IS DENSITY-DEPENDENT RESOURCE HARVEST A RELIABLE HABITAT INDICATOR FOR CONSERVATION AND MANAGEMENT?

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ABSTRACT

Adaptive foraging decisions emerge from environmental conditions that alter fitness. Under most circumstances fitness varies with population density. So it should be possible to use density-dependent foraging not only as a surrogate for fitness, but also as an assay for habitat quality. We tested this prediction by measuring the quitting-harvest rates of red-backed voles foraging in artificial resource patches located in three different habitats where we manipulated population density. Quitting-harvest rates were less in safe foraging trays located under cover than in risky trays in the open. Voles avoided risky trays in old field and alder field habitats, and foraged all trays in a dense alder forest habitat to similar low harvest rates. Quitting-harvest rates declined with density in experiments conducted in 2005 but not in similar experiments during 2006. We interpret these complex results as evidence that rapid food renewal during the 2006 experiments increased the voles' foraging costs, and their quitting-harvest rates, in artificial food patches. Continued foraging in the trays would compromise the voles' abilities to forage elsewhere in the habitat. This conclusion is bolstered by significant differences in rainfall between years that precipitated vegetation recovery in 2006 shortly before we initiated our experiments. Our results demonstrate that we may not be able to use behavior alone to estimate population density in variable environments. So we outline more effective research designs that should allow other scientists to not only detect density-dependent foraging, but also spatial and temporal variation in habitat quality.

Keywords: conservation, density dependence, giving-up density, habitat quality, habitat selection, optimal foraging

INTRODUCTION

Optimal foraging theory provides a unique avenue with which to explore adaptive behaviors. Most organisms forage under conflicting demands. They attempt to acquire resources from their environment while seeking safety, or engaging in other non-foraging activities that enhance fitness. These inevitable conflicts allow us to use foraging and space-use behaviors to estimate habitat quality (Morris, 1988, 1994; Pusenius and Schmidt, 2002; Persson and Stenberg, 2006; Stenberg and Persson, 2006), carrying capacity (Sutherland and Anderson, 1993; Percival et al., 1998; Gil et al., 2001; van Gils et al., 2004; Morris and Mukherjee, 2007), predation risk (Brown, 1988, 1992; Brown et al., 1999; Hughes and Ward, 1993), species interactions (e.g., Brown, 1988, 1989; Morris, 1988, 1989, 1999; Brown et al., 1997) and spatial–temporal patterns of animal abundance (Morris, 1997, 2001). We should, therefore, be readily able to apply foraging and habitat-selection theory to conservation and management (Morris, 2003).

Theories of optimal foraging predict, for example, that individuals should use foraging patches as long as the profit obtained from foraging exceeds its cumulative costs (Brown, 1988, 1992; Houston and McNamara, 1999; Brown and Kotler, 2004; van Gils et al., 2004). Costs include the metabolic expenses of foraging in a particular patch, risks of being killed by predators while in the patch, and lost opportunities to pursue alternative activities instead of foraging in that patch. Thus, with appropriate experiments, one can assess chemical and metabolic differences in foraging costs (Schmidt, 2000; Davidson and Morris, 2001; Shochat et al., 2004), differences between patches and habitats in foraging risk (Brown and Alkon, 1990; Brown et al., 1992a,b; Kotler et al., 1994, 1999; Kotler and Blaustein, 1995; Jacob and Brown, 2000; Morris and Davidson, 2000; Orrock and Danielson, 2005), differences in foraging efficiency among competing species (Brown et al., 1997; Kotler et al., 1998), density-dependent resource harvest (Bowers et al., 1993; Morris, 1997; Davidson and Morris, 2001; Mohr et al., 2003; Morris and Mukherjee, 2007), and scales of habitat use (Morris, 1997; Druce et al., 2006).

Theory promises much more. If foraging behavior depends on population density, and if we can quantify that behavior with relatively simple field experiments on foraging animals, then we should be able to use those same simple experiments to back-calculate population size. To do so assumes, however, that the relationship between foraging behavior and density is consistent from one place to another and through time. It may not be. Carrying capacities are likely to vary in time and space, and foraging strategies might also vary. So we need studies, such as the one we describe below, that contrast density-dependent foraging among habitats at different times.

We begin by reviewing how we can use density-dependent resource harvest to estimate habitat quality. We highlight problems associated with temporal variation in carrying capacity. Then we describe experiments where we used density-dependent resource consumption by red-backed voles to measure the quality of alternative habitats. We contrast results from two different years that illustrate annual differences in quality associated with climatic variation. We discuss the value of density-dependent resource harvest in management and conservation, and conclude with advice on developing more effective and powerful protocols for foraging studies.

THEORETICAL CONTEXT

When fitness is correlated with the net rate of energy gain, individuals maximizing the fitness obtained from foraging should feed in a resource patch until

$$QHR = C + \frac{\mu F}{\frac{\partial F}{\partial e}} + \frac{\Phi_t}{p\left(\frac{\partial F}{\partial e}\right)} \tag{1}$$

where QHR = quitting-harvest rate in the resource patch, C = the metabolic cost of foraging in the patch, μ = the instantaneous rate of being killed by a predator while foraging in the patch, F = the fitness obtained by foraging in the patch, Φ_t = the marginal fitness value of time that could be allocated to activities other than foraging in the patch, p = the probability of survival over the foraging interval, and $\partial F/\partial e$ = the marginal value of energy in terms of fitness (the forager's energetic state, Brown, 1992; Brown and Kotler, 2004). Thus, density dependence in QHR emerges from potentially complicated relationships of prey density with metabolic costs of foraging, predation rates, fitness, the value of missed opportunities, survival, and the marginal value of energy. The cumulative response will depend on such things as habitat, predator responses, temporal–spatial variation in carrying capacity, seasonal differences in food availability and foraging costs, whether each additional individual has a similar effect to all others, and whether an individual's impact varies with population density.

