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Density-dependent foraging effort of Deer Mice (*Peromyscus maniculatus*)

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Summary

1. Little is known about how population density affects the foraging behaviour of individuals. Simple models are developed to predict the net effect of density on the quitting-harvest rates of optimal foragers. The theory was tested with experiments that measured the foraging behaviour of free-ranging Deer Mice under control and reduced densities.

2. An increased density of conspecifics may (a) reduce the costs of foraging by increasing competition for resources (reduces the energetic state of the forager; competition hypothesis) or (b) increase the costs of foraging by increasing the value of time spent on social activities (social benefits hypothesis).

3. A reduction in the costs of foraging caused by competition will reduce the quitting-harvest rate of an optimal forager, whereas an increase in the value of alternative activities will increase the quitting-harvest rate. Both hypotheses predict a reduction in optimal foraging time with increased density.

4. The hypothesis that applies to Deer Mice (*Peromyscus maniculatus*, Wagner) was assessed by measuring their foraging activity and quitting-harvest rates at control and reduced population densities on four study plots located in boreal forest in north-western Ontario, Canada.

5. Deer Mice increased their *per capita* foraging activity and their quitting-harvest rates when population densities were reduced. The results confirm the very important role of competition in the behaviour of optimal foragers.

Key-words: Competition, giving-up density, quitting-harvest rate

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Introduction

An animal behaving optimally should allocate time between foraging and non-foraging activities in such a way as to maximize fitness. In this light, an animal should quit foraging when the marginal benefit (energy-intake rate) no longer exceeds the marginal costs of foraging, including the missed opportunities of not engaging in alternative fitness-enhancing activities (Schoener 1971; Brown 1988). Any factors that influence the costs of foraging will also influence the optimal time that an animal should devote to foraging. The harvest rate at which it quits foraging (quitting-harvest rate) will be modified accordingly. Quitting-harvest rates of seed-eating rodents, for example, increase in the face of increased foraging costs arising from metabolic expenditures (Kotler, Brown & Mitchell 1993a; Bozinovic & Vásquez 1999), predatory risk (Brown *et al.* 1988; Kotler *et al.* 1988, 1993b; Kotler, Brown & Hasson 1991; Hughes, Ward & Perrin 1994; Bouskila 1995) and missed opportunities of not foraging elsewhere (Brown, Morgan & Dow 1992; Kotler 1996). It is likely that a significant component of each of these costs is related to changes in population density and associated differences in competition for resources. A test for the density dependence of quitting-harvest rates is long overdue, as is an evaluation of the explicit processes by which population density influences foraging effort. We examine both issues.

Increased population density may also influence foraging activity by increasing the benefit of engaging in social activities (e.g. courtships, matings, the value of defending one's territory). The reduced costs of foraging caused by competition, as well as the increased benefit of engaging in alternative activities, can be differentiated by their effect on the quitting-harvest rates of individuals. If increased competition reduces the energetic state of each forager, individuals will place a higher value on obtaining energy than on alternative activities and forage to a lower quitting-harvest rate. Conversely, social benefits associated with increased

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population density will cause individuals to place less value on foraging and will increase quitting-harvest rates.

We begin by developing simple models that predict density-dependent effects on the quitting-harvest rates of optimal foragers. We then test for density-dependent foraging by estimating quitting-harvest rates (obtained from the giving-up density, GUD, of resources in artificial foraging patches; Brown 1988) of free-ranging Deer Mice (*Peromyscus maniculatus*, Wagner). We test whether Deer Mice are energy maximizers and differentiate between the 'competition' and 'social benefits' hypotheses by manipulating Deer Mouse densities and measuring the respective GUDs. Our focus is the net response of quitting-harvest rates to population density that will allow us to assess the role of competition on foraging.

THE EFFECT OF POPULATION DENSITY ON QUITTING-HARVEST RATES

An animal using a strategy that maximizes its fitness will quit foraging when the marginal benefit no longer exceeds the marginal costs of foraging, including the cost of not engaging in alternative fitness enhancing activities (Brown 1988; Mitchell *et al.* 1990). Thus, a fitness maximizer quits foraging when

$$f(n)v = VC + (\partial G/\partial t_a)/(\partial G/\partial x_1), \qquad \text{eqn 1}$$

where the left-hand side is the rate of resource harvest as an increasing function of the available resource density in the habitat, n, multiplied by the per unit energy value of the resource, v. VC is the additional energetic cost of foraging (above basal metabolism), $\partial G/\partial t_a$ is the marginal increase in fitness, G, with time spent on alternative activities, t_a, and $\partial G/\partial x_1$ is the marginal increase in fitness with the energetic state, x_1, of the forager (Mitchell *et al.* 1990, eqn 9). The last term in equation 1 is the marginal benefit, converted to an energetic currency, of engaging in alternative non-foraging activities. Alternative activities are considered together as a missed opportunity cost of foraging (Brown 1988) because their benefit is not realized while an animal is foraging.

