these

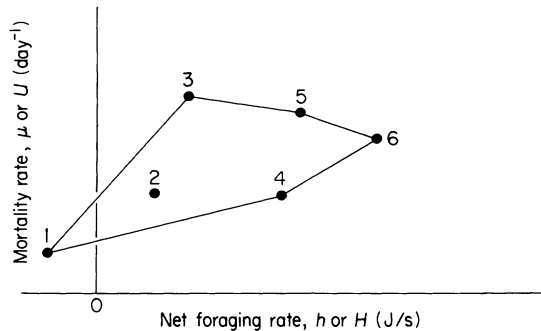


FIG. 1. Six available habitats are characterized by the net foraging rate and the mortality rate a forager expects in each. Mortality rate is minimized for a given "target" long-term net foraging rate by using Habitats 1 and 4 if the "target" is between the net foraging rates in those two habitats, and by using Habitats 4 and 6 if the "target" lies between those two net foraging rates. Habitats 2, 3, and 5 are never in the optimal set.

points define the feasible combinations of U and H , and the solution to the problem will lie along a lower bound of the least polygon (convex hull) of these points. For example, Fig. 1 depicts a case with $n = 6$ habitats. The least polygon is the solid line. Allocation of all time to a single habitat i of course yields $H = h_i$ and $U = \mu_i$. Allocation of nonzero time to two habitats yields a value of U and H on a straight line connecting those two points, and allocation of time to three or more habitats in the figure results in U and H in the interior of the polygon. The solution of the example is clear by inspection. If $H' \leq h_1$, then U is minimized by $\mathbf{p}^* = [1, 0, 0, 0, 0, 0]$. If $h_1 < H' < h_4$, then $\mathbf{p}^* = [p_1, 0, 0, p_4, 0, 0]$, where $p_1 + p_4 = 1$. If $H' = h_4$, then $\mathbf{p}^* = [0, 0, 0, 1, 0, 0]$; if $h_4 < H' < h_6$, then $\mathbf{p}^* = [0, 0, 0, p_4, 0, p_6]$, where $p_4 + p_6 = 1$; finally, if $H' = h_6$, then $\mathbf{p}^* = [0, 0, 0, 0, 0, 1]$. If $H' > h_6$, then there is no solution. Habitats 2, 3, and 5 are never in the optimal set for any value of H' .

The graphical solution generalizes to any number of habitats, and trade-offs of mortality and foraging rate within a habitat could be represented as a set of points for each habitat. (Interestingly, the optimal behavior within a habitat would then depend upon the options outside of the habitat.)

From the graphical solution we can make several observations. First, the optimal habitats to be used can be specified if we know only that H' lies in one of the above intervals (e.g., Habitats 1 and 4 if h_4 exceeds the gut-processing capacity, or if consumption of a maintenance ration met by h_4 is assumed). Second, if H' were known precisely, the exact time budget could also be specified (e.g., if H' corresponded to the midpoint of the 1-4 line, then $\mathbf{p}^* = [0.5, 0, 0, 0.5, 0, 0]$). Third, \mathbf{p}^* contains at most two nonzero elements. Fourth, the combination of Habitat 1 and Habitat 6 is never optimal for any value of H' (the line connecting those points lies above some other time budgets in the figure).

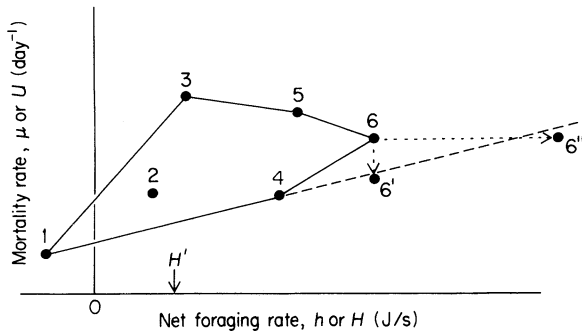


FIG. 2. Given that the "target" rate H' lies between the net foraging rates in Habitats 1 and 4, the solution is to "use Habitats 1 and 4." However, a switch to "use Habitats 1 and 6" would occur if the point representing Habitat 6 were moved below the dashed line.

