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OPTIMALLY FORAGING MICE MATCH PATCH USE WITH HABITAT DIFFERENCES IN FITNESS

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Abstract. We tested the fundamental assumption of the “optimality paradigm” that the foraging behavior of individual organisms corresponds to what we would expect if it had been honed by natural selection to match habitat differences in reproductive success. First, we used long-term studies of life history and habitat selection in white-footed mice to illustrate that the fitness of females living in the forest is greater than that of females living in forest-edge habitat. Second, we used short-term foraging studies to evaluate whether food patches located in the forest provided more value to foragers than did those in the edge. Third, we used foraging studies and data on the occurrence of predators to demonstrate that animals foraging in areas with little cover face higher risks than when they forage in areas with more cover. We confirmed three a priori predictions: (1) Individual mice abandoned foraging patches at higher harvest rates in edge habitat than they did in forest. (2) Individuals harvested resource patches to lower quitting harvest rates under cover than they did when patches were located in the open. (3) The difference in quitting-harvest rate between “open” and “covered” patches was less in the safe forest habitat than it was in the risky edge habitat. Our results yield an impressive fit with our previous knowledge of habitat differences in reproductive success and substantiate the premise that short-duration strategic decisions by individuals match habitat differences in fitness.

Key words: *fitness; foraging; giving-up density (GUD); habitat selection; life history; natural selection; patch use; Ontario; Peromyscus; predation risk.*

INTRODUCTION

Optimality theories in ecology are built on the assumption that evolution by natural selection molds animal behavior in ways that maximize reproductive success. A behavior is optimal when the marginal rate of increase in fitness benefits is equal to the marginal rate of increase in fitness costs. Often, however, the theories are based on maximizing a surrogate of fitness (e.g., the gain of energy from the environment), with tests measuring the surrogate (e.g., mean harvest rate) rather than the underlying currency of evolutionary fitness. An exception is Ritchie's (1990) study of Columbian ground squirrels. Individuals whose diet deviates from their optimum mix of monocots and dicots have much lower survival and reproduction than do squirrels whose diet is close to their optimum. But the optimality paradigm (Rosenzweig and Abramsky 1997) can be used to predict patterns in ecological populations and communities only if populations tend to evolve toward

their respective optima. Does the average behavior exhibited by members of a population correspond with what we would expect if they were maximizing evolutionary fitness? We provide a partial answer to this crucial question by testing whether the relative “profit” obtained from different habitats by foraging rodents agrees with a priori predictions based on long-term estimates of fitness in those same habitats.

We begin by assessing differences in fitness of white-footed mice occupying nest boxes in forest and forest-edge habitats. We demonstrate that higher mortality in the edge habitat corresponds with higher risks of predation, and that our estimates reflect true differences in mortality rather than dispersal between habitats. We use foraging experiments to calculate quitting-harvest rates of individual mice, then use those data to assess three critical a priori hypotheses: (1) Mice should quit foraging at a higher harvest rate in patches located in edge habitat than in patches located in forest. (2) Mice should quit foraging at a higher harvest rate in patches located in the open than in patches located under cover. (3) The difference in quitting-harvest rates between patches located in the open and patches located under cover should be less in the forest than in the edge

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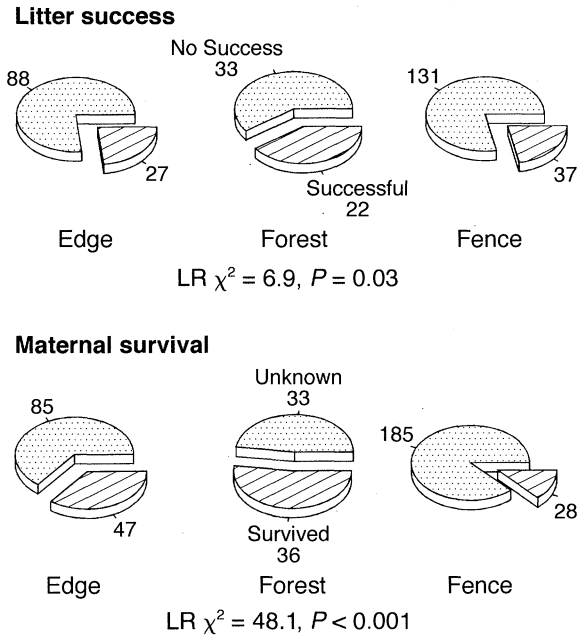