The decision of when to quit foraging is governed by an important principle that emerges from equation 1. The marginal benefit of foraging (left-hand side of equation 1) decreases with foraging time as available resource density in the habitat declines while the marginal costs of foraging (right-hand side of equation 1) increase (Fig. 1). Two effects increase marginal costs with time spent foraging:

1. The marginal value of energy, $\partial G/\partial x_1$, decreases as the energy state of the forager increases (i.e. diminishing returns to fitness in energy, Schoener 1971; Mitchell *et al.* 1990).
2. The marginal value of time spent on alternative activities, $\partial G/\partial t_a$, increases with the energetic state of the animal (i.e. complementary inputs to fitness).

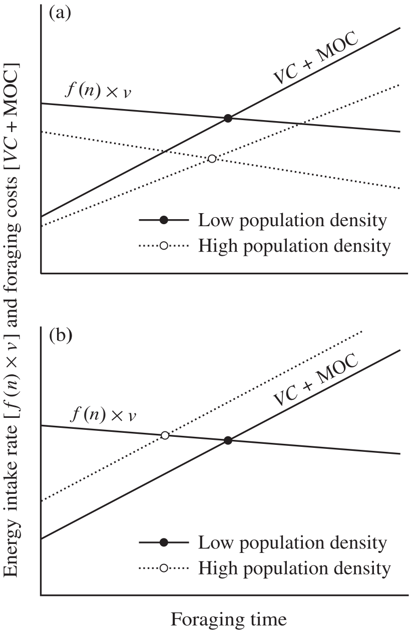

Fig. 1. The 'competition' and 'social benefits' hypotheses for density-dependent quitting-harvest rates of optimal foragers. Energy-intake rate [$f(n)v$] decreases with foraging time as resource density in the habitat, n, declines. Missed opportunity costs (MOC) increase with foraging time because the value of time spent on alternative activities increases with the energetic state of the animal. The additional energetic expenditure of foraging (VC) is independent of foraging time. A fitness maximizer will quit foraging when the marginal benefit equals the marginal costs (i.e. at the intersection of the two functions). (a) Competition (high *vs* low density) increases the depletion rate of resources thereby reducing an individual's energy-intake rate and energetic state at any given foraging time. MOC is similarly reduced by competition because individuals experience diminishing returns to fitness in energy. Competition reduces the optimal quitting-harvest rate. (b) An increased value of engaging in social activities increases MOC at higher population density. Optimal quitting-harvest rate increases with increased population density. Curvilinear functions yield qualitatively similar conclusions.

The marginal benefit and costs in equation 1 eventually equalize at which time the animal quits foraging in favour of alternative activities.

The effect of increased population density on the optimal quitting harvest rate depends on how population density influences the marginal benefit and costs of foraging. If increased population density reduces the availability of resources in the habitat (competition hypothesis), equation 1 is satisfied at a lower harvest rate for two reasons (Fig. 1a): the energy-intake rate is reduced and the mean energetic state of foragers is reduced thereby reducing $\partial G/\partial t_a$ and increasing $\partial G/\partial x_1$ (Mitchell *et al.* 1990). If, on the other hand, increased population density increases the value of alternative activities such as finding or attracting mates, territorial defence and other social interactions (i.e. $\partial G/\partial t_a$ is increased, social benefits hypothesis), equation 1 will be satisfied at a higher harvest rate (Fig. 1b). While each mechanism is likely to operate simultaneously, the net effect of population density yields unique predictions that can be tested with estimates of marginal harvest rate (Fig. 1).

A comparison of marginal harvest rates between habitats differing only in population density can be made from the resource densities remaining in abandoned resource patches (GUDs). Imagine animals foraging in identical, non-renewing resource patches. Within a patch, harvest rate declines as a forager reduces the resource density. An optimal forager abandons the patch when its marginal harvest rate in the patch equals the marginal harvest rate for the habitat. The density of resources remaining in the patch is, then, a relative measure of the marginal harvest rate for the habitat.

