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PARADOXICAL AVOIDANCE OF ENRICHED HABITATS: HAVE WE FAILED TO APPRECIATE OMNIVORES?

DOUGLAS W. MORRIS¹

Department of Biology and Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario P7B 5E1 Canada

Abstract. Omnivores have not figured prominently in our understanding of food webs and prey dynamics even though they can have substantial direct and indirect effects on the structure of ecological communities and on the dynamics of interacting species. The important role of omnivores is implicated by the paradoxical results of a food-supplementation experiment. The experiment was designed to test theories that predict how habitat change affects the distribution of habitat-selecting species. According to theories of habitat selection, a quantitative change in habitat (as caused by supplemental food) should increase consumer population size and alter habitat selectivity. Related theories of patch use predict that consumers should increase their use of enriched patches. A two-year experiment on two species of small mammals in Canada's boreal forest failed to alter population densities of red-backed voles, but did cause a dramatic shift in vole habitat use. Rather than increasing their use of feeding stations as predicted by classical theory, voles avoided them. Deer mice did not respond to the experimental treatments. The paradoxical results occurred because omnivorous black bears altered prey behavior by increasing predation risk at feeding stations. Revised theory confirms the indirect omnivore effect, and demonstrates that the behavioral paradox is far more likely for omnivores than for other types of predators. The behavioral paradox of enrichment highlights not only important new, and potentially stabilizing, roles for omnivores, but also the pervasive influences of behavior and habitat selection on population dynamics and regulation.

Key words: boreal forest; competition; deer mice, ecology of fear; food web; habitat selection; ideal-free distribution; omnivore; paradox of enrichment; population regulation; predation risk; red-backed voles.

INTRODUCTION

On occasion, great ecological insights emerge from “failed” experiments. Perhaps the most famous example is Schroder and Rosenzweig's (1975) reciprocal removal experiment on two competing kangaroo rats. When Schroder and Rosenzweig removed *Dipodomys ordii* from its preferred desert grassland, they expected invasion by the closely related *D. merriami*. Instead, the grids were quickly repopulated by Ord's kangaroo rats. When they removed *D. merriami* from its favored desert scrub, the area was reinvaded by Merriam's kangaroo rats. Even though the two seed-eating rodent species are similar, the experiment revealed stereotyped habitat preferences that reduced competition to near

zero. The result was anathema to those ecologists who believed that competition could be estimated from niche (and habitat) overlap. Rosenzweig (1979) had a better idea. The species are in fact strong competitors; so strong that the persistent threat of competition creates the very habitat preferences that eliminate our ability to measure their competitive interaction. Rosenzweig's invention of isoleg theory proved the point, and his clever metaphor to the ghost of competition cemented the concept firmly in the minds of community ecologists.

I report on a similar “failed” experiment in Canada's boreal forest that also reveals an extremely interesting and potentially widespread effect. My assistants and I enriched habitats exploited by red-backed voles (*Clethrionomys gapperi*). Study plots contained an equal mixture of “shrub” and “moss” habitat. We added sunflower seed and rodent chow on different plots at stations representing either shrub, moss, or a mixture of

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 Corresponding Editor: B. J. Danielson.

¹ E-mail: douglas.morris@lakeheadu.ca

the two. In the second year of the experiment we reversed the treatments. Voles avoided the enriched patches. When we reversed the treatments, voles reversed their preferences. We think we know why. Omnivorous black bears foraged extensively on the enriched patches and increased the risk of predation to small mammals.

I begin by describing the context and design of the field experiment. I demonstrate how the experiment's paradoxical results can be interpreted in the light of increased predation risk from omnivorous predators. I develop a simple theory that links the behavioral paradox of enrichment to theories of habitat selection. I then use the theory to evaluate the relative roles of predators vs. omnivores on prey habitat use and population regulation, as well as their respective influences on the structure of food webs.

CONTEXT OF THE EXPERIMENT

Theories of habitat selection predict that the spatial distribution of individuals should reflect the fitness that they can expect to achieve in different habitats (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 1988, 2003; Appendix A). Fitness will depend on resource levels (e.g., Sutherland 1983, Pulliam and Caraco 1984, Fagen 1987, Morris 1994), on the efficiency of harvesting those resources (Morris 1988), and on the risks associated with their harvest (Brown 1988). I attempted to test the theory with a multi-year experiment using red-backed voles as the primary model organism. The experiment was centered on food-supplementation treatments (increased resource), that allocated those supplements differentially to preferred (shrub), less preferred (moss), or a shrub–moss mixture of habitats. According to current theory and intuition, vole densities should have increased in treated plots relative to controls, and the increase should have been greater in preferred habitat (with its associated high foraging efficiency and low risk of mortality) than in secondary or mixed treatments.