FIG. 1. Litter success and maternal survival of white-footed mice living in nestboxes in southwestern Ontario, Canada, was higher in forest than in forest-edge or fencerow habitats (hierarchical loglinear analysis; likelihood ratio (LR) chi square [Norušis 1992]). Successful litters were those that yielded at least one recruit to the nestbox population of mice (sample based on marked litters [≤ 20 days old; Layne 1968] born in spring and autumn 1981–1991 [data for 1982 excluded because boxes were not checked in the autumn of that year]). Maternal survival was estimated as survivors until the next reproductive season versus mothers whose survival was unknown (sample based on marked mothers observed with litters ≤ 20 days old in spring or autumn 1981–1991 [data for 1982 excluded]; the sample is larger than for litter-success because very young litters were unmarked).

habitat. We use the proportion of resources consumed in rich and poor patches to test whether white-footed mice followed a fixed quitting-harvest rate or a fixed search-time foraging strategy. We combine all results to reveal the link between foraging and its fitness consequences.

THE STUDY SYSTEM

White-footed mice (*Peromyscus leucopus*) are semi-arboreal, nocturnal, North American rodents that readily occupy wooden nestboxes in the northeastern part of their geographic range. We have, since 1981, individually marked and monitored the subsequent survival of lactating females and their nursing offspring in interior forest, adjacent forest edge, and tree-dominated fencerow habitats in an agricultural mosaic in southern Ontario. Most litters produced by this population of white-footed mice are unsuccessful at producing any recruits to the adult population of nestbox-inhabiting mice (Morris 1986), a result corroborated by other researchers (Jacquot and Vessey 1998). Litters born in the spring of the year have much higher recruitment

than do litters produced in autumn. Few litters are produced during the summer breeding hiatus. Despite these seasonal differences, the success of litters born in edge and fencerow habitats is much less than the success of litters born in forest (Fig. 1, top).

Maternal survival from spring to autumn, and vice versa, is also higher in forest than it is in either of the other habitats (Fig. 1, bottom). There are no differences in the duration of breeding, or in the proportion of animals breeding, among habitats. Female white-footed mice whose nests are located in the forest (30–90 m from the agricultural fields) have higher fitness than do females whose nests are located in forest near the edge (< 10 m from fields), or in fencerows (< 5 m from fields) (Morris 1996).

Differences in survival correlate well with our knowledge of habitat use by predators. A much higher proportion of weasel scats, of partially consumed rodents, and of weasels themselves (*Mustela frenata*) in our boxes occur in the fencerow habitat than in forest or edge (Fig. 2). Over the years, our casual observations of feral dogs, feral cats, foxes (*Vulpes fulva*), coyotes (*Canis latrans*), long-eared owls (*Asio otus*), and carnivore tracks have always been associated with fencerow and edge habitats (but all are more visible there than in the forest). Mice are also at risk, during forays into the fields, of “consumption” by agricultural machines that farmers operate frequently after dark. The pattern from weasels, and the supporting but circumstantial evidence on other sources of mortality, suggests that predation on mice is greater near, and within, fields than it is within the forest.

A role for dispersal?

Are the differences in “survival” caused by differences in our ability to detect dispersing animals in the three habitats? There are at least two reasons to suspect not. First, most emigration in white-footed mice, as in many other rodent species, occurs shortly after weaning (Wolff 1997, Wolff et al. 1988). It is difficult to reconcile juvenile-biased dispersal with our convincing evidence of differences in adult survival. Second, low juvenile survival in edge and fencerow habitats is inconsistent with our tests of dispersal.

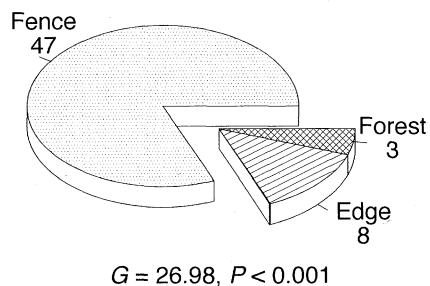


FIG. 2. Weasels visited fencerow nestboxes far more frequently than they visited nestboxes in either forest or forest-edge habitats (data include all evidence of weasel visits).