Habitat 1 might be called a "Refuge" (lowest mortality rate, such as a burrow or brushpile), but the solution is never to use Habitat 6 and then spend the rest of the time in the "Refuge." Rather, if Habitat 6 is to be used, the complementary time is to be spent in Habitat 4. This is unchanged if Habitat 1 were an absolute refuge ($\mu_1 = 0$).

The fifth observation is the most crucial because it allows us to specify the quantitative changes necessary to produce switches in the optimal solution. In the example, assume $h_1 < H' < h_4$, so that the solution is to "use Habitats 1 and 4." A switch to "use Habitats 1 and 6" occurs in the solution if the point (h_6, μ_6) is moved below the dashed line in Fig. 2. For example, a switch in the solution occurs if the mortality rate in Habitat 6 is reduced sufficiently (point 6') or the net foraging rate raised sufficiently (point 6''). A final observation is that one habitat can replace another in the optimal set without either habitat being altered. For example, moving the point representing Habitat 1 sufficiently to the right (increasing h_1) while holding Habitats 4 and 6 constant can change the solution from "use Habitats 1 and 4" to "use Habitats 1 and 6."

The algebraic characterization is as follows. Call the habitat with the smallest μ_i the Refuge, and denote its foraging and mortality rates as h_R and μ_R , respectively. If the animal is to forage at a mean rate $H \leq h_R$, then obviously it should just stay in the Refuge. If it is to forage at a higher mean rate, we proceed as follows. Of the habitats for which $h_i > h_R$, denote that which minimizes $(\mu_i - \mu_R)/(h_i - h_R)$ as Habitat A (graphically, by raising the slope of a line through the point (h_R, μ_R) until the line touches another habitat's point; for simplicity, we assume this is a single point). Of the habitats for which $h_i > h_A$, denote the one that minimizes $(\mu_i - \mu_A)/(h_i - h_A)$ as Habitat B. Of the habitats for which $h_i > h_B$, denote that which minimizes $(\mu_i - \mu_B)/(h_i - h_B)$ as Habitat C, and proceed analogously. An animal would minimize U by using only R and A if $h_R < H' < h_A$, by using only A and B if $h_A < H' < h_B$, only B and C if $h_B < H' < h_C$, etc.

In the present application of the model to creek chubs, $n = 3$ "habitats": an absolute refuge (Habitat 1, or R) with no food, and two foraging areas (Habitats 2 and 3). The solution is, "Use the Refuge, plus the area with the lowest ratio of $(\mu_i - \mu_R)/(h_i - h_R)$." This does not rely on the value of H' , except that $H' < h_2, h_3$, which we assured by using resource levels that produced satiation if foraged upon continuously. The Refuge was absolute ($\mu_R = 0$) and provided no food, so h_R is just the metabolic rate, assumed to be similar in each habitat. Thus "use the Refuge, plus the area with minimal $(\mu_i - \mu_R)/(h_i - h_R)$ " simplifies to, "use the Refuge, plus the area with minimal μ_i/f_i ," where f_i is the gross foraging rate (i.e., $h_i = f_i + h_R$). The units of μ and f are arbitrary.

In the case applied to the creek chubs, then, the model's solution reduces to an especially tractable and intuitive form: in addition to the refuge, the forager uses the foraging habitat with the lowest ratio of mortality rate to gross foraging rate; i.e., "while foraging, minimize μ/f ." Thus, with the foodless refuge present, we require only estimates of mortality rates and gross foraging rates in the alternative areas to predict preferences by the fish.

METHODS

The utility of the "minimize μ/f " rule was tested with juvenile creek chubs in an experimental field stream. The stream consisted of wooden channels, 42 cm wide, laid directly into a stream bed (more completely described in Fraser and Cerri 1982). Experiments were conducted in a 2.4-m linear section of the stream (Fig. 3). The central refuge (30 × 42 cm) was an area screened with 13-mm mesh hardware cloth that prevented passage by predatory adult creek chubs but not the smaller foragers (juvenile chubs). The densities of food (*Tubifex* spp. worms burrowed into mud) and predators (adult creek chubs) were manipulated in the two foraging areas flanking the refuge. This arrangement imitated local headwater streams, in which adult creek chubs are the only piscivorous fish. The experimental section was cleaned daily with a suction pump to prevent colonization by invertebrates, and upstream blocking nets prevented drifting organisms from entering the experimental arena. Water current was maintained at ≈ 1 cm/s, and depth at 12 cm.