METHODS

Several assistants and I manipulated habitat richness in a large homogeneous fragment of boreal forest in northwestern Ontario, Canada (48°55' N, 89°55' W; Appendix B). In 1991 we established eight 1-ha replicate study plots, arranged with two columns and four rows. We separated each 100 × 100 m plot from its neighbors by an intervening equal-sized, 1-ha area that we avoided during the entire study. The outside margin of the “checkerboard” was at least 200 m from the edge of disturbed habitat (roads and small cutblocks). Each study plot was composed of a 6 × 6 sampling grid with 20-m spacing between the 36 sample points.

We began by measuring habitat and vegetation at all sampling stations, and then summarized the data with principal-components analysis to create a single composite variable representing habitat variation (Appen-

dix C). We used pretreatment vole data to measure habitat preference along the habitat gradient so that we could define, for each plot, two equal groups of stations representing preferred (shrub), and less preferred (moss) habitat.

We estimated habitat use by trapping small mammals with “Longworth” live traps for several trapping periods (each station trapped over three consecutive nights) in 1991 through 1994 (Appendix B). We complemented our habitat-use data from live-trapping with counts of rodent tracks (an estimate of “activity density”; Kotler 1985; Appendix B).

We collected control data on small-mammal abundance during three trapping periods in 1991. We collected experimental data in 1992 and 1993 (nine trapping periods each year) followed by a second control year in 1994 (eight trapping periods). Each field season began in mid-May and ended in early September. I estimated population densities and recruitment for each plot during each trapping period (Appendix B).

Beginning in 1992, I randomly assigned the eight field plots to four treatment groups for supplemental feeding in the 1992 and 1993 field seasons. Two plots (1 and 6) served as natural controls. The controls received no supplement in either year. Plots 4 and 7 served as “quantitative” controls. I selected nine stations at random from each of the shrub and moss habitats. The 18 stations received supplemental food in 1992. The other 18 stations on plots 4 and 7 received food in 1993. The remaining plots received “qualitative” treatments. Plots 2 and 5 received supplemental food in the “shrub” habitat. All 18 shrub stations on each plot received supplemental food in 1992. Plots 3 and 8 received supplemental food in the “moss” habitat. I reversed the treatments in 1993 (plots 2 and 5 received food in the moss habitat, plots 3 and 8 received food in the shrub habitat). We trapped all plots again in 1994 for comparison with the pretreatment data collected in 1991 (temporal control).

The six treatment plots received the twice-weekly food supplements. We calculated the expected energetic needs of voles when at maximum density (30 voles per plot from the 1991 data; mean August density = 29.125 voles), then doubled that value (Appendix D). We broadcast two forms of resources, sunflower seeds and rodent chow (to ensure access to both energy and essential nutrients), at the calculated rate (totaling four times the energetic requirements of voles).

I compared vole population numbers, habitat selectivity, and recruitment on treatment plots with the natural controls to assess the influence of supplemental food (Table 1). I compared “shrub and moss treatments” with the quantitative controls to evaluate possible differences in foraging efficiency or risk associated with food located in alternative habitats. I repeated the tests with deer mice, the second most abundant rodent species.

TABLE 1. A brief summary of key predictions and results from a field experiment that supplemented food for red-backed voles in preferred and less preferred habitats in boreal forest located in northern Ontario, Canada.

Contrast	Prediction	Result
Density (pre- vs. posttreatment)†	pre \equiv post	pre > post
Density (treatments vs. controls)	treatments > controls	treatments \equiv controls
Density (year 2 vs. year 3)	yr 2 \equiv yr 3	yr 2 \equiv yr 3
Recruits (pre- vs. posttreatment)	pre \equiv post	pre > post
Recruits (treatments vs. controls)‡	treatments > controls	treatments \equiv controls
Recruits (year 2 vs. year 3)	yr 2 \equiv yr 3	yr 2 \equiv yr 3
Electivity (pre- vs. posttreatment)	pre \equiv post	pre \equiv post
Electivity (year 2 vs. year 3; controls)	yr 2 \equiv yr 3	yr 2 \equiv yr 3
Electivity (year 2 vs. year 3; quantitative)§	yr 2 \equiv yr 3	yr 2 < yr 3
Electivity (year 2 vs. year 3; preferred)	yr 2 > yr 3	yr 2 < yr 3
Electivity (year 2 vs. year 3; less preferred)¶	yr 2 < yr 3	yr 2 > yr 3

† Pre- and posttreatment data were collected in year 1 and year 4 (before and after the experiment).

‡ Treatment plots received supplemental food; controls did not.

§ Quantitative treatments received food at both preferred and less preferred habitats.

|| Received food in preferred shrub habitat in year 2 and in less preferred moss habitat in year 3.