TABLE 1. Observed and expected dispersal (animals that occupied a nestbox in a habitat different from their natal habitat) of white-footed mice marked as littermates in nestboxes in three habitats in a 50-ha study area in southwestern Ontario.

Habitat	Observed	Expected
Fencerow	16	37.04
Edge	53	40.44
Forest	27	20.52

Note: Expected values were calculated as the product of overall dispersal rate (6.67%) multiplied by the number of mice marked as littermates in each habitat ($G = 17.5$; $P < 0.001$).

We searched our data to identify mice born in a nestbox in one habitat that later occupied a nestbox found in another. We calculated dispersal rates in each habitat by comparing the proportion of young mice known to have dispersed relative to the total population of marked mice born in nestboxes in each habitat. There was a significant difference in dispersal rates among habitats, but not in the direction predicted by the dispersal hypothesis. Dispersal rates were higher in forest and edge habitats than they were in fencerows (Table 1).

We were concerned that our comparison among habitats might itself be biased by differential abilities to detect dispersing individuals. We conducted a second analysis on the subset of dispersers moving between adjacent boxes in forest and edge habitats. We reasoned that if low juvenile survival in forest edge is caused by dispersal, the proportion of individuals dispersing from edge to adjacent forest boxes should be higher than the proportion dispersing from the same forest boxes in the other direction. The dispersal rates were virtually identical (Table 2). We conclude that white-footed mice have higher fitness in forest than in forest-edge habitat.

Patch use by foraging mice

We evaluated whether white-footed mouse foraging behavior corresponded to habitat differences in fitness by assessing patch-leaving rules of mice using identical, depletable foraging patches in each habitat (Brown 1988). Optimal foragers should, if they have evolved to maximize the average rate of resource harvest, leave a patch when the benefit obtained from foraging is balanced by the summed energetic costs, the risk of predation, and the cost associated with opportunities lost from other fitness-enhancing activities (Brown 1988). Assuming that rodents harvest resources with diminishing rates through time (e.g., a type II functional response), the quitting-harvest rate of the final forager to exit a patch can be estimated by the mass (giving-up density, GUD) of the remaining resources.

Quitting-harvest rate is an optimal patch-leaving rule in depletable patches when animals forage for randomly distributed resources with diminishing returns and

when foragers can assess the quality of the foraging patches (Brown and Mitchell 1989). Animals that cannot assess resource abundance within a patch, or differences between patches, can nevertheless optimize their foraging if they leave patches after a fixed search-time (Brown and Mitchell 1989). Fixed search-time is an optimal foraging strategy when resources fit a Poisson distribution (Iwasa et al. 1981). A fixed-time strategy may also be employed by animals living in capricious environments where individuals hedge their foraging bets by visiting numerous patches irrespective of the resource density in any single patch. Fixed-time foragers should, nevertheless, adjust their foraging time relative to the quality of their foraging range, and relative to the risks they take while foraging at a particular location. Giving-up densities should, for both quitting-harvest rate and fixed-time foragers, provide an accurate assessment of the quality of adjacent habitats, and of the location, within which the patch occurs.

Field experiments

During August 1996 we selected 11 foraging sites in each habitat (forest or edge) subject to the constraints that each site corresponded to one of our long-term nestbox locations, that the minimum distance between successive sites within a habitat be ≥ 30 m, and that each site would be accessible to foragers whose nest was located in either habitat (all foraging stations in forest were located within 50 m of the edge; white-footed mice foraging distances are on the order of 50 m [Stickel 1968]). We were unable, given the scale of our study area, to pair edge stations with adjacent ones in forest.