A CAVEAT

Increased competition may result in equation 1 being satisfied at a higher harvest rate if energy-starved animals experience accelerating returns to fitness in energy (i.e. $\partial G/\partial x_1$ increases with the energy state of the animal, e.g. Caraco, Marindale & Whittam 1980). By reducing the mean energy state of the animals and thus decreasing $\partial G/\partial x_1$, increased competition may increase rather than decrease MOC (Mitchell *et al.* 1990). An increase in the quitting-harvest rate at higher population densities could be consistent with both the social benefits hypothesis and the competition hypothesis. Regardless, a density-dependent reduction in quitting-harvest rate will always signify density-dependent competition for resources.

ENERGY MAXIMIZERS *VS* TIME MINIMIZERS

The foraging model represented by equation 1 assumes that animals are 'energy maximizers' (Schoener 1971). An energy maximizer always realizes a fitness benefit from additional energy intake and quits foraging only when the costs equal this benefit (equation 1). An alternative foraging goal might be to minimize the time spent obtaining a fixed energy requirement (i.e. animals may be 'time minimizers', Schoener 1971). A time minimizer acquires no fitness benefit from surplus energy and, thus, quits foraging when its requirement is satisfied. We can, however, differentiate between the two foraging goals by examining the effect of density on the foraging activity of individuals (Mitchell *et al.* 1990). If increased population density reduces individuals' mean harvest rates, then time minimizers must increase foraging activity to obtain the same energy requirement (Mitchell *et al.* 1990). Conversely, energy maximizers should reduce foraging activity with increased resource competition (Mitchell *et al.* 1990). The social benefits hypothesis also predicts reduced foraging activity with increased population density for energy maximizers (Fig. 1b).

A SUMMARY OF THE PREDICTIONS

The competition hypothesis predicts that, at increased population density, individuals forage longer in each resource patch and abandon patches at a lower giving-up density. The social benefits hypothesis predicts that, at increased population density, individuals spend less time in each resource patch and abandon patches at a higher giving-up density. At the scale of a habitat containing multiple resource patches both hypotheses predict a reduction in the mean foraging activity of individuals.

Materials and methods

STUDY AREA AND SMALL MAMMAL CENSUS

In July and August 1995, the activity level and giving-up densities of Deer Mice under control and density-reduced conditions was measured in boreal forest in northwestern Ontario, Canada. Four study plots were established each consisting of 16 stations (4 × 4 grid) at 20-m intervals in a 30-ha stand of Trembling Aspen (*Populus tremuloides*, Michx.). Deer Mice, Red-Backed Voles (*Clethrionomys gapperi*, Vigors) and Yellownose Voles (*Microtus chrotorrhinus*, Miller) were the most abundant small mammal species on the plots with estimated mean densities of 36, 33 and 8 animals ha^{-1}, respectively (minimum number known alive, Hilborn, Redfield & Krebs 1976; determined by live-trapping). Also present, but in low numbers, were Woodland Jumping Mice (*Napaeozapus insignis*, Miller), Meadow Jumping Mice (*Zapus hudsonius*, Zimmermann) and Phenacomys (*Phenacomys intermedius*, Merriam).

Each plot was live-trapped with a minimum of four biweekly censuses before the start of a density-reduction experiment, followed by one census 6–10 days after the end of the experiment. Each census lasted two consecutive nights during which time three baited Tomahawk live-traps were set at each station. Traps were checked each morning and the intervening evening. Animals were identified to species and individually marked before being released at the point of capture. All captured Deer Mice were given the same unique toe-clip to aid in identifying tracks for activity estimates (see below).

DENSITY-REDUCTION EXPERIMENTS

Six experimental trials were conducted to test for the effect of population density on foraging activity by Deer Mice and their quitting-harvest rates. Deer Mouse density in each trial was manipulated by removing (and subsequently returning) animals from a study plot. Foraging activity and quitting-harvest rate were estimated at both high (control) and low (approximately half of the animals removed) population densities. Removed animals were maintained in holding cages for two nights while the responses of the remaining animals were measured. There was a total of six experimental trials. Two plots received one trial, two others received a second trial 9 days after the end of the first when population densities had increased through recruitment. Populations continued to increase during, and between trials. Even though the removals lasted only 2 days, immigrants could jeopardize our attempts to manipulate density, and to collect valid control data. Both problems were addressed by applying the density-reduction treatment before the control in three trials and after the control in the other three trials.

Quitting-harvest rates were estimated with GUDs in identical artificial foraging patches (Brown 1988). A mixture of 2·0 g prescreened, unhusked millet seed (>2 mm diameter, mean mass = 7·3 mg seed^{-1}) and 300 ml of screened sand (grain size <0·5 mm) was poured into unused 1 l cardboard milk cartons. Deer Mice readily dug to the full depth of the sand (2 cm) making all seeds in a patch accessible. A 3 × 7 cm^2 opening at one end of each carton served as an entrance to the patch. GUD was estimated as the number of millet seeds remaining in a patch after a night's foraging. Millet-in-sand foraging patches have been used to assess GUDs of Deer Mice elsewhere in their range (Morris 1997) and of many seed-eating rodents (e.g. Brown 1988; Kotler *et al.* 1991, 1993a,b; Hughes *et al.* 1994; Ziv *et al.* 1995).