¶ Received food in less preferred habitat in year 2 and in preferred habitat in year 3.

Though we encountered bears during the main experiment and made casual notes of their presence on the plots, we did not quantify their activity. So, in August 2004, we repeated the experiment by adding the same amount of resources at the same stations as in 1992. We added food twice weekly for two fortnights. Then we searched each plot for omnivores and recorded bear activity as digs (feeding sites where bears had ripped open the forest floor to consume seeds and chow) and fecal piles (many of which included partially digested sunflower seeds).

Statistical design

I analyzed the data on vole and mouse population sizes, habitat choice (electivity; here based on shrub and moss categories), and recruitment with a full three-factor repeated-measures analysis of variance (GLM procedure, SPSS 2001) in a balanced split-plot design (treatment group analyzed as a between-subjects random effect; trap period analyzed as a within-subjects fixed effect). A significant treatment effect would document the influence of supplemental food. A significant year \times treatment interaction would demonstrate that effects related to the addition of food depend on which habitat the food is added to. I used a comparable simplified analysis (paired *t* tests) to assess the track data. The clear pattern of bear activity did not require statistical analysis.

RESULTS

A single principal component accounted for 44% (eigenvalue = 3.08, Kaiser-Meyer-Olkin measure of sampling adequacy [KMO] = 0.80) of the common variation in the final set of seven screened habitat variables (Appendix E). The habitat axis comprised a gradient from small shrubs (*Vaccinium*) and dense herbs on a moss-covered forest floor at one end (positive values), to large shrubs (e.g., *Alnus*) with their associated deep litter of leaves and woody debris at the other (negative values).

Voles and mice

Clethrionomys dominated the entire small-mammal community with 65% of the individuals (1123 of 1718) and 71% of all captures (4798 of 6750). *Peromyscus maniculatus* was the second most abundant species (285 individuals [17%], 1225 captures [18%]). The remaining proportions were divided among 12 additional species (Appendix F). No other species comprised >5% of the community.

Red-backed voles had a clear and obvious preference for habitat along the gradient. Habitat electivities declined more-or-less linearly from "shrub" to "moss" (electivity = 0.7 to -0.06 with ranked principal-component [PC] scores, $F_{1,23} = 203.5$, $P < 0.001$, $R^2 = 0.89$; Fig. 1). Deer mouse preferences were somewhat more complicated. Mice tended to avoid extreme stations at both ends of the gradient (Fig. 1). Consequently, I partitioned habitats in two at the median PC score. Stations with a low (negative) value for PC1 were classified as shrub, stations with a high value were classified as moss. All subsequent electivity values were recalculated to reflect these two habitat categories (positive values indicate preference for shrub habitat, negative values indicate a preference for moss).

Clethrionomys also dominated our data on mammal tracks, and in a proportion similar to that in the live-trap data (68%; Appendix F). The track data mirrored the trap-revealed preference of red-backed voles for shrub habitat. The mean number of tracking tubes containing vole tracks was greater in shrub than in moss, and in each habitat more tubes contained *Clethrionomys* tracks when placed under cover than in the open (Appendix G). Though deer mouse tracks were less abundant, the habitat preference was similar to that of voles (marginally more tracked tubes in shrub than in moss, and more tubes with tracks under cover than in the open). The preference of both species for shrub habitat, and for cover in both habitats, suggests that predation and habitat-dependent risk play key roles in rodent abundance and distribution.

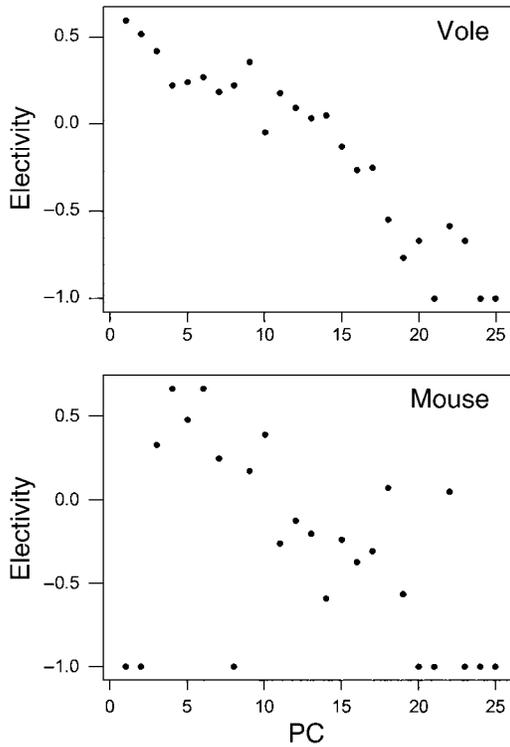


FIG. 1. Red-backed vole habitat preference (estimated by Ivlev's index of electivity using all vole captures from 1991; see Appendix C) declined linearly along a principal-component gradient from "shrub" to "moss" habitat. Deer mice avoided extreme sites.