We established identical foraging patches by charging $30 \times 25.5 \times 15$ cm opaque plastic water bottles (2.5 gallons) with either 4 g or 6 g of uniformly-sized (> 2 mm diameter) millet mixed thoroughly in 1.5 L of silica sand (70 grain) (Morris 1997). Each foraging site was composed of one bottle located in an area with no understory and little ground vegetation (open), and another located within 2 m placed under shrubs or saplings (cover). We assumed that animals approaching and leaving open bottles were at higher risk from visually searching predators than were those foraging in bottles under cover.

TABLE 2. Observed and expected dispersal (animals that occupied a nestbox in a habitat different from their natal habitat) of white-footed mice marked as littermates in adjacent nestboxes in forest and edge habitats in a 50-ha study area in southwestern Ontario.

Habitat	Observed	Expected
Edge	15	17.43
Forest	12	9.57

Note: Expected values were calculated as the product of overall dispersal rate (4.49%) multiplied by the number of mice marked as littermates in each habitat ($G = 0.91$; $0.5 < P < 0.1$).

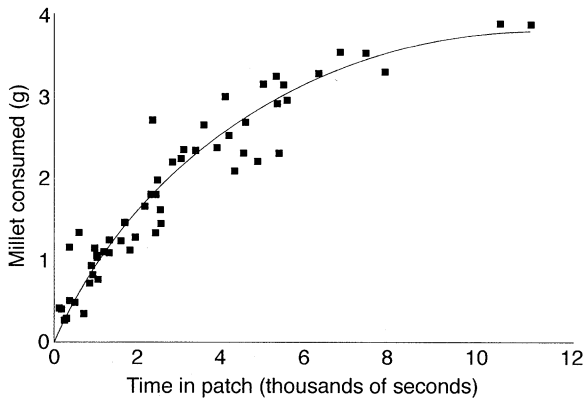


FIG. 3. The harvest rate of millet declined with the amount of time that white-footed mice foraged in artificial resource patches.

Each day we checked all bottles during daylight, sieved the residual millet left by nocturnally-foraging white-footed mice, recharged the sand with millet, and replaced each bottle in its original location. White-footed mice are the only abundant nocturnal rodents at our research site. We checked all tracks in the sand and found none that belonged to any other seed predator (some raccoon prints were preserved in the sand near the single 3.4-cm openings of our bottles when they reached in to explore the contents). The sieved millet was returned to the lab, cleaned of feces and loose hulls, dried for a constant interval in a microwave oven, and weighed to the nearest 0.01 g.

We tested the assumption of diminishing returns by allowing six different white-footed mice to forage in bottles in experimental $60 \times 60 \times 30$ cm high chambers under red light. We cut the bottles in half so that we could observe foraging rodents and, with a separate stop watch, recorded the amount of time each foraged. The superb fit of the data to a curve of diminishing returns (Fig. 3) allowed us (for 4-g bottles) to convert our field data on GUD to quitting-harvest rate by solving the integral of Holling's disk equation.

Following Kotler and Brown (1990), the rate of millet harvest in our resource patches given by Holling's disk equation is $dN/dt = -aN/(1 + ahN)$ where N is the final mass of millet (GUD), a is a white-footed mouse's attack rate, and h is a mouse's handling time for millet. Inverting the disk equation and subsequent integration yields an equation for time foraging in the patch, t , by which one can use regression to calculate a . Specifically,

$$t = (1/a)(\ln[N_o/N_f]) + h(N_o - N_f)$$

where subscripts denote initial and final abundances of millet in the patch (see also Royama 1971, Rogers 1972). For white-footed mice the regression was highly significant ($F_{2,53} = 879.96$, $P < 0.0001$), with $a = 4.12 \times 10^{-4}/s$ ($t_{53} = 10.01$, $P < 0.0001$) and $h = 548.56$ s/g ($t_{53} = 4.34$, $P = 0.0001$). The quitting-harvest-rate

(g millet/hr) for any GUD is found by converting seconds to hours, then substituting a and h into the disk equation (Kotler and Brown 1990). This approach is likely to be biased because the two independent variables in the multiple regression are correlated with one another. We repeated the analysis by estimating h from the mean times that six captive mice spent foraging on 0.1 g piles of millet (16 seeds, search time assumed to be zero) on top of the sand in their foraging trays ($h = 1054.3$ s/g). We substituted this value into the equation for t and calculated a by regression ($F_{1,54} = 267.09$, $P < 0.0001$), $a = 2.38 \times 10^{-4}/s$ ($t_{54} = 16.34$, $P < 0.0001$). The results from the ANOVA based on quitting-harvest rates using these values were identical to those we report below.