Deer Mouse activity was estimated as a score equal to the number of Deer Mouse tracks accumulated overnight on tracking paper in plastic tubes (40 mm diameter × 30 cm, van Apeldoorn *et al.* 1993). The unique toe-clip given to all Deer Mice allowed us to distinguish their tracks from the similar tracks of other species present on the study plots.

At dusk, one foraging patch was placed at each station along with one tracking tube in line with and within 10 cm of the foraging patch entrance. All patches and tubes were collected the following morning. Activity scores and GUDs at each station were averaged over the two nights of each experiment. *Per capita* activity for each round was calculated by dividing the total activity score from all stations by the minimum number of Deer Mice known alive on the plot.

EXPERIMENTS TO TEST ASSUMPTIONS

Using the giving-up density in a patch as a relative measure of the marginal harvest rate for the habitat is based on three assumptions. The assumption that harvest rate declines as a forager depletes a patch was tested by observing eight captive Deer Mice as they foraged in our resource patches under red light.

The assumption that a Deer Mouse abandons a foraging patch according to the marginal harvest rate in the patch was tested by comparing the proportions of millet harvested from foraging patches containing initial millet densities of 1, 2, 4, 8, 16 and 32 g patch^{-1}. With increasing initial density, the proportion of millet harvested will decrease, stay the same, and increase for fixed-harvest, fixed-time and quitting-harvest-rate rules, respectively (Valone & Brown 1989). Six foraging stations were established (2 × 3 grid) at 60 m intervals in the same aspen stand used for density-reduction experiments. On each of six consecutive nights, four foraging patches of equal initial millet density were placed at the corners of a 10 m × 10 m square centred at each station. The six levels of initial millet density were assigned to the six stations and six nights using a Latin square design (Tabachnick & Fidell 1989). All foraging patches were collected each morning.

Measuring GUDs with and without habitat resource augmentation tested the assumption that the quitting-harvest rate in a foraging patch increases with the marginal harvest rate for the habitat. Two foraging patches were placed 60 cm apart at each of eight stations on each of the four study plots for one night. One patch contained fine sand (grain size <0·5 mm), the other coarse sand (1 mm <grain size <1·4 mm). The sand treatment was used as a supplemental test for the assumption that Deer Mice abandon patches on the basis of quitting-harvest rates (Davidson 1998). Assuming that search rates differ in patches with different substrates (Price & Heinz 1984; Ziv *et al.* 1995; Hughes *et al.* 1994; Davidson 1998), GUDs will vary with the substrate in a patch (Brown 1988).

One half of the stations on each plot were selected at random and 40 g of millet seed was scattered within a 1-m radius. Control stations were located a minimum of 60 m from the nearest augmented station. The experiment was reversed (control stations became treatment stations and vice versa) three nights later.

All statistical analyses were performed using SPSS software (version 6·1, SPSS Inc., Chicago, IL, USA, Norušis 1994). GUDs were transformed to natural logarithms, when necessary, to stabilize variance and normalize the data.

Results

HARVEST RATE DECLINED AS A FORAGER DEPLETED THE RESOURCES IN A PATCH

Only one of the eight rodents consistently consumed the millet seeds while in the patch. The harvest rate for this individual was notably low compared with the other seven animals (Fig. 2). The data for this animal were excluded from the analysis. The remaining rodents carried seeds to their shelters before eating them. None of these animals cached the seeds. Boxes contained hulls, but no seeds, at the end of the experiment. Polynomial regression of harvest on foraging time yielded a significant and positive linear term, and a significant and negative quadratic term ($P < 0.001$ for both, Fig. 2). The constant and cubic terms were not significant ($P = 0.72$ and $P = 0.29$, respectively). Deer mice experienced diminishing harvest rates in artificial resource patches.