Adequate numbers of voles necessary for reasonable estimates of habitat choice (set, arbitrarily, at 10 captures per plot per period) were available only in the late summer of each year. Preference for shrub habitat (electivity) during this time was similar among treatments and in the two control years (1991 and 1994, $F_{1,4} = 0.21$, $P = 0.67$) despite much higher densities and recruitment in 1991 ($F_{1,4} = 24.31$, $P = 0.008$ and $F_{1,4} = 46.81$, $P = 0.002$, respectively; Table 1, Fig. 2). No interaction was close to statistical significance (set at $P = 0.05$).

Densities in the two treatment years were not different, but did increase during the summer (period main effect, $F_{1,4} = 14.63$, $P = 0.019$, analyses restricted to periods 8 and 9; Fig. 3). Most importantly, voles altered their selection of habitat depending on which treatment was applied in each year (year \times treatment interaction, $F_{1,4} = 31.38$, $P = 0.003$; Table 1, Fig. 4). Habitat selection in the two types of control plots was similar in both years, and reflected *Clethrionomys*' clear preference for shrub habitat. But the paradoxical pattern of habitat choice in the other treatments was opposite expectation. Voles "avoided" supplemental feeding stations in both years. When treatments received food in shrub habitat, voles increased their use of moss. When treatments received food in moss, voles preferred the

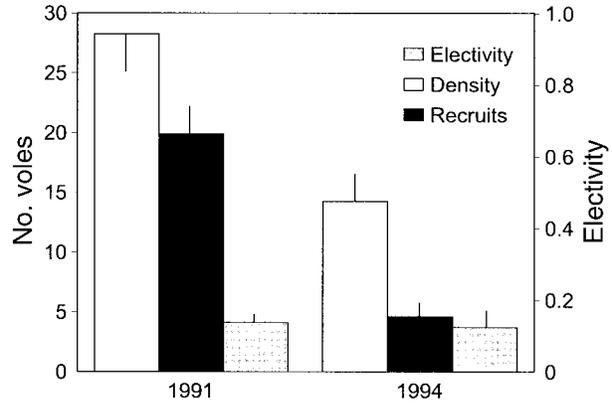


FIG. 2. Vole density and recruitment were greater in 1991 than in 1994, but habitat preference (electivity) was similar. Values are mean \pm SE; $N = 8$ plots.

shrubs. And, when we reversed treatments in 1993, the voles also reversed their preference!

The response by deer mice was also a paradox. Deer mice were indifferent to the experiment (Appendix H). Habitat electivity and densities were similar between the two control years ($P > 0.3$ for each). Densities tended to be higher in period 9 than in period 8 ($F_{1,4} = 5.63$, $P = 0.08$), and there was a suggestion that electivity also varied through time (year \times period interaction in electivity [$F_{1,4} = 5.73$, $P = 0.075$]). But the theory's predicted year \times treatment interaction in habitat electivity was "highly nonsignificant" ($F_{3,4} = 0.39$, $P = 0.77$).

No other effect or interaction was significant for either species (there was a hint of a year \times trap period interaction for vole recruitment [$F_{1,4} = 5.54$, $P = 0.08$]). The number of vole recruits was virtually identical in both periods in 1992, but was much greater in period 9 than 8 in 1993 (mean recruits = 10.88 and 6.00, respectively). The detection of recruits depends critically on the timing of live trapping and a pulse of recruits from synchronized reproduction could easily be restricted to a single trapping period. Such an effect could produce the apparent year \times trap period inter-

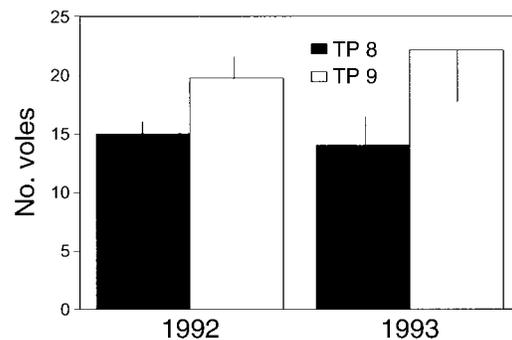


FIG. 3. Vole density in eight 1-ha study plots was greater in trap period (TP) 9 than in trap period 8 during both 1992 and 1993.