If individuals forage similarly and behave independently, then it is reasonable to assume that each additional individual will approach the average effect of all individuals, and that QHR will decline linearly with increasing population density. But if individuals forage in social groupings, if different classes of individuals forage at different times or in different places, or if predation and missed opportunities are related to group behavior, then it could be extremely difficult to predict the cumulative effect of density on resource harvest. No matter how complicated the interactions might be, however, one can use the relationship between density and QHR to assess density-dependence in fitness, and thus habitat quality.

QHRs decline linearly with density in "non-social" deer mice (Morris, 1997; Davidson and Morris, 2001) and red-backed voles (Morris and Mukherjee, 2007), but have not yet been investigated in truly social species. Whether QHRs are linear with density or not, theory suggests that they can be used to measure a habitat's carrying capacity because the marginal value of energy is reduced for individuals that curtail reproduction. When population size exceeds carrying capacity, individuals that forego reproduction in favor of survival can often achieve higher fitness than those individuals that continue to reproduce (Morris and Mukherjee, 2007). The relationship between density and quitting-harvest rate will thus be different above carrying capacity than it is below (Morris and Mukherjee, 2007).

We confirmed the theory with experiments on red-backed voles (Morris and Mukherjee, 2007) where we estimated quitting-harvest rates from the amount of food remaining in standardized resource patches (giving-up density, GUD, Brown, 1988). But quitting-

harvest rates estimated from artificial patches may be insensitive to density for at least four different reasons. (1) Renewal rates in some environments may match resource depletion. Quitting-harvest rates would remain more or less constant because renewal exceeds the ability of foragers to draw down the capital of their habitats. Such an effect may occur in gerbils whose GUDs are lower in summer (when seed resources in the Negev Desert are renewed daily in wind-blown sands) than in winter, when seed renewal is blocked by damp immobile soil (Kotler et al., 2004). (2) Resource depletion may be associated with reduced energetic costs of foraging. Thus low gerbil GUDs in summer could reflect high rodent densities (depleting resources), but may be unreliable cues of density-dependence unless one corrects for seasonal differences in thermo-regulatory costs of foraging (B.P. Kotler, pers. comm.). (3) Animals may not be able to distinguish among different giving-up-densities when patches are designed to ensure diminishing returns (harvest rates) with time spent foraging (Brown, 1988; Brown et al., 1992a). Quitting-harvest rates in such patches change rapidly when animals consume an inter-mediate amount of food, but slowly when animals eat either most of the food (amount of food eaten is asymptotic to food abundance) or little of it (consumption is linear with time in the patch). (4) Quitting-harvest rates may also be insensitive to density when foragers are incapable of assessing patch quality or resource abundance in the habitat. But if individuals are incapable of assessing patch and habitat quality, then we should almost never observe density-dependent foraging. And, if animals cannot distinguish among quitting-harvest rates when GUDs are high (and if we have measured low GUDs in the same system at other times), then we must conclude that foraging costs have also changed through time.

To summarize, we predict a density-dependent reduction in GUD when increased population density depresses per capita resource availability (reduced habitat quality). The marginal value of energy increases and GUDs decline. But we do not know how frequently a panoply of countervailing effects might destroy our ability to detect a den-sity-dependent foraging signal. Many of these effects will be associated with seasonal or other temporal changes in habitat quality. So we explore the relationship between resource harvest and density across habitats and between years.

METHODS

We evaluated density-dependent declines in quitting-harvest rates of red-backed voles (*Myodes gapperi*) during August 2006 in six of 12 adjacent 50 m × 50 m galvanized metal enclosures (the six experimental enclosures comprised a 2 × 3 matrix; fences were 0.75 m high buried to a depth ≥0.5 m) near Lake Superior in northwestern Ontario, Canada (the Lakehead University Habitron). Two 9.25 cm diameter ground-level circular metal gates were spaced at equal distances along each internal wall so that voles could either move between adjacent enclosures (gates open), or live within a single enclosure (gates closed). The enclosures are arranged as adjacent pairs in three different habitats that represent different stages of secondary succession. Old field (enclosures 1 and 2) was dominated by vernal species such as strawberry (*Fragaria virginiana*), milfoil

(*Achillea millefolium*), and dandelions (*Taraxacum* spp.) giving way to a dense mixture of native and domestic grasses, red clover (*Trifolium pratense*), aster (*Aster ciliolatus*), and goldenrod (*Solidago* spp.) in autumn. We maintained the habitat in an old-field state by cutting all shrubs ≥1 m tall in spring. Alder field (enclosures 5 and 6) was similar to the old field but with invading alder shrubs (*Alnus rugosa*) 1–3 m tall that were not cut. Alder forest (enclosures 9 and 10) was a thick undisturbed 5-m tall alder forest. Hand-planted red-pine saplings (*Pinus resinosa*, ≤3 m tall) were scattered throughout the old field and alder field habitats, but not in the alder forest.

We set Sherman live traps under aluminum covers on each plot's 4 × 4 grid (spaced at 12.5 m intervals) in late afternoon every third day. We checked and replaced used traps at 12 hr, and checked them again 6 hr later when traps were removed. We washed all traps entered by rodents in detergent, then sanitized, rinsed, and dried them before reuse. We marked animals uniquely with metal ear tags, and recorded their tag number, weight, sex, sexual condition (reproductive or not), and body length before release at the point of capture.