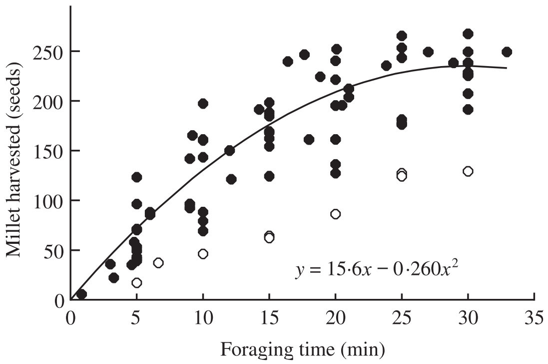

Fig. 2. Deer Mice experienced a diminishing harvest rate with time spent foraging for 2·0 g of millet seeds in artificial resource patches (300 ml sand; $N = 72$). Open points represent observations from a single individual that consumed seeds while in the patch (excluded from the analysis). All other animals carried seeds back to their shelters.

THE PATCH-LEAVING RULE FOR DEER MICE APPEARED TO BE BASED ON HARVEST RATE

Mean GUD increased significantly with initial millet density (Fig. 3a, Table 1). Patches initially containing 32 g of millet were abandoned at relatively high millet densities with high variance (Fig. 3a), suggesting that some animals were sated at this level of resource. These data were excluded from the analyses. GUD increased with initial millet density for the remaining patches. The result is consistent with two different expectations of optimal foragers.

1. Foragers should abandon patches at higher quitting-harvest rates if the resource density of the habitat is increased (the marginal value theorem, Charnov 1976; average resource density in our experiments increased because all four patches at any one station contained the same initial millet density).
2. Animals could be using a Bayesian foraging strategy that underestimates the resource level in rich patches while overestimating the resource level in poor patches (Valone & Brown 1989). Bayesian foragers will, like these Deer Mice, have higher GUDs in rich than in poor patches (Valone & Brown 1989; see Olsson & Holmgren 1999) and Olsson *et al.* (1999) for predictions where foragers optimize the potential gain rates of clumped prey in patches rather than instantaneous rates).

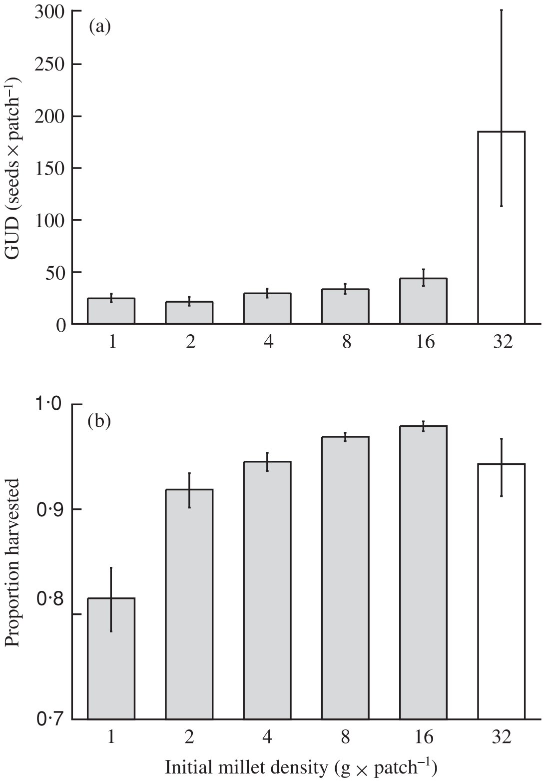

Fig. 3. The effect of initial millet density on the foraging behaviour of Deer Mice harvesting artificial resource patches in boreal forest in northwestern Ontario. (a) Giving-up densities of millet (GUDs) increased with initial millet density. (b) The proportion of millet harvested increased at a declining rate with increasing initial millet density. Open bars represent the data for very high millet density (32 g patch^{-1}) that was not included in the statistical analyses. Bars represent means; vertical lines represent one standard error about the mean.

The proportion of millet harvested also increased significantly with initial millet density but followed a more complex pattern ($P < 0{\cdot}01$ for all polynomial contrasts, 32 g treatment excluded, Table 1, Fig. 3b). The significant quadratic term demonstrates that the rate of increase in the proportion of millet harvested declined with increased initial millet density. The decline is expected because the proportion of millet harvested has an upper limit of one. The significant cubic and fourth-order terms correspond to continued flattening of the curve as it approaches its asymptote (Table 1). The salient point is that the increase in the proportion of millet harvested is inconsistent with fixed-harvest (predicts a declining proportion) and fixed-time (predicts a constant proportion) foraging rules.