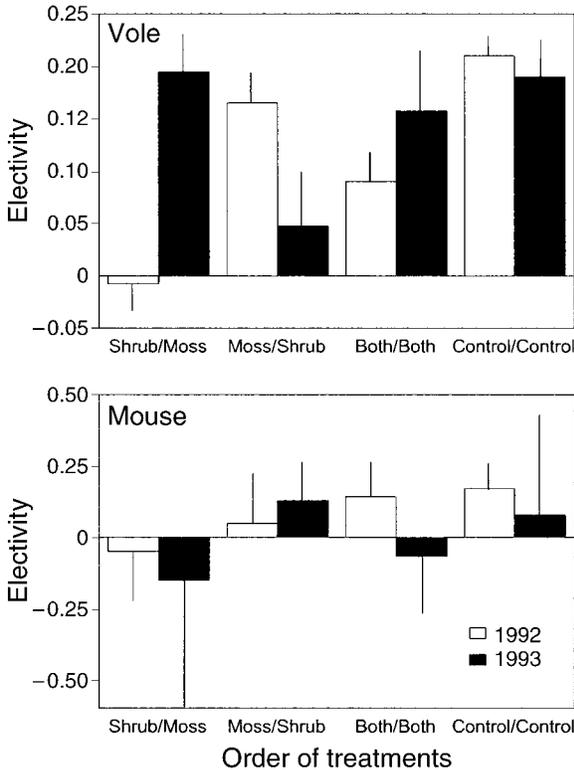


FIG. 4. Vole habitat choice (electivity; positive values indicate preference for shrub habitat) depended on which treatments were applied to study plots in two different years. Habitat choice reversed with reversals in treatment. Deer mice had no preference for any treatment. Values are mean \pm SE; $N = 4$. Shrub/Moss represents plots receiving food in the shrub habitat in 1992 and in the moss habitat in 1993, Moss/Shrub represents plots receiving food in the moss habitat in 1992 and in the shrub habitat in 1993, Both/Both represents plots receiving food in both habitats (but at a different set of stations) in both years, and Control/Control represents control plots in both years.

action. But the interaction, even if it truly exists, does not influence the dramatic paradox in habitat selection.

Omnivores

Could the paradox be caused because predators were attracted to the enriched sites? Perhaps, but only if prey were more abundant (or more easily captured) than at other sites. The opposite was true. The dominant small-mammal prey, red-backed voles, were more abundant at control than at food-supplemented stations. But two omnivores, in addition to small mammals, exploited the enrichment sites. Black bears (*Ursus americanus*) foraged for sunflower seeds at night as well as during the daytime, and Gray Jays (*Perisoreus canadensis*) became persistent sunflower seed robbers. Jays learned quickly about the distribution of feeding stations (Appendix I). Even though there were abundant seeds for jays, voles, and bears, *Clethrionomys* must have feared the potentially serious threats from ravaging bears and voracious jays with an appetite for small rodents.

The 2004 experiment pointed an incriminating finger directly toward bears. Black bears were active on all treatment plots, yet were virtually absent from the controls. Bears were active both day and night, and they disturbed an equally large proportion of feeding stations on all treated plots (Appendix J). Jays, squirrels, and other potential omnivores were conspicuously sparse.

Caveats

There are at least four additional hypotheses that could account for the habitat-selection paradox by voles (but not for the increased activity of bears). Full details are in Appendices K, L, and M.

H_1 . The habitat-selection paradox could occur simply because the electivity measures are constrained by the number of captures (the opportunity to occupy a single habitat during the experiment was lost when more than one half of all traps contained animals). I rejected the hypothesis because estimates of trap competition revealed a potential problem in only five of the 32 possible comparisons (8 plots, 2 periods, 2 years) used in my analyses, and because the pattern of habitat use in these cases was most often opposite to expectation.

H_2 . Voles in the vicinity of feeding stations may not have been attracted to traps. This hypothesis failed because the capture rate of voles was not different between feeding plots and the controls without food.

H_3 . Dominant voles may have excluded subordinates from the rich foraging sites. I rejected this hypothesis because the sex ratio, body-size distribution, and age class distribution of voles did not vary predictably with the foraging treatments.

H_4 . The food-addition experiments may have failed to increase habitat quality because supplemented resources were consumed by many different competitors. The hypothesis failed because, despite the disturbances by bears, there was always an abundance of supplemental food available for voles and mice.

DISCUSSION

Red-backed voles are habitat selectors. Voles possessed a strong preference for shrub-covered sites and altered their habitat selection in response to supplemental food. But there were no detectable treatment effects in vole density or recruitment. And, the habitat use by voles was opposite to both intuitive and theoretical expectations. Intuition and patch-use theory predict increased use of enriched patches by consumers. When we added food to shrub habitat, voles responded by increased exploitation of moss. When we added food to the moss habitat, they responded by choosing shrubs. When we reversed the treatments, the voles reversed their preference. Competition, whether for traps or for resources, was insufficient to explain the pattern. Deer mice, the second most abundant species, failed to respond to the experiment at all.