The calculation of functional response parameters from Holling's disk equation is plagued with controversy, and many techniques generate biased estimates of both a and h (Juliano and Williams 1987). To test whether our estimates were biased, and to overcome any problems if they were, we recalculated quitting-harvest rates independent of biological assumptions. First, we fitted the mass of seeds consumed by the mice to a quadratic equation with a multiple linear regression forced through the origin (mass of millet eaten = 8.29×10^{-4} [time in seconds] - 4.58×10^{-8} [time]²; $F_{2,53} = 1002.6$, $P < 0.0001$, $R^2 = 0.97$). We differentiated the solution to estimate the instantaneous quitting-harvest rate (QHR), then calibrated QHR with GUD by regressing the estimate on $\ln(N_f)$ (linearizes the relation, $F_{1,53} = 560.9$, $P < 0.0001$, $R^2 = 0.91$). We used the calibration curve to recalculate our field estimates of QHR, converted the estimate to hours, and repeated all analyses. The two estimates of QHR were virtually identical ($r = 0.999$ for both day 1 and day 2 of the experiment), as were the results from the ANOVA.

Foraging behavior and fitness

Our long-term study of reproductive success yields a series of a priori, one-tailed predictions to test, with confidence, whether foraging animals adjust their use of each habitat to match differences in fitness. Animals compensating for high mortality rates should leave patches at higher foraging rates (higher GUDs) than individuals experiencing lower foraging costs. Individual white-footed mice should, on average, abandon patches at higher harvest rates in edge habitat than they do in the forest (GUD in forest < GUD in edge). Individuals should harvest patches to lower average quitting-harvest rates in safe sites than in risky ones (GUD under cover < GUD in open). The difference in quitting-harvest rate between risky (open) and safe (cover) sites should be less in the safe forest habitat than in the risky edge (the difference between open and cover GUDs in forest < the difference between open and cover GUDs in the edge).

At the end of a seven-day acclimation period when mice were foraging at all sites, we initiated an exper-

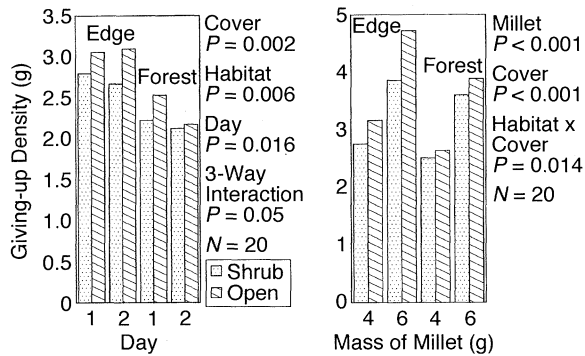


FIG. 4. Left: The mass of millet remaining after foraging was higher in patches in the open (risky) than in paired patches located under shrubs (safe), and it was higher in forest-edge habitat than in forest. The difference between shrub-covered and open sites was less in the forest on the second day of the experiment than it was on the first. Right: The mass of millet was higher when patches contained 6 g of millet than when they contained 4 g, and it was higher in patches in the open than under shrubs. The difference between open and shrub-covered patches was higher in the "risky" edge habitat than it was in the "safe" forest habitat.

iment consisting of two rounds of foraging over two days where all bottles contained 4 g of millet. The intent of the two-day design was to assess whether any differences in GUD were associated with temporal variation in foraging behavior as might occur in response to day-to-day changes in weather and cloud cover. One site in the edge habitat was unused on the second night of the experiment. It and a randomly selected one in the forest were deleted from the analyses that require a balanced design.