Red-backed voles in the Habitron have high capture rates (often 100%, Morris and Mukherjee 2007), so we used the number of different captured animals as our estimate of density in each enclosure. No other small-mammal species occupied the enclosures during the experiment, and all voles were descendants of animals introduced in 2005 (e.g., Morris and Mukherjee, 2007; Oatway and Morris, 2007).

After we completed each 18-hr live-trapping rotation, and removed all traps from the enclosures, we placed four artificial food trays made from opaque plastic water bottles (9.5 l with a single 3-cm opening) in pairs at two permanent trapping stations in each enclosure (24 bottles in total). We placed one tray of each pair under the protective cover of alder or red pine, and another in the "open" approximately 1–2 m away. Each bottle contained 4.0 g of sized millet seed (> 2 mm diameter) mixed thoroughly in 1.5 l of screened (60–90 grain) silica sand. We collected bottles 48 hr later, before the next trapping rotation, and used soil sieves to separate the sand from residual millet. We weighed the cleaned millet with an electronic balance to the nearest 0.01 g (the giving-up density, GUD). We trained the voles to use the trays for seven days (4–11 August 2006). Animals were free to move among subsets of enclosures during this time (part of another experiment). All procedures involving animals were conducted under an animal care protocol evaluated and approved by Lakehead University's Animal Care Committee, which is certified by the Canadian Council on Animal Care.

The animals we used here had access to multiple enclosures before our experiment began. On 12 August 2006 we ensured that the experimental animals were restricted to single enclosures by closing all gates, then allowed them to habituate to their restricted surroundings for the next 4 days before starting the experiment. On 16 August we randomly selected four male and four female voles living under identical conditions in another enclosure, and moved them to enhance densities in the six experimental enclosures so that we had a reasonable range of densities for the experiment (initial densities ranged from 4 to 13 animals per enclosure, 50 animals in total). We designed these and all subsequent density adjustments to maintain equal sex ratios of immigrants placed

in each enclosure. We further manipulated densities by moving animals among the six enclosures during regular trapping rotations between 19 and 28 August (5 different treatment densities at three-day intervals).

We hoped to target one enclosure of each pair of similar habitats with an initial low density for graduated increases, and one with high density for graduated reductions (10 different densities in each habitat between 4 and 13 animals; these densities are rough approximations of the range of densities observed in free-living populations in our area [Morris, 2005a]). But our reductions and augmentations were complicated by slight increases in population size through juvenile recruitment (we captured no more than 55 animals in total during any trap check), and by a small number of voles that learned how to move among enclosures (≤ three individuals during any treatment interval). Thus, we manipulated densities to ensure that (1) each enclosure received immigrants and contributed emigrants, (2) each underwent periods of increased and reduced density, and (3) there was no consistent pattern among enclosures in the sequence of additions and reductions. So although we manipulated densities successfully and without systematic bias, the recruits and a handful of demonically clever adults kept us from reaching our targeted values (old field = 8 different densities between 4 and 13 animals, alder field = 6 different densities between 5 and 11 animals, alder forest = 6 different densities between 5 and 13 animals).

We compared the 2006 results with a similar experiment completed in the alder-forest enclosures between 17 July and 25 August 2005 to evaluate the possible role of inter-annual variation on density-dependent resource harvest. Anticipating differences, we searched for a climatic correlate by contrasting mean monthly precipitation and temperature from May through August each year using data from an Environment Canada weather station (Thunder Bay AWOS [ID = 6048264, 48.367 N, 89.317 W], ~30 km away from the Habitron).

We included GUD data in our analyses only where both trays at a station were foraged. We excluded data from unforaged trays because (1) we could not be certain that the animals actually discovered (or remembered) that the unused trays were available for foraging and (2) even if the animals were aware of the trays then the GUD for these trays was equal to the initial resource density. If all four trays in the enclosure were foraged, then we calculated the mean GUDs for the two open trays, and separately for the two shrub-covered trays. Otherwise we used the values from the single pair of foraged trays (with one exception [enclosure 1, addressed in the results], there was always at least one station where both trays were foraged). We log-transformed all data ($\log_{10}$ [GUD + 1]) to estimate the quitting-harvest rate of the final animal(s) using the tray(s). The transformation linearizes the relationship between GUD and *QHR* and is an effective estimate of harvest rate for small mammals that forage for millet in sand-filled trays with diminishing returns (Morris and Davidson, 2000; Davidson and Morris, 2001; Morris, 2001; Brown and Kotler, 2004).

We began our analysis by evaluating whether the 2006 estimates of *QHR* differed between covered and open trays (paired *t*-test on the mean values of the two tray types in each enclosure at each density) and whether they depended on density or differed among

enclosures (GLM, tray type, and enclosures treated as fixed effects, with density as a covariate). We repeated the analyses using only data from the two enclosures where we had data on density and *QHR* in both 2005 and 2006 (tray type and enclosures treated as fixed effects, year as a random factor, with vole density as a covariate). *QHR* did not vary with density in 2006, so we used regression to assess whether *QHR* varied with density in 2005 alone. We calculated the difference between *QHR* in open versus covered trays, and evaluated whether the difference depended on density or enclosure (GLM). All analyses were performed in either MINITAB (Version 12) or SPSS (Version 15).

Reviewers questioned whether our data screening was too conservative and recommended including unforaged trays in our calculations. We recalculated all mean values and recomputed all statistical tests. The results were, with one minor exception, unchanged. So other than that exception, we report only our original analyses.