Meanwhile, at a smaller scale of habitat use revealed by their tracks, voles preferred the protective cover of shrubs over open areas. The preference was clear in all years and in both shrub and moss habitat. The pattern of microhabitat use is consistent with numerous studies on small mammals that have demonstrated higher predation risk in the open than under protective cover (e.g., Brown et al. 1988, Kotler et al. 1991, 1992, Brown et al. 1992, 1994, Kotler and Blaustein 1995, Morris 1997, Morris and Davidson 2000). The pattern in microhabitat use is also consistent with the larger-scale preference of voles for shrub habitat in our control data. Vole habitat use suggests a major role of predators, and the risk of predation, in their habitat choice. Indeed, predators may play a crucial role in maintaining separate habitat preferences for voles and deer mice (Morris 1996). But why should that risk be related to supplemental feeding?

A theory

Imagine that prey individuals have a choice of foraging at two sets of identical sites, that they use the sites in a way that maximizes an individual's fitness, and that an individual's expected fitness is equal in both sets at equilibrium (an ideal-free distribution; Fretwell and Lucas 1969). Following Brown and Kotler (2004),

$$p_1 F_1(N_1) = p_2 F_2(N_2) \tag{1}$$

where p is the probability of surviving predation, F is the fitness of survivors, and N is the number of individuals using the two types of sites (subject to the constraint that the total number of individuals is a constant $N = N_1 + N_2$). For simplicity, assume that fitness is a linear and negative function of the number of individuals using a particular type of site:

$$F_i(N_i) = W_i - b_i N_i \tag{2}$$

where W is the maximum fitness achieved at low density. When the sites are identical, each set should have an equal number of individuals:

$$N_2 = N_1. \tag{3}$$

Now, imagine that we add supplemental food (A) to all sites in one of the sets (2). Then,

$$p_{2A}(W_{2A} - b_{2A}N_{2A}) = p_1(W_1 - b_1N_1)$$

such that $W_{2A} > W_1$. Following rearrangement,

$$N_{2A} = \left(\frac{W_{2A}}{b_{2A}} - \frac{p_1 W_1}{p_{2A} b_{2A}} \right) + \frac{p_1}{p_{2A}} \frac{b_1}{b_{2A}} N_1. \tag{4}$$

Eqs. 3 and 4 represent the linear habitat isodars (Morris 1987, 1988) where fitness is identical in "control" and manipulated sites, respectively. In the absence of predation, the intercept of Eq. 4 will be positive, and more individuals will occupy sites (Eq. 2) following food addition than before (when densities were equal; Eq. 3). But with predation, a behavioral paradox of prey distribution ($N_2 > N_{2A}$) will occur (for all values of N)

only if the intercept of Eq. 4 is ≤ 0 , and if the slope is less than unity (diverging isodars). Since, in our example, the two types of sites are otherwise identical, the slopes of the fitness curves can be assumed equal ($b_{2A} = b_2 = b_1$, e.g., Morris 1988; the slopes could differ if foraging behavior changes with resource density). Thus, for the paradox to occur, the risk of predation must be greater in the manipulated set ($p_{2A} > p_1$), and

$$W_{2A} < \frac{p_1}{p_{2A}} W_1 \tag{5}$$

(the prediction of unequal predation risk could be verified by careful foraging experiments in the two types of sites, e.g., Brown 1988, Brown and Kotler 2004).

Are omnivores or "obligate" predators most likely to cause the paradox? Consider, first, the case for omnivores. Assume, as in the case of adult black bears, that the omnivore is not at risk from other predators. Assume, as well, that consumption of prey is incidental and forms a negligible component of the omnivore's diet. Following similar logic as above, the omnivore's isodar is given by

$$O_{2A} = \frac{W_{O2A} - W_{O1}}{b_{O2A}} + \frac{b_{O1}}{b_{O2A}} O_1 \tag{6}$$

where O is the number of omnivores and subscripts identify the omnivore and the two types of sites. Thus, omnivores will be attracted to the augmented sites directly by the additional food (the omnivore isodar intercept with supplemental food is greater than zero) and $O_{2A} > O_2$. For omnivores, there is no paradox. But the increased presence of omnivores at supplemented sites can create a paradox for their prey. Even if consumption of prey by omnivores is only incidental, more omnivores are present at augmented sites and predation risk will increase ($p_{2A} > p_1$). Meanwhile, the omnivore is consuming the added resource, and the augmentation's incremental fitness to prey will be less than if the omnivores were absent. And if omnivores are the first to arrive at manipulated sites, or if they are more efficient at consuming the added food than are prey, the supplement may fail to increase the "total" fitness of prey individuals at augmented sites ($W_{2A} < W_1$). Each effect will reinforce inequality (Eq. 5).