We analyzed the experiment with both GUD and quitting-harvest rate (QHR) via two mixed-model repeated-measures ANOVAs (Norušis 1992; habitat treated as a between-subject random effect, cover and day treated as fixed within-subjects effects). The results confirmed our a priori predictions (Fig. 4, left). GUD and QHR were much lower in bottles under cover than in the open ($F_{(GUD)1,18} = 13.75$, $P = 0.002$ and $F_{(QHR)1,18} = 14.39$, $P = 0.001$), much lower in forest than in the edge ($F_{(GUD)1,18} = 9.52$, $P = 0.006$ and $F_{(QHR)1,18} = 8.87$, $P = 0.008$), and were lower on day 2 than on day 1 ($F_{(GUD)1,18} = 7.03$, $P = 0.016$ and $F_{(QHR)1,18} = 8.11$, $P = 0.01$). Most importantly, the difference in both GUD and QHR between open and covered bottles was greater in the risky edge habitat than in the safe forest when animals foraged intensely on the second day (three-way interaction; $F_{(GUD)1,18} = 4.26$, $P = 0.05$ and $F_{(QHR)1,18} = 4.08$, $P = 0.06$).

Immediately following completion of the first experiment we initiated a second that also lasted for two days. Each site included one bottle with 4 g of millet and one with 6 g. We selected one half of the sites in each habitat at random, ensured that the selected sites were interspersed throughout each habitat, and placed

the 6-g bottle under cover. The 6-g bottle was located in the open in the other half of the sites. We reversed the treatment on the second day. The proportion of millet consumed should be greater in the 6-g bottles if mice use quitting-harvest-rate as their patch leaving rule (Brown 1989, Brown and Mitchell 1989, Valone and Brown 1989).

But white-footed mice might use an alternative "fixed search-time" rule. The probability of a resource item being consumed is, for a fixed search-time foraging strategy, independent of the number of items in the patch (density-independent resource harvest; Brown 1989, Brown and Mitchell 1989, Valone and Brown 1989). The ratio of items in a poor patch relative to a rich one is the same after harvest as it is before. Letting I_i = initial resource density in patch i , and F_i = final resource density (GUD), $I_p/I_r = F_p/F_r$, thus, $I_p/F_p = I_r/F_r$. The proportion of resource consumed is the same in both poor and rich patches. No other common strategy yields this prediction.

Again, one site in the edge habitat was unused on the second day of the experiment. That site and a randomly selected forest site were deleted from the analyses.

White-footed mice appeared to use a fixed-time rule. The proportion of millet consumed was not significantly different between 4-g and 6-g bottles (repeated measures ANOVA [Norušis 1992] on arcsine-transformed proportions with the initial mass of millet and cover treated as fixed within-subjects factors and with habitat as a random between-subjects factor; $F_{1,18} = 1.96$, $P = 0.18$).

The fixed search-time strategy of white footed mice foraging in 4-g versus 6-g patches does not exclude the possibility that they might adjust quitting-harvest rates to larger differences in patch quality, nor does it imply that their foraging is, in some respect, suboptimal. Round-tailed ground squirrels (*Spermophilus tereticaudus*) and pocket mice (*Perognathus amplus*) used a fixed-time strategy when exploiting patches varying in resource density by approximately 10–20%, but switched to a fixed quitting-harvest rate when resource densities were twice as great in one patch as in the other (Valone and Brown 1989). Desert birds, lacking the olfactory abilities of rodents, used a fixed-time strategy across all resource densities (Valone and Brown 1989), a result corroborated on Crested Larks (*Galerida cristata*) in Israel (Kotler and Brown 1999). Fox squirrels (*Sciurus niger*), tested across a two- to three-fold difference in patch quality, used a fixed-harvest rate strategy (Morgan et al. 1997). Thus, the 50% difference in patch quality in our experiments may have been below the assessment abilities of white-footed mice foraging in these novel patches. Regardless, our test of the main hypothesis was confirmed (Fig. 4, right). The difference in GUD between open and covered bottles was again greater in the edge than in the forest ($F_{1,18} = 7.39$, $P = 0.01$).

The results of our two-week foraging experiments were redundant with the results of our multiyear study of white-footed-mouse life history. White-footed mice foraged resources to a lower GUD and quitting-harvest rate in the relatively safe forest habitat where their fitness was high than they did by foraging in the risky edge habitat where their fitness was low. The strategic decisions of mice foraging in different habitats are consistent with underlying differences in reproductive success.

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