RESULTS

VOLES WERE SELECTIVE IN THEIR USE OF FORAGING STATIONS

The voles had an opportunity to provide 20 different estimates of quitting-harvest rate in each enclosure during the 2006 experiment, but they used the trays unequally. Voles avoided trays in enclosure 1 (old field) most of the time (foraging in both trays at a station only once). So we excluded this enclosure from all subsequent analyses. And although one-half of the potential trays were used in enclosure 5 (alder field), voles foraged in both trays at only one of the two stations where the covered tray was located under a large alder (~3 m tall). By way of contrast, all trays in the alder forest were used in both years. So even though the enclosures replicated habitat, the voles' use of space differed among them.

VOLES FORAGED LESS IN RISKY THAN IN SAFE PATCHES

Quitting-harvest rates were greater in open than under cover in 2006 (paired $t = 3.59$, $P = 0.001$, $N = 25$, mean $GUD_{open} = 3.20$, mean $GUD_{cover} = 2.85$), but the difference was unequal among enclosures ($F_{4,20} = 6.39$, $P = 0.002$, GLM on the difference between [*QHR* open] minus [*QHR* cover]). The difference between open and covered trays in enclosure 5 (alder field) was greater than in enclosures 2 (old field), 6 (alder field), and 9 (alder forest; post-hoc contrasts with Bonferroni corrections for multiple comparisons). There was no difference between open and covered trays in the two alder-forest enclosures where we had reliable *QHR* data in both years (paired $t = 0.96$, $P = 0.35$, $N = 34$; data pooled for 2005 and 2006). These important results confirm that the voles recognized our trays as distinct foraging patches, and that they modified their quitting-harvest rates to reflect differences in patch quality. Voles avoided risky (open) patches in habitats where we could place the open trays without obstruction to the sky (old field and alder field). But voles did not recognize differences between trays in the alder forest where it was impossible for us to locate trays outside of the closed forest canopy. These results are also crucially important because they demonstrate that voles alter their foraging when feeding in habitats that differ in structure.
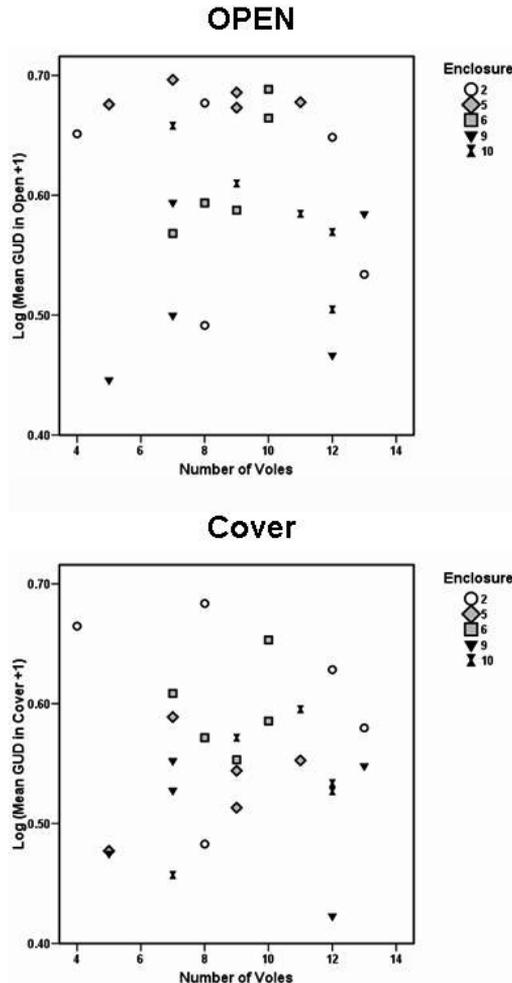
Fig. 1. Differences between open and covered foraging trays used by red-backed voles during 2006 in five different enclosures representing old field (open symbols), alder field (gray diamonds and squares), and alder forest (dark triangles and hourglasses) habitats in northern Ontario, Canada.

Differences between open and covered microhabitats were retained in our additional analysis that included unforaged trays (paired $t = 3.43$, $P = 0.002$, $N = 30$), but there was no difference in our estimates of quitting-harvest rates among enclosures ($F_{5,24} = 2.25$, $P = 0.55$). This single exception between the results of analyses excluding unforaged trays, versus those including unforaged trays, is unsurprising because the GUDs of the unforaged trays are identical to one another.

Fig. 2. Differences in quitting-harvest rates ($\log_{10}$ [mean GUD + 1]) of red-backed voles living at a range of densities in two enclosures of alder forest in 2005 versus 2006. Quitting-harvest rates declined consistently with increased density in 2005, but were independent of density in 2006.

QHR WAS VARIABLE BUT DECLINED WITH DENSITY IN ONLY ONE OF TWO YEARS

Density treatments during 2006 varied threefold, from 16 to 52 voles ha^{-1} (4 to 13 voles enclosure^{-1}). Despite dramatic variation in the number of voles, density had no effect on *QHR*. Quitting-harvest rates in 2006 did not covary with density (GLM, $F_{2,18} = 0.29$, $P = 0.75$), despite rather considerable variation (Fig. 1). Densities in 2005 were somewhat lower but nevertheless spanned a ninefold range (4 to 36 voles ha^{-1} (1 to 9 voles enclosure^{-1}). When data for 2005 and 2006 were pooled, *QHR* declined with density (GLM, $F_{1,59} = 6.78$, $P = 0.012$) and was smaller in 2005 than in 2006 ($F_{1,59} = 5.4$, $P = 0.024$). No other effect or interaction was significant. Knowing that *QHR* did not vary with density in 2006, we asked whether the significant covariation in density was caused by density-dependent *QHR*s in 2005. It was. Quitting-harvest rates in 2005 declined significantly with population density ($F_{1,46} = 36.9$, $P < 0.001$, Fig. 2). These results demonstrate that the relationship between *QHR* and density also depends on other sources of heterogeneity.