We estimated the mortality rates of juvenile chubs in the presence of different densities of adult chubs, and their rate of resource intake at different densities of *Tubifex* worms. These estimates were made prior to and independent of the choice experiments. In particular, to measure gross foraging rates, *Tubifex* worms were allowed to burrow in mud in plastic trays for 30 min; the worms then showed the typical behavior of waving the posterior portion of their bodies in the water column. Window screening with 3.2-mesh was fitted flush with the surface of the mud prior to adding

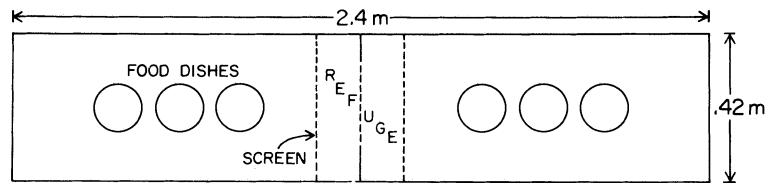


FIG. 3. Experimental section of the field stream.

the worms. This eliminated feeding attempts by adult chubs in the subsequent choice experiments; without the screens, adult chubs consumed worms by sucking the mud into their mouths. Juvenile chubs, 30–38 mm total length (TL), which had been fasted overnight, fed readily on the worms, and the volume ingested while foraging continuously for 1 min was determined by pumping stomachs. Mortality rates were determined in the experimental stream by confining eight juveniles with a given adult density (one, two, or three adult chubs, 135–178 mm TL, randomly assigned) over a 24-h period. Previous pilot experiments showed a strong effect of predator density on the mortality rate of foragers (as was confirmed in the present experiment), but detected no effect of forager density.

The choice experiments were conducted as follows. In each trial, one of the two foraging areas contained one predator and three 14 cm diameter Petri dishes, each containing 0.17 *Tubifex* worms/cm². In the first experiment, the other contained two predators and either 0.17, 0.33, 0.50, or 1.0 worms/cm² in the Petri dishes. Based on the model and the results of the mortality and foraging experiments, the chubs were predicted to prefer the one-predator area at the first two densities, but switch to the two-predator area at the two highest densities (see Results). The second experiment offered a three-predator area as an alternative to the one-predator area, with densities of 0.65 and 1.0 worms/cm² at the three-predator area; these densities also bracketed the predicted switch point.

In a given trial (replicate), the side to receive one predator was chosen randomly, and the predators were randomly assigned from a pool of four adult chubs (135–178 mm TL). Eight foragers were then drawn randomly from a pool of 32 juvenile chubs (30–47 mm TL, $\bar{X} = 35.0$, $SE = 0.7$) and stocked in the refuge. When a majority had left the refuge (usually within 1 min) the location of foragers and the activity level of each predator (1 = inactive to 4 = chasing a forager) were recorded at 1-min intervals for 26 min from an observation platform. The 26-min period precluded substantial resource depletion. No forager was used twice in one day, all fish were fed to satiation at the end of the day, and the foragers fasted overnight. Eight replicates, each with eight fish, were conducted for each treatment.

Preference for the high-hazard (two- or three-predator) area during a trial was calculated as $t_B/(t_A + t_B)$,

where t_A = proportion of time spent at a feeding dish in the one-predator area, and t_B = proportion of time spent at a feeding dish in the two- or three-predator area. Individual fish were not distinguished.

RESULTS

The juvenile chubs readily left the refuge and sampled the two foraging areas. The fish foraged semi-independently, leaving the refuge as singletons, or occasionally in loose temporary associations. The chubs clearly treated the refuge as such, and across all trials spent 42% of the time (range 7–77% for individual trials) in the refuge, which comprised 12% of the test area. Across all trials, 13% (range 1–35% for individual trials) of the time was spent at a feeding dish and 45% (range 14–72%) out of the refuge but not foraging at a dish, usually along edges of a foraging area. Overall, 9984 fish-minutes were recorded. When feeding at a dish, the fish fed vigorously in both the initial trials to measure foraging rate, and in the choice experiments.