So a behavioral paradox (Eq. 5) will depend on the omnivore's ability to consume the added resource (and the paltry prey in this example) as well as how large of a threat it poses to prey. But even if the intercept of Eq. 4 is positive, the slope will be < 1 , and the manipulated isodar (Eq. 4) will cross over the control isodar (Eq. 3). It is thereby possible that a prey species living at low density (such as the deer mouse) could respond positively to the manipulation, or not at all (where the two isodars cross one another). A prey species living at high density (vole) would always exhibit the behavioral paradox of enrichment.

Now, consider the case for obligate predators. Imagine, first, that prey abundance is determined in habitat i solely by predators (Lotka-Volterra dynamics):

$$\frac{dP_i}{dt} = e_i a_i N_i P_i - d_i P_i \quad (7)$$

where P is the number of predators, e is the efficiency with which they convert prey into new predators, a is the per capita attack rate of predators on prey, and d is the predator's instantaneous death rate. Predator fitness in i is given by dividing both sides of Eq. 7 by the number of predators. In our example comparing control and food-augmented sites, the predator's fitness in both types of sites is thus equal when

$$e_{2A} a_{2A} N_{2A} - d_{2A} = e_1 a_1 N_1 - d_1$$

which, when converted to the isodar, yields the equilibrium distribution of prey:

$$N_{2A} = \frac{e_1 a_1}{e_{2A} a_{2A}} N_1 - \left(\frac{d_1 - d_{2A}}{e_{2A} a_{2A}} \right). \quad (8)$$

Eq. 8 demonstrates that the number of prey occupying food-augmented vs. control sites is unaffected by the number of predators. There can be no behavioral paradox unless prey are more easily captured when food is added than when it is absent ($a_{2A} > a_2$), or if predator mortality is larger in food-supplemented sites.

Strict predators, in contrast with omnivores, will be attracted to enriched sites only indirectly because more prey should be present there (predators have no direct effect on W_{2A}). Meanwhile, the probability that a prey individual survives predation (p) will depend on the predator's numerical and functional responses. If prey are easier to catch when food is added (as may occur at moderate prey densities in a Type III functional response), the risk of predation would increase at those sites, as would the number of predators. But under many circumstances, and across most prey densities, the risk to a prey individual should decline with prey abundance (and especially when prey share risk and vigilance). We conclude that a predator-induced behavioral paradox of enrichment, while not impossible, is nevertheless unlikely.

Thus, both theory and data have revealed a behavioral paradox comparable to the numerical paradox described by Rosenzweig (1971) over 30 years ago. Omnivores, by feeding in rich sites at the same trophic level as their prey, increase predation risk and alter prey distribution. When predation risk is high, prey species are unable to take advantage of spatially heterogeneous productive patches, and resources are channeled upward to the next trophic level (omnivores).

Implications

The short-term enrichment paradox mirrors that seen with apparent competition (Holt 1977, Holt and Kotler 1987) where shared predators subsidize their diet of

rare prey species by concentrating on abundant ones. Predator populations increase, and the net interaction between prey is negative, even if they otherwise do not compete for shared resources. But in the short term, predators that aggregate or increase their foraging activity and efficiency in patches rich in one prey species increase the risk of predation for other potential prey. Prey alter their behavior and distribution, and thereby modify both fitness and population size (Holt and Kotler 1987).

The behavioral paradox of enrichment functions similarly. Omnivores, keying on the shared resources of intermediate prey, increase the prey species' risk of predation. The very resources that make a patch valuable to prey are depreciated by their attractiveness to omnivores. The effect on prey is likely to be of far greater magnitude than the mortality and apparent competition caused by strict predators. Predators win only through increased prey abundance and any associated increases in prey capture rates. Omnivores can win twice, once by foraging on rich resources at a lower trophic level than their prey, and again through potential prey attraction to the enriched sites. But prey that coexist with omnivores lose in at least four different ways. Prey lose through resource competition with the omnivore, through interference in their ability to harvest resources, through predator-induced mortality, and through both short- and long-term apparent competition.