QHRS VARIED AMONG ENCLOSURES

Quitting-harvest rates in both open and covered trays in 2006 varied among enclosures (GLM, covariate of density removed, overall analysis $F_{8,38} = 4.44$, $P = 0.001$, open $F_{4,20} = 5.05$, $P = 0.006$, cover $F_{4,20} = 3.03$, $P = 0.04$). These results need to be interpreted cautiously because the variance in open trays was heterogeneous among enclosures and often asymmetrical (Fig. 3). Variances were much less heterogeneous in covered trays.
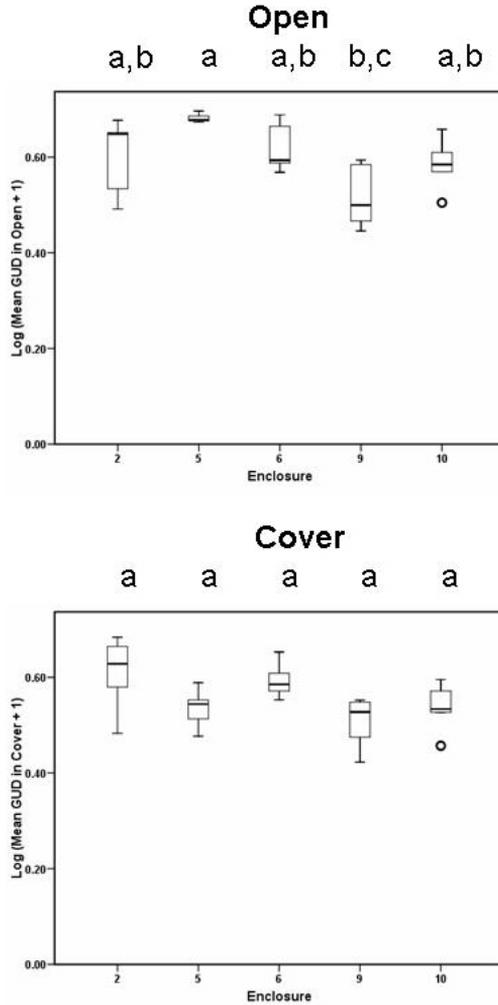
Fig. 3. Quitting-harvest rates in risky (open) and safe (cover) foraging trays used by red-backed voles foraging in five enclosures representing three different habitats near Thunder Bay, northern Ontario, Canada, during 2006: old field (2), alder field (5 and 6), and alder forest (9 and10). Letters indicate significant differences ($P \leq 0.05$).

Yet it is clear that voles foraged less in the open in enclosure 5 (alder field) than did voles foraging in enclosure 9 (alder forest, Fig. 3). There was no significant difference in *QHR* among any of the other comparisons (post-hoc contrasts with Bonferroni correction for multiple comparisons).
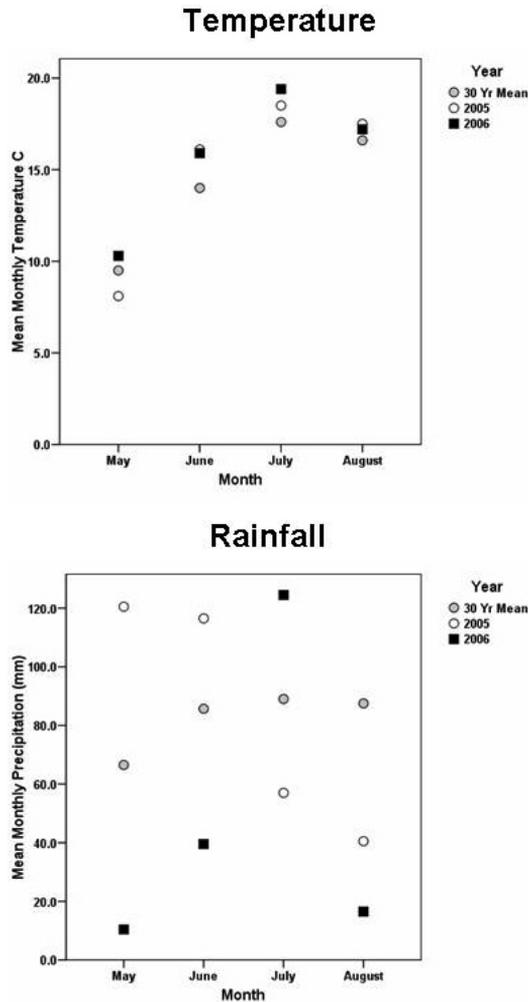
Fig. 4. Differences in mean monthly temperature and precipitation between 2005 and 2006 at Thunder Bay, northern Ontario, Canada. Reference data (gray fill) were based on a 30-yr average from 1971 to 2000.

CLIMATE DURING THE SUMMER OF BOTH YEARS WAS WARMER AND DRIER THAN NORMAL

Climate records revealed a clear and consistent increase in mean monthly temperature in northern Ontario (Fig. 4). Except for May 2005, mean monthly temperatures were approximately two degrees higher than the 1971–2000 30-yr average. Precipitation, however, was less than the long-term average during 2005 and 2006. The precipitation pattern varied dramatically between years. May and June 2005 were wetter than normal,

but gave way to a prolonged summer drought. May and June 2006 were exceptionally dry. A heavy downpour associated with severe thunderstorms on 31 July broke the drought, but only temporarily (Fig. 4).