The independently measured mortality and foraging rates (Fig. 4 and 5), together with the “minimize μ/f ” rule, specified the food level at which the two- or three-predator area was predicted to become preferred over the one-predator area with 0.17 worms/cm². These levels are shown in Fig. 6 (e.g., in Fig. 6A, the predicted switch point was at 0.80 worms/cm² in the three-predator area; given estimates of $\mu = 0.15$ and 0.34 in the presence of one and three predators, respectively, and 0.17 worms/cm² in the one-predator area, μ/f in the three-predator area was lower than in the one-predator area only if food levels exceeded 0.80 worms/cm² in the three-predator area). Foraging chubs switched to feeding at the three-predator area as predicted by the model (Fig. 6A). The switch was real: at 0.65 worms/cm² the preference was significantly less than 0.5, and at 1.0 worms/cm² significantly greater than 0.5 (arcsine \sqrt{x} transformation, two-tailed t tests, $n = 8$, $P < .05$ in each case). Each data point in Fig. 6 is the preference for the high-predator area during one trial (each trial contained 8 fish, so the mean preference is actually based on 64 fish).

Foragers also switched from the one-predator area to the two-predator area as predicted by the “minimize μ/f ” rule (Fig. 6B). In this series, we used four food levels to ask whether the shift was gradual or better described by a step function. This was done with three planned orthogonal contrasts. Denoting the four food

levels as 1, 2, 3, and 4 (1 = lowest food), the contrasts were: (a) 1 vs. 2; (b) 3 vs. 4; (c) (1 and 2) vs. (3 and 4). Contrast (a) was not statistically significant (arcsine-transformed, $F = 0.2279$, $df = 1, 28$, $.75 > P > .50$), nor was contrast (b) ($F = 0.3227$, $df = 1, 28$, $.75 > P > .50$). However, contrast (c) was highly significant ($F = 9.40$, $df = 1, 28$, $P < .005$). Thus, the switch appears to be better described as a step function than as a gradual shift. Again, the switch in preference was real: the preference at (1 and 2) was < 0.5 , and the preference at (3 and 4) was > 0.5 (arcsine-transformed, two-tailed t tests, $n = 16$, $P < .05$ in each case). Note that the shift in preference to the more hazardous area occurred at a lower resource density in the 2 vs. 1 predator trials than in the 3 vs. 1 predator trials.

The fish spent less time in the refuge as the resource density in the high-hazard area increased (Fig. 7). Predator density also affected the time in the refuge (regression with untransformed data: time in refuge = $-0.046 + 0.25$ predator number [2 or 3] $- 0.21$ worm density, $P < .02$ for each effect, with same significance on arcsine-transformed data).

Predator activity level varied among trials, and we feel that this increased the variance in the data in Fig. 6. For example, at 0.5 worms/cm² in Fig. 6B, the replicate that departed strongly from the predictions (the trial for which preference = 0) was a trial in which the two predators quickly attacked foragers entering the two-predator area, while the single predator was less active. Overall, however, there was no significant partial correlation between preference and predator activity levels in the two areas during a trial. This was surprising, but may reflect two cancelling effects: high predator activity should decrease the attractiveness of an area (hence negative correlation between activity and number of foragers), but lack of foragers should

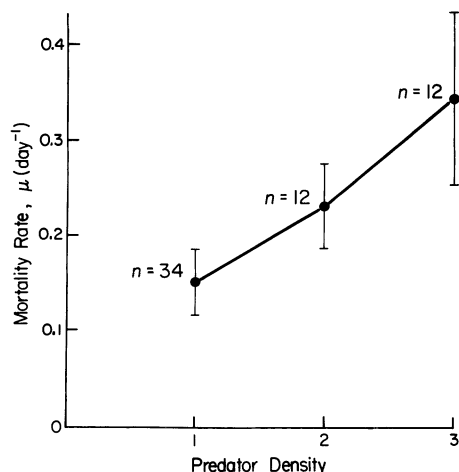


FIG. 4. Mortality rate (probability of death per day) of juvenile creek chubs as a function of predator density (no. adult chubs) in a compartment. Vertical bars = ± 1 SE. n = number of replicates.