Table 1. Significant effects of initial millet density in a foraging patch on giving-up density ($\log_e$ transformed) and the proportion of millet harvested (square-root-arcsine transformed) by Deer Mice foraging in boreal forest in northwestern Ontario (repeated measures ANOVA)

Source	df	*F*	*P*
Giving-up density			
Constant	1,5	1990·41	<0·001
Polynomial contrasts			
Linear component	1,5	7·83	0·04
Proportion of millet harvested			
Constant	1,5	8656·71	<0·001
Polynomial contrasts			
Linear component	1,5	46·30	0·001
Quadratic component	1,5	36·15	0·002
Cubic component	1,5	15·00	0·01
Fourth power component	1,5	15·74	0·01

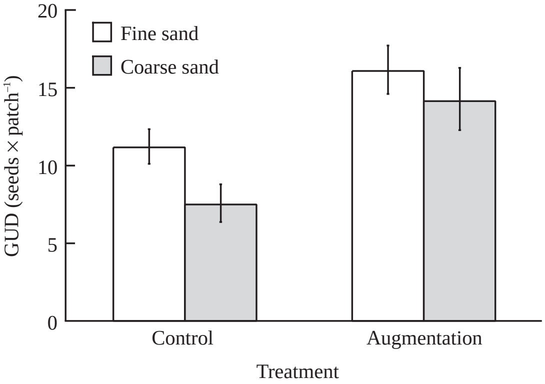

Fig. 4. Mean giving-up density of Deer Mice foraging in artificial resource patches was higher in patches containing fine sand than in patches containing coarse sand and higher under resource augmentation than in controls ($N = 32$). Bars represent means; vertical lines represent one standard error about the mean.

Table 2. Significant effects on giving-up densities (log$_e$ transformed) for Deer Mice foraging in artificial resource patches containing fine and coarse-sand substrates, with and without resource augmentation (32 stations on four study plots, repeated measures ANOVA)

Source	df	*F*	*P*
Plot	3,28	9·85	<0·001
Augmentation	1,28	8·76	0·006
Substrate	1,28	9·01	0·006
Substrate × plot	3,28	3·11	0·04

Mean GUDs were significantly higher in fine than in coarse sand (13·4 and 10·3 seeds patch^{-1}, respectively; Fig. 4, Table 2). A significant interaction between study plot and substrate was caused by atypically high GUDs in two patches containing coarse sand on plot 4. Both of these data were statistical outliers (>3 standard deviations from the grand mean). The interaction disappeared when the data were reanalysed excluding these outliers; no other terms changed in significance.

Higher GUDs in fine sand are consistent with a lower search rate in fine than in coarse sand. However, no significant effect of substrate on search rate was detected in observations of Deer Mice foraging in both substrate types (Davidson 1998). The fine sand packs closer (smaller particle size) and has a higher bulk density than the coarse sand (1·73 and 1·57 g cm^{3}, respectively). On average, a forager must displace a larger mass of sand per seed harvested from fine sand than from coarse sand. Deer Mice may expend energy at a faster rate (higher foraging cost) when searching through fine compared to coarse sand. The high GUDs in fine sand are consistent with this 'elevated cost' hypothesis, and also support our earlier observation that the mice abandoned patches according to a quitting-harvest rate rule.

Table 3. Population densities (MNA) of Deer Mice in control and density-reduction treatments for six experimental trials. Half the density reductions were conducted during the first census (trials 2, 4, 6); the other half were conducted 9 days later during the second census

Trial	MNA		Percentage reduction in MNA
	Control	Treatment	
1	29	19	34·5
2	22	14	36·4
3	9	9	0·0
4	23	7	69·6
5	33	14	57·6
6	18	7	61·1

QUITTING-HARVEST RATES IN PATCHES INCREASED WITH THE MARGINAL HARVEST RATE OF THE HABITAT

Mean GUDs were significantly higher with resource augmentation than without (15·1 and 9·1 seeds patch^{-1}, respectively; Fig. 4, Table 2). The result demonstrates that quitting-harvest rates were higher when the marginal harvest rate for the habitat was higher.

Mean GUD also varied among the study plots (Table 2). The study plots varied in Deer Mouse and vole density, and may have varied in predatory risk, level of resources, or other factors that influence GUDs.

POPULATION REDUCTION TREATMENTS REDUCED DEER MOUSE DENSITY BY UP TO 70% COMPARED WITH CONTROLS

The observed reduction in Deer Mouse density relative to controls ranged from 0 to 70% among the six trials (Table 3). Deviations from our objective of 50% reduction were caused by natural changes in the population densities over the 9 days between the control census and our density-reduction treatments. The increase in the number of Deer Mice caused by juvenile recruitment in one trial (3) was equal to the number of animals removed. A substantial difference between treatment and control densities was observed in all other trials (Table 3).

PER CAPITA ACTIVITY OF DEER MICE DECREASED AT HIGHER POPULATION DENSITIES

There was a significant negative relationship between *per capita* activity of Deer Mice and their population density ($r = -0{\cdot}72$, $P = 0{\cdot}009$, Fig. 5). Deer Mice decreased their foraging activity as population density increased. The result is inconsistent with the hypothesis that Deer Mice are time minimizers.