DISCUSSION

Voles traded off food for safety. They foraged less in risky (open) trays than they did in safer ones (cover). But the trade-off varied among enclosures. Voles avoided all trays in enclosure 1 (old field) and used only one pair in enclosure 5 (alder field). And the difference in QHR between risky and safe trays in enclosure 5 was greater than in (most) others. Voles used the safe tray in the protective shelter of a large alder much more than the nearby tray exposed to the open sky. And though voles foraged most intensely in the thick alder forest, they did not distinguish between the trays that were always located under the forest canopy. It thus appears that some stations in "open" habitat were so risky that voles refused to forage in either tray. And trays located at other stations in closed habitat were deemed equally safe even though we did our best to maximize natural differences in cover.

These results identify a serious problem for anyone interested in comparing quitting-harvest rates among habitats. If you aim to assess differences in predation risk, then take great care to ensure that the relative differences between safe (e.g., sheltered) versus risky (unsheltered) foraging sites are equal in each habitat. Maintaining relative differences will often be best achieved by using standardized artificial shelters in place of naturally occurring cover (e.g., Morris, 1997, 2001; Morris and Davidson, 2000).

Voles foraged very differently in 2006 than they did in 2005. Density had no effect on quitting-harvest rate in 2006 even though it was negative and linear in the same enclosures in 2005. The 2006 data are different from all of our laboratory's other data on density-dependent quitting-harvest rates. Typically, GUD and QHR decline linearly with increasing population density (Morris, 1997, 2001; Morris and Davidson, 2000; Davidson and Morris, 2001; Morris and Mukherjee, 2007). The 2006 data are exceptionally odd because QHR was higher than during 2005, even though vole densities were greater. There are two "obvious" explanations. (1) The voles used a different foraging strategy in 2006 than in 2005, and one that differed dramatically from the density-dependent pattern of foraging observed in all other rodent species that members of our laboratory have studied. (2) The costs of foraging were much higher in 2006 than in our previous studies.

Although we cannot exclude the possibility of an altered foraging strategy, we consider this hypothesis unlikely. If foraging costs were similar between years, the more-or-less invariant quitting-harvest rates in 2006 imply that voles were using either a fixed time or fixed amount harvest rule. Fixed time is an optimal strategy when animals cannot assess patch quality (Iwasa et al., 1981; Brown and Mitchell, 1989; Valone and Brown 1989). There is no reason to assume that animals in 2006 were incapable of assessing, patch quality when animals in 2005 could clearly do so. We also do not understand why

animals in 2006 should adopt a fixed amount strategy unless it was associated with high rates of food renewal elsewhere in the habitat (missed opportunities). We thus view the "altered cost of foraging" hypothesis as the more parsimonious explanation for inter-annual differences in vole foraging behavior.

Metabolic foraging costs were fixed across trays by our standardized protocol, which used identical substrate, substrate volume, seed type, seed size, initial seed density, mixing rules, foraging bottles, and foraging duration in both years. So if costs differed, they should be associated with either predation risk or missed opportunities (eq 1). Voles did not differentiate between open and covered foraging trays in the alder forest habitat. This lack of discrimination could imply that overall predation risks were similar between years. But it is more likely, in the forest, that open and covered microhabitats are equally safe sites in which voles cannot discriminate differences in risk even if the average risk varies among years. So differences in foraging costs between years might have been caused by an increase in both predation risk and missed opportunities.

Ironically, our design did not include an explicit test to evaluate missed opportunities. With 20/20 hindsight we recommend that tests for missed foraging opportunities (e.g., by supplementing the available food supply) should be incorporated into foraging studies whenever feasible. But before you do so, we advise you to consider carefully whether the supplements will carry over onto other treatments. Subsequent treatments in the same location, such as our density manipulations, are likely to be biased by changes in the marginal value of energy if individuals hoard the supplemental food (Kotler, 1997; Ovadia et al., 2001), or otherwise store it (e.g., as fat).

We can, however, use the climate data to test indirectly for increased missed opportunity costs during 2006. The intense July thunderstorm in 2006 broke a prolonged drought and generated an unusual spurt of late-summer vegetative growth that would normally be unavailable to omnivorous red-backed voles. The opposite climate pattern dominated late summer 2005 when drought curtailed any late-season growth. It is thus likely that voles foraging during August 2006 did so in habitats with superabundant food while voles foraging during July and August 2005 did so when resource renewal was either constant or in decline.

Regardless as to cause, it is quite clear that the pattern of quitting-harvest rates with density can vary dramatically through time. Yet it is equally transparent that quitting-harvest rates do often vary with density and provide a method to estimate habitat quality (e.g., Morris and Mukherjee, 2007). Sadly, it now appears that we cannot shortcut estimates of density with foraging behavior alone. All is not lost, however. If we collect quitting-harvest rates at standard densities, for example, we should be able to use those data to estimate the spatial and temporal stochasticity in habitat quality because any differences in *QHR* could not depend on density. And we can probably determine the relative roles of predation risk and missed opportunities with similarly appropriate field designs.

Our research also includes lessons on how to design experiments that record harvest-rates while manipulating density. It will often be advantageous, for example, to use a geometric series of densities in pilot studies to identify the appropriate range of densities where quitting-harvest rates vary with population size. Such a design would have the

additional advantage of detecting potentially wide variance in habitat quality. The disadvantage is that the field research will require more time, and thus increase the likelihood that habitat quality will change during the experiment.