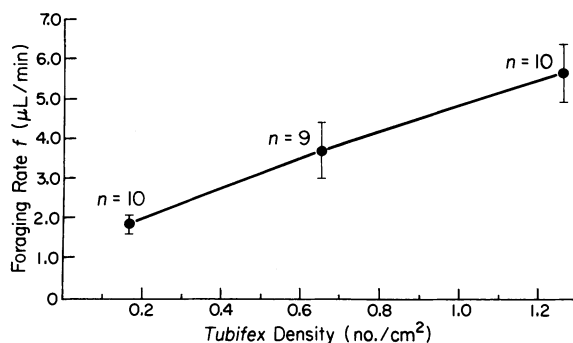


FIG. 5. Foraging rates of creek chubs on *Tubifex* worms burrowed in mud, as a function of *Tubifex* density (worms/cm²). n = number of replicates. Vertical bars = ± 1 SE. Foraging rate = $1.147 + 4.29(\text{Density}) - 0.058(\text{Density})^2$, $r = 0.62$.

decrease predator activity (hence positive correlation between activity and number of foragers).

DISCUSSION

The simple rule, "when foraging, minimize μ/f ," correctly specified preference in a field setting with live predators. The success of the rule might be attributable to an alternative statement of the rule: the criterion

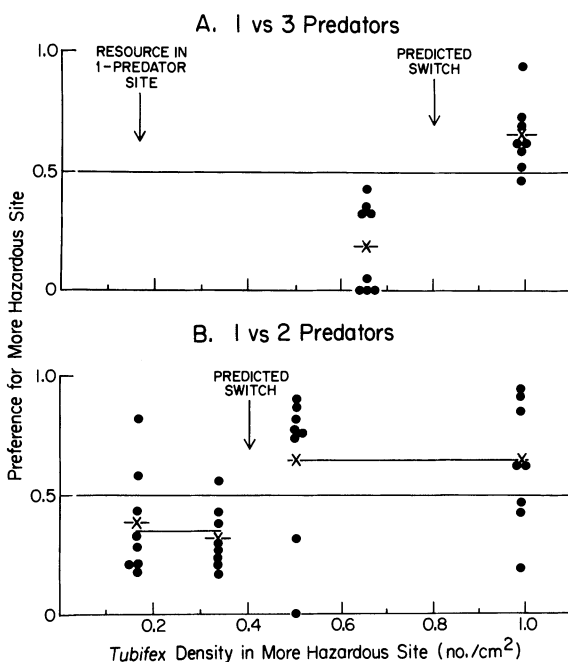


FIG. 6. Results of choice experiments. Resource level in the one-predator area was 0.17 worms/cm² in each trial, and resource level was varied in the two- or three-predator area. Panel A: choice between a one-predator area and a three-predator area. Panel B: choice between a one-predator area and a two-predator area. A point on the figure represents the preference for feeding at the more hazardous area during one trial. \times = treatment means; horizontal bars = pooled means for orthogonal contrasts.

“prefer Habitat A over Habitat B if $\mu_A/f_A < \mu_B/f_B$ ” can be rearranged to “Prefer A if $\mu_A/\mu_B < f_A/f_B$.” This rearrangement greatly reduced the sophistication required of both the experimenter and the forager, since the rule is seen to depend only upon the relative levels of mortality and intake in the two sites, not the absolute levels. This alternative statement means that even if measurements of absolute mortality and foraging rates include systematic errors, the measurements remain useful if the relative magnitudes are still somewhat accurate. We measured absolute mortality and foraging rates, but what really mattered was that two predators were about 1.5 times as hazardous as one predator, not the absolute levels. This is also of substantial practical importance if relative rates can be estimated more feasibly than absolute rates; one needs only to know whether an animal is x times as likely to be preyed upon, and obtains y times as much food, in one area as another. We caution, however, that this simplification applies to the present case, with an absolute refuge included in the optimal set, but not to others.