GIVING-UP DENSITIES INCREASED WHEN POPULATION DENSITY WAS REDUCED

Mean GUD was higher when we removed animals in four of the six trials ($P = 0{\cdot}005$, 0·06, 0·04, 0·001,

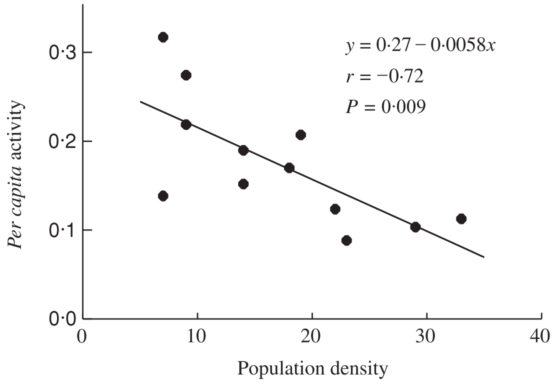

Fig. 5. *Per capita* activity (total number of tracks at all stations/MNA) of Deer Mice decreased with increasing Deer Mouse density (MNA) on four study plots in boreal forest in northwestern Ontario.

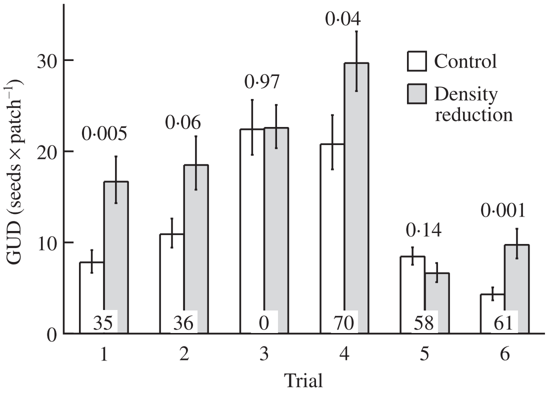

Fig. 6. Comparison of mean giving-up densities (±1 standard error) of Deer Mice foraging in artificial resource patches at high (control) and low (density reduction) population densities in boreal forest in northwestern Ontario. The percentage reduction in Deer Mouse density between the control and the density-reduction treatments for each trial is superimposed on each pair of bars. Proportions above bars represent *P*-values for separate paired *t*-tests ($N = 16$ for each trial).

respectively, Fig. 6). As expected, there was virtually no difference in mean GUD in trial 3 ($P = 0·97$, Fig. 6) where the control and treatment densities were identical. Mean GUD appeared lower in the reduction treatment of trial 5 but the difference was not statistically significant ($P = 0·14$). The result from trial 5 may have been caused by a relatively large increase in vole density between the time of the control and its respective treatment (68·2% increase compared with a mean increase of 21·4% in all other trials). Nonetheless, the density-reduction treatments tended to increase GUDs for foraging Deer Mice.

Table 4. Summary of hierarchical regression analysis of mean giving-up density on vole density (sum of MNA for Red-Backed and Yellownose Voles), total activity score (total number of Deer Mouse tracks from all stations), and Deer Mouse density (MNA), respectively

Step	Variable entered	R^2 change	df	*F*	*P*
1	Vole density	0·34	1,10	5·13	0·05
2	Total activity score	0·31	1,9	8·08	0·02
3	Deer Mouse density	0·18	1,8	8·84	0·02
Model		0·83	3,8	13·4	0·002

QUITTING-HARVEST RATES WERE NEGATIVELY DENSITY DEPENDENT

The differences in GUDs that we observed in our experiments may have been caused by differences in Deer Mouse density, activity or by changes in the density of coexisting Red-Backed and Yellownosed Voles. Mean GUD on a plot was negatively correlated with total activity (sum of Deer Mouse tracks; $r = -0·56$, $N = 12$, $P = 0·06$) and vole density ($r = -0·58$, $N = 12$, $P = 0·05$). Total activity was positively correlated with Deer Mouse density ($r = 0·66$, $N = 12$, $P = 0·02$). When vole density and total Deer Mouse activity were controlled in a three-variable hierarchical regression, Deer Mouse density had a significant and negative effect on mean GUD (mean GUD = 52·2 – 0·77 vole density –0·10 total activity –0·63 Deer Mouse density, $R^2 = 0·83$, $F_{3,8} = 13·4$, $P = 0·002$, Table 4). The decrease in GUD with increased Deer Mouse density cannot be attributed solely to an increase in the Deer Mouse activity at foraging patches. Quitting-harvest rates for Deer Mice were negatively density dependent.