Quitting-harvest rates vary with an individual's state, with the risk of predation, with the social context within which the individual lives, and with differences in habitat quality. Most of these phenomena depend on population density, but possibly in different directions. It is thus somewhat remarkable that a clear density-dependent foraging signal has been observed so consistently in previous research that looked for it. But it is also remarkable that red-backed voles in 2006 failed to alter their quitting-harvest rates over a threefold range bracketing their maximum population densities in northern Ontario. If our interpretation of climate-mediated missed opportunities is correct, then the list of ecological impacts associated with climate change will need to include unexpected resource pulses that temporarily improve and equalize habitat quality. Adaptively foraging individuals leave resource patches when their quitting-harvest rates are still high. But rather than be disappointed by the results, we should still be able to map stochastic changes in resource supply through their effect on quitting-harvest rates (Morris, 2001). We may then be able to use those mappings to help understand spatial and temporal dynamics, to gain deeper appreciations of temporally variable food webs, and perhaps even to forecast future population responses. No matter what success we may achieve, we must incorporate our deepening knowledge of adaptive ecologically-significant behavior into conservation and management.

Conservation biologists and managers might wonder whether or not they can apply foraging studies, such as ours on small rodents, to other taxa. To do so they must overcome at least two problems: (1) Experiments must include effective methods to estimate population density, spatial distribution, and harvest rates; (2) The experimental design must be logistically feasible for species that live in difficult environments, and for species with broad spatial distributions and long generation times.

Several creative studies document the ability to conduct these sorts of experiments on difficult taxa and at large spatial scales. Stenberg and Persson (2006) have learned how to measure quitting-harvest rates for benthic fishes. Druce and coworkers (2006) have done the same for rock hyraxes and klipspringers. Kotler and coworkers have measured giving-up densities of Nubian ibex (Kotler et al., 1994; Hochman and Kotler, 2006a,b), Altendorf and coworkers (2001) have done the same with mule deer, as have Rieucau et al. (2007) for white-tailed deer, and Morris (2005b) for snowshoe hares. Several ecologists have used similar techniques on birds (including northern bobwhite [Kohlmann and Risenhoover, 1998], waterfowl [Amano et al., 2006], and passerines [Shochat et al., 2004]), as well as bats (Sánchez, 2006), and termites (Korb and Linsenmair, 2002).

Nevertheless, and despite calls to link behavior with its population dynamic consequences (Lima, 1998), there are relatively few examples of density-dependent foraging. The logistics of conducting these studies, especially on large and widely distributed species, is daunting and often beyond the capabilities of academic research scientists. Managers often face a different problem where they have a mandate and resources for population monitoring and assessment, but few resources for field experiments. Rather

than viewing these two solitudes as a barrier to overcome, we see it as an opportunity to merge the population expertise of management and conservation research with behavioral ecology. Behavioral ecologists need to work more closely with managers to link foraging with population dynamics in time and space. Only then will we be able to truly assess the conditions under which behavior yields unbiased estimates of habitat quality that can be applied to management and conservation.

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REFERENCES

Altendorf, K.B., Landré, J.W., López Gonazález, C.A., Brown, J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer. J. Mammal. 82: 430–439.

Amano, T., Ushiyama, K., Fujita, G., Higuchi, H. 2006. Foraging patch selection and departure by non-omniscient foragers: a field example in white-fronted geese. Ethology 112: 544–553.

Bowers, M.A., Jefferson, J.L., Kuebler, M.G. 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). Oikos 66: 229–236.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22: 37–47.

Brown, J.S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecol. Monogr. 20:1–20.

Brown, J.S. 1992. Patch use under predation risk. I. Models and predictions. Ann. Zool. Fenn. 29: 301–309.

Brown, J.S., Mitchell, W.A. 1989. Diet selection on depletable resources. Oikos 54: 33–43.

Brown, J.S., Alkon, P.A. 1990. Testing values of crested porcupine habitats by experimental food patches. Oecologia 83: 512–518.

Brown, J.S., Kotler, B.P. 2004. Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7: 999–1014.

Brown, J.S., Morgan, R.A., Dow, B.D. 1992a. Patch use under predation risk. II. A test with fox squirrels, *Sciurus niger*. Ann. Zool. Fenn. 29: 311–318.

Brown, J.S., Arel, Y., Abramsky, Z., Kotler, B.P. 1992b. Patch use by gerbils (*Gerbillus allenbyi*) in sandy and rocky habitats. J. Mammal. 73: 821–829.

Brown, J.S., Kotler, B.P., Mitchell, W.A. 1997. Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. Evol. Ecol.11: 757–771.

Brown, J.S., Laundré, J.W., Gurung, M. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. J. Mammal. 80: 385–399.

Davidson, D.L., Morris, D.W. 2001. Density-dependent foraging effort of deer mice (*Peromyscus maniculatus*). Funct. Ecol. 15: 575–583.

Druce, D.J., Brown, J.S., Castley, J.G., Kerley, G.I.H., Kotler, B.P., Slotow, R., Knight, M.H. 2006. Scale-dependent foraging costs: habitat use by rock hyraxes (*Procavia capensis*) determined using giving-up densities. Oikos 115: 513–525.

Gill, J.A., Sutherland, W.J., Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. Proc. R. Soc. London B. 268: 369–376.

Hochman, V., Kotler, B.P. 2006a. Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behav. Ecol. 18: 368–374.

Hochman, V., Kotler, B.P. 2006b. Effects of food quality, diet preference and water on patch use by Nubian ibex. Oikos 112: 547–554.