For the forager, the alternative statement means that the animal's behavior need only reflect the relative levels: if one site appears x times as hazardous, do not forage there unless it yields at least x times the intake rate. This simplicity may explain why the foragers were able to show the appropriate preferences within a brief 26-min trial. Indeed, the preferences appeared early in the trials; for instance, data from only the first 13 min of the trials gave nearly as strong agreement with the predictions as did the entire 26-min trial. Nine of the 48 trials were contrary to the predictions over the 26-min trials (Fig. 6); over the first 13 min, 10 were incorrect, and over only the final 13 min, 12 were incorrect (in three trials both the first and second 13-min intervals were incorrect). This pattern suggests that the animals employed a quickly implemented rule of thumb. Such a rule might manifest itself as a probability of leaving a site following a predator's approach. Qualitatively, we were impressed by the “tenacity” the foragers showed in the presence of three predators and the highest food level; in these trials, foragers would commonly circle around predators and resume feeding, while at the lower food level they would shift to the one-predator site or the refuge.

The foraging minnows spent less time in the refuge as the food level increased in the environment. This is instructive: if the fish had behaved according to a goal of obtaining some set ration “requirement,” the fish would instead be expected to spend more time in the refuge as the food density increased (i.e., to use the higher foraging rate to reduce its total exposure to predators). However, the fish exhibited the opposite behavior: across treatments, they spent less time in safety as the food level increased, thus accepted a higher total exposure to predators for the higher reward.

We chose the resource type, resource densities, and length of the time trial so as to preclude substantial

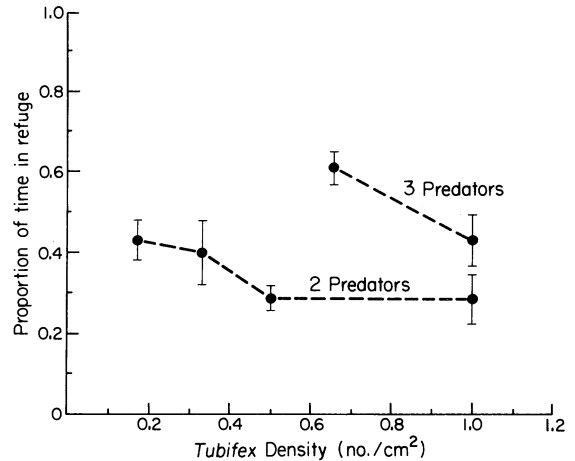


FIG. 7. Proportion of time in the Refuge as a function of *Tubifex* density in the more hazardous area. Since the food level in the one-predator area was held constant, the density axis could be re-scaled linearly to represent the average food density in the environment. Vertical lines = 1 SE, n = eight replicates (each with eight fish).

resource depletion during a trial, as is likely to mimic foraging on many benthic invertebrates in streams and lakes. In many cases, however, depletion might be substantial. In these cases, we would expect omniscient foragers to deplete “patches” so as to equalize μ/f in each patch at departure.

Since site selection by individuals can structure populations and communities, we are encouraged that the model and feasible measurements can accurately predict shifts as resource levels and mortality threat change. More broadly, the “minimize μ/f ” rule (i.e., deaths per unit energy) provides a simple alternative to the “maximize energy intake per unit time” criterion (i.e., maximize f , i.e., energy per unit time) that has been instructive in long-term choices of diets, patches, and habitats among which mortality hazard does not vary. However, the rule applies exactly only if the refuge is absolutely safe, the metabolic costs in each habitat are identical, and the solution specifies that some time should be spent in the refuge (this final condition occurs if the “target” H' is less than the net foraging rate in the site satisfying the rule). If these conditions do not hold, modifications apply. For example, if the mortality rate in the refuge is nonzero, but the other conditions apply, the full model reduces to “minimize $(\mu - c)/f$,” where c is the mortality rate in the refuge. Thus manipulation of hazard in the refuge influences optimal behavior while out of the refuge. Similarly, if the metabolic cost in the refuge is decidedly different from the other sites (e.g., different current speed or temperature), the full model reduces to “minimize $\mu/(f + k)$,” where k is the difference between the metabolic costs in and out of the refuge. In yet other cases (e.g., no refuge, or constraining the animals to use only one habitat per day), the solution may require the ad-

ditional step of determining precisely an optimal H' (the present model minimizes total mortality for a given value of H'). This step requires analysis at the interface of foraging and life history theory, in which the immediate cost of death is weighed against long-term benefits of body growth (Werner and Gilliam 1984) or other benefits (e.g., Iwasa 1982, Abrams 1984, Iwasa et al. 1984, Lima 1986, Mangel and Clark 1986, McNamara and Houston 1986).

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