Adaptive prey responses include avoidance of rich patches, and increased vigilance and apprehension that compromise the omnivore's otherwise best-of-all-worlds strategy. Adaptive prey are repelled by the omnivore's use of rich patches. In the case of asymmetric relationships between large omnivores and small prey (bears and voles), prey avoidance of rich patches will have an insignificant effect on the omnivore's use of augmented sites. But when omnivores and prey are of similar size, prey avoidance of rich sites may reduce the attractiveness of those sites to the omnivore. The net value of each site to the omnivore would depend on such things as resource abundance and renewal, the omnivore's foraging and digestive efficiency, and the value placed on consuming prey rather than the prey's resources. Regardless, each prey response reduces overall prey foraging efficiency. Prey fitness and population size are less than they otherwise would be. In the case of red-backed voles, predation risk appears to exceed the benefit of supplemental food and voles shift their activity to less risky and less profitable sites. The food web is "compartmentalized" by habitat, and the food has no net benefit on vole population dynamics.

Somewhat similar habitat shifts have often been associated with intra-guild predation (e.g., Polis et al. 1989). The behavioral paradox of enrichment is special, not because prey alter their behavior in response to predators, but because their resource attracts omnivores. Prey may nevertheless congregate at enriched

patches when either the patches are exceptionally rich, or when competing omnivores represent small risks. As they do so, additional predators may alter their patch selection to mirror that of the prey (or other more abundant prey, including omnivorous members of the predator guild). Prey distribution will then depend on the frequency, duration, and relative value of resource patches, as well as the risks of direct and indirect predation.

Omnivores visiting rich patches will have a disproportionate effect on the trade-offs between food and safety of their prey. Unlike predators, whose risk to prey may decline with the amount of time the predator lingers in a patch (e.g., a detected predator is not nearly as dangerous as a stealthy one), the opposite is likely to apply to omnivores. True, the risk of predation from omnivores may also decline with time, but so, too, does the food value of the patch. Prey that could otherwise tolerate a declining level of predation risk in a rich patch exploited only by other equally brave conspecifics may not be able to balance the risk against the depleting value of a patch harboring a hungry omnivore. The resulting paradox could even produce an inverse relationship between resource abundance and the local population density of consumers if omnivores concentrate only on the richest patches. Exciting new predictions will emerge when the prey also possess omnivorous diets. Food web models that fail to account for such coadaptive behaviors are very likely to misrepresent the flows of energy and nutrients, and possibly misinterpret the dynamics and stability of the community.

It is unclear how frequently predation risk from omnivores may have caused food supplementation, food web, habitat-selection, and predator manipulation studies (e.g., Sih et al. 1985) to “fail.” It is even possible, despite the “smoking gun” of our 2004 “bear experiment,” that omnivores were not responsible for the paradoxical use of enriched habitats by red-backed voles. Even so, the concept deserves our attention. Competitive omnivory is potentially widespread and adds substantially to the panoply of behaviorally mediated “third-party” trophic effects that influence the distribution and abundance of species, and that may act to stabilize communities. It may even be time to discard cherished ecological notions about top-down vs. bottom-up processes (control by omnivores, if we can call it that, is not only top-down and bottom-up, but also horizontal and diagonal). As we do so, we need to pay more attention to how the dynamics of populations, the interactions among species, the structure of communities, the resulting implications to food webs, and the “ecology of fear” (Brown et al. 1999), are played out through adaptive habitat selection. Ignore habitat, or ignore behavior, and you risk misinterpreting both the processes, and their emergent patterns, in populations and communities.

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APPENDIX A

A review of the underlying theory predicting how habitat use should respond to habitat change is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A1.

APPENDIX B

A description of field sites as well as trapping and tracking methods used to assess density and habitat use by red-backed voles is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A2.

APPENDIX C

A description of vegetation and habitat measurements and analysis to assess the effects of habitat change on red-backed voles is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A3.

APPENDIX D

A description of the methods to determine how much supplemental resource should be added to experimental plots is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A4.

APPENDIX E

A table summarizing the results of a principal-components analysis on the common variation of seven habitat variables is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A5.

APPENDIX F

A table documenting the cumulative number of small-mammal individuals, total captures, and tracks recorded on eight 1-ha study plots in northern Ontario, Canada, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A6.

APPENDIX G

A table documenting habitat preferences of red-backed voles and deer mice as indicated by their tracks is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A7.

APPENDIX H

A table documenting the indifferent response of deer mice to food supplements is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A8.

APPENDIX I

Evidence demonstrating increased presence of omnivores at feeding stations avoided by red-backed voles is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A9.

APPENDIX J

An illustration of the results from a 2004 replicate of the original experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A10.

APPENDIX K

A description of the tests of four alternative hypotheses that could possibly account for the behavioral paradox of enrichment observed in red-backed voles is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A11.

APPENDIX L

An illustration of how vole habitat choice (electivity) varied among plots and between the two years of the supplemental feeding experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A12.

APPENDIX M

A table documenting abundances of sunflower seeds and mouse-chow pellets at feeding stations used to augment resources consumed by red-backed voles is available in ESA's Electronic Data Archive: *Ecological Archives* E086-138-A13.