Houston, A.I., McNarara, J.M. 1999. Models of adaptive behaviour. Cambridge University Press, Cambridge, UK.

Hughes, J.J., Ward, D. 1993. Predation risk and distance to cover affect foraging behavior in Namib desert gerbils. Anim. Behav. 46: 1243–1245.

Iwasa, Y.M., Higashi, M., Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. 117: 710–723.

Jacob, J., Brown, J.S. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91: 131–138.

Kohlmann, S.G., Risenhoover, K.L. 1998. Effects of resource distribution, patch spacing, and pre-harvest information on foraging decisions of northern bobwhites. Behav. Ecol. 9: 177–186.

Korb, J., Linsenmair, K.E. 2002. Evaluation of predation risk in the collectively foraging termite *Macrotermes bellicosus*. Insectes Soc. 49: 264–269.

Kotler, B.P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. Oikos 78: 274–282.

Kotler, B.P., Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? Oikos 74: 251–258.

Kotler, B.P., Gross, J.E., Mitchell, W.A. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. J. Wildl. Manage. 58: 299–307.

Kotler, B.P., Dickman, D.R., Brown, J.S. 1998. The effects of water on patch use by two Simpson Desert granivores (*Corvus coronoides* and *Pseudomys hermannsburgensis*). Aust. Ecol. 23: 574–578.

Kotler, B.P., Brown, J.S., Knight, M.H. 1999. Habitat and patch use by hyraxes: there's no place like home? Ecol. Lett. 2: 82–88.

Kotler, B.P., Brown, J.S., Bouskila, A., Mukherjee, S., Goldberg, T. 2004. Foraging games between gerbils and their predators: seasonal changes in schedules of activity and apprehension. Isr. J. Zool. 50: 255–271.

Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision making? Bioscience 48: 25–34.

Mohr, K., Vibe-Petersen, S., Jeppesen, L.L., Bildsøe, M., Leirs, H. 2003. Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs. Oikos 100: 459–468.

Morris, D.W. 1988. Habitat-dependent population regulation and community structure. Evol. Ecol. 2: 253–269.

Morris, D.W. 1989. Habitat-dependent estimates of competitive interaction. Oikos 55: 111–120.

Morris, D.W. 1994. Habitat matching: alternatives and implications to populations and communities. Evol. Ecol. 8: 387–406.

Morris, D.W. 1997. Optimally foraging deer mice in prairie mosaics: a test of habitat theory and absence of landscape effects. Oikos 80: 31–42.

Morris, D.W. 1999. Has the ghost of competition passed? Evol. Ecol. Res. 1:3–20.

Morris, D.W. 2001. Learning from the games animals play: using behavior to assess spatial structure and stochasticity in natural populations. Ann. Zool. Fenn. 38: 37–53.

Morris, D.W. 2003. How can we apply theories of habitat selection to wildlife conservation and management? Wildl. Res. 30: 303–319.

Morris, D.W. 2005a. On the roles of time, space, and habitat in a boreal small-mammal assemblage: predictably stochastic assembly. Oikos 109: 223–238.

Morris, D.W. 2005b. Habitat-dependent foraging in a classic predator-prey system: a fable from snowshoe hares. Oikos 109: 239–254.

Morris, D.W., Davidson, D.L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. Ecology 81: 2061–2066.

Morris, D.W., Mukherjee, S. 2007. Can we measure carrying capacity with foraging behavior? Ecology 88: 597–604.

Oatway, M.L., Morris, D.W. 2007. Do animals select habitat at small or large scales? An experiment with meadow voles (*Microtus pennsylvanicus*). Can. J. Zool. 85: 479–487.

Orrock, J.L., Danielson, B.J. 2005. Patch shape, connectivity, and foraging by oldfield mice (*Peromyscus polionotus*). J. Mammal. 86: 569–575.

Ovadia, O., Ziv, Y., Abramsky, Z., Pinshow, B., Kotler, B.P. 2001. Harvest rates and foraging strategies in Negev Desert gerbils. Behav. Ecol. 12: 219–226.

Percival, S.M., Sutherland, W.J., Evans, P.R. 1998. Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. J. Appl. Biol. 35: 57–63.

Persson, A., Stenberg, M. 2006. Linking patch-use behavior, resource density, and growth expectations in fish. Ecology 87: 1953–1959.

Pusenius, J., Schmidt, K. A. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. Oikos 98: 251–262.

Rieucau, G., Vickery, W. L., Laquerre, B. 2007. An innovative use of white-tailed deer (*Odocoileus virginianus*) foraging behaviour in impact studies. Can. J. Zool. 85: 839–846.

Sánchez, F. 2006. Harvest rates and patch-use strategy of Egyptian fruit bats in artificial food patches. J. Mammal. 87: 1140–1144.

Schmidt, K.A. 2000. Interactions between food chemistry and predation risk in fox squirrels. Ecology 81: 2077–2085.

Shochat, E., Lerman, S.B., Katti, M., Lewis, D.B. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. Am. Nat. 164: 232–243.

Stenberg, M., Persson, A. 2006. Patch use behavior in benthic fish depends on their long-term growth prospects. Oikos 112: 332–341.

Sutherland, W.J., Anderson, C.W. 1993. Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. J. Theor. Biol. 160: 223–230.

Valone, T.J., Brown J.S. 1989. Measuring patch assessment abilities of desert granivores. Ecology 70: 1800–1810.

van Gils, J.A., Edelaar, P., Escudero, G., Piersma, T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. Oikos 104: 197–204.