Discussion

Deer Mouse foraging is markedly density dependent. *Per capita* foraging activity of these energy maximizers declined with increased population density, a result predicted by both the competition and social benefits hypotheses. The role of competition is confirmed by the density-dependent quitting-harvest rates. Although we cannot reject the hypothesis that increased population density increased the value of engaging in social activities, the net effect of competition is clear; quitting-harvest rates declined with increased population density. We suspect that the density-dependent reductions in the foraging activity of gerbils (Abramsky & Pinshow 1989; Mitchell *et al.* 1990; Hughes *et al.* 1994) also reflect density-dependent competition for resources. The competition hypothesis is supported as well by the documented effect of interspecific competition on foraging behaviour (e.g. Abramsky & Pinshow 1989; Mitchell *et al.* 1990; Hughes *et al.* 1994; Bouskila 1995).

The negative correlation between vole density and the quitting-harvest rate of Deer Mice suggests a competitive interaction between these species. Yet many other studies have rejected competitive coexistence between voles and mice (e.g. Grant 1972; Morris 1983, 1996; Wolff & Dueser 1986; Barry, Heft & Baummer 1990). Our use of artificial foraging patches may have presented an unnatural medium for competition between these apparent non-competitors.

Although Red-Backed Voles harvest few millet seeds, they may consume enough to significantly influence the energy state of Deer Mice. Captive Red-Backed Voles do little more than shallow digging in the foraging patches, collecting only the seeds near the surface of the sand. Captive voles abandon foraging patches at relatively high GUDs compared to Deer Mice held under identical conditions (mean GUD ± SE = 213·6 ± 10·3 and 18·0 ± 5·6 seeds patch^{-1}, respectively, n = 12 for each). When a patch is used by more than one species, the measured GUD is that of the species with the lower GUD. All foraging patches in the study were well dug through with all GUDs ≤80 seeds patch^{-1} indicating that the measured GUDs were those of Deer Mice. Note, however, that any patch use by voles will reduce the mean density of resources in the habitat thereby influencing quitting-harvest rates of Deer Mice. The magnitude of the effect should increase with vole density.

Alternatively, increases in vole density may have been associated, spuriously, with unmeasured factors that influenced the GUDs of Deer Mice. The correlated decrease in Deer Mouse GUDs may have been simply a response to temporal changes in resource density. It is also possible that Deer Mice became more efficient in the artificial foraging patches over time. We have no independent data to test these hypotheses, but it is crucial to reiterate that, regardless of any influence by voles or foraging experience, the quitting-harvest rates of Deer Mice were negatively density dependent.

We assumed that tracks left in tracking tubes represented foraging activity. The assumption seems reasonable because tracking tubes were placed adjacent to foraging patches. Yet it is possible that our estimates of *per capita* foraging activity were biased because our study populations were not closed. Our density estimates could not account for any Deer Mice that may have moved onto the plots while densities were supposed to be depressed by Deer Mouse removal. If immigrating mice did not have the unique toe-clip used to identify tracks, then our estimates of *per capita* activity were unbiased. It is possible, however, that some marked mice immigrated from nearby plots and inflated our estimates of *per capita* activity. Regardless, the possible immigration of mice onto the plots has no effect on our general interpretation of density-dependent foraging because, if anything, it would have made negatively density-dependent quitting-harvest rates even more difficult to detect.

Our confidence in density-dependent reduction in GUDs is bolstered by similar results in western Canada (Morris 1997, 2001). Mean GUD for Deer Mice foraging in millet-in-sand patches along transects crossing prairie–badland boundaries was negatively correlated with Deer Mouse density (Morris 1997). Density-dependent GUDs of Deer Mice in boreal forest confirm Morris's interpretation that the density-dependent GUDs reflected competition among prairie Deer Mice. The importance of competition is reflected in the rapid responses of Deer Mice to reduced density. Quitting-harvest rates increased in the boreal forest when competitors were removed for just 2 days. In western Canada, Deer Mouse GUDs increased when competitors were simply restrained from foraging (in live traps) for only a few hours (Morris 2001). At least two non-independent mechanisms can account for these rapid changes in foraging behaviour: (1) animals may recognize an improvement in habitat quality with reduced density (perhaps by using surrogate cues related to density) and (2) reduced density allows remaining individuals to forage more profitably, thereby increasing their energetic state and reducing the marginal value of energy. Regardless as to mechanism, it is dramatically clear that we must not underestimate the dominant influences of density on the behaviour of optimal foragers.

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