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EFFECT OF POPULATION DENSITY ON THE FORAGING EFFORT OF DEER MICE

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ABSTRACT

I investigated theoretically and experimentally the influence of population density on the foraging behaviour of individuals. An increased density of conspecifics may 1, reduce the benefit of foraging by increasing competition for resources (competition hypothesis) or 2, increase the costs of foraging by increasing the value of time spent on social activities (social benefits hypothesis). Both will reduce optimal foraging time. However, a reduction in the benefit 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. I tested for density dependence of the foraging behaviour of deer mice by assessing foraging activity and quitting-harvest rates at control and reduced population densities on four study plots in boreal forest in northwestern Ontario. I assessed quitting-harvest rates by measuring the giving-up densities of resources in artificial foraging patches. Tests of crucial assumptions supported the use of this technique for deer mice. Deer mice demonstrated a density-dependent decrease in both *per capita* foraging activity, as measured by tracking, and quitting-harvest rates. The results support the competition hypothesis. The density-dependent decrease in quitting-harvest rates may have important implications to the distribution and abundance of optimal foragers.

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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 factor that influences the benefit or costs of foraging will influence the optimal time that an animal should devote to foraging and, thereby, the harvest rate at which it quits foraging (quitting-harvest rate). Quitting-harvest rates of seed-eating rodents, for example, increase in the face of increased foraging costs arising from metabolic expenditures (Kotler et al. 1993a), predation risk (Brown et al. 1988, Kotler et al. 1988, 1991, 1993b, Hughes et al. 1994, Bouskila 1995), and missed opportunities of not foraging elsewhere (Brown et al. 1992b, 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. Yet, surprisingly, no one has yet tested for density dependence of quitting-harvest rates, nor has anyone examined the explicit processes by which population density influences foraging effort.

Increased density-dependent competition should reduce each individual's mean harvest rate thereby reducing the benefit of foraging relative to alternative activities (Mitchell et al. 1990). Consistent with this view, the foraging activity of some small mammals is clearly density dependent. *Per capita* foraging activity of gerbils (*Gerbillus allenbyi*, *G. pyramidum*, and *Gerbillurus tytonis*), as measured by sand-tracking, decreased at higher population densities in the Negev and Namib deserts (Abramsky and Pinshow 1989, Mitchell et al. 1990,

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Hughes et al. 1994).

Increased population density may also influence foraging activity by increasing the benefit of engaging in social activities. Animals may gain more fitness benefit from density-dependent social activities than they do from foraging. The rate of random encounters between conspecifics increases directly with population density (Mosimann 1958) and the rate of input to fitness from some social activities (e.g., courtships, matings, the value of defending one's territory) should increase with encounter rates.

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

I begin by exploring the possible density-dependent effects on the quitting-harvest rates of optimal foragers. I 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*) living in boreal forest in northwestern Ontario. I test the three assumptions required to use the GUD technique to estimate quitting-harvest rates. 1. The harvest rate in a foraging patch is an increasing function of the resource density in the patch. 2. The decision to quit foraging in a patch is based on the marginal harvest rate in that patch. 3. The quitting-harvest rate for

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a patch increases with the marginal harvest rate for the habitat. I differentiate between the "competition" and "social benefits" hypotheses by manipulating deer-mouse densities and measuring the respective GUDs. I conclude with a brief discussion of the implications of density-dependent harvest rates to the distribution and abundance of optimal foragers.

OPTIMAL FORAGING UNDER INCREASED POPULATION DENSITY

The Model

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,

$$f(n)v = VC + (\partial G/\partial t_a)/(\partial G/\partial x_1) \qquad (1)$$

where the left-hand side is the rate of resource harvest as an increasing function of the available resource density, 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, eq. 9, a derivation of eq. 1 is given in the appendix). The last term in eq. 1 is the marginal benefit, converted to an energy currency, of engaging in alternative non-foraging activities. Alternative activities are considered together as a missed opportunity cost of foraging (MOC, 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

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emerges from eq. 1. The marginal benefit of foraging (left-hand side of eq. 1) decreases with foraging time as available resource density declines while the marginal costs of foraging (right-hand side of eq. 1) increase. Marginal costs increase with foraging time for two reasons. 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). The marginal benefit and costs in eq. 1 eventually equalize at which time the animal quits foraging in favour of alternative activities.

The effect of population density on quitting-harvest rates and foraging activity

The effect of increased population density on the optimal quitting-harvest rate depends on how population density influences the marginal benefit and marginal costs of foraging. If increased population density reduces either the marginal benefit or the marginal costs, then eq. 1 is satisfied at a lower harvest rate. If the marginal benefit or costs are increased, then eq. 1 is satisfied at a higher harvest rate.

An increased number of competitors may increase the depletion rate of the resources in the habitat (the competition hypothesis, Fig. 1A). Assuming that harvest rate declines with mean resource density in the habitat, increased population density will reduce harvest rate. In addition, the reduced energetic state of the forager reduces its MOC. Thus, increased competition reduces both the marginal benefit and the marginal costs of foraging, thereby reducing the quitting-harvest rate. Note that any change in optimal foraging time with

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Figure 1. The competition hypothesis for density-dependent quitting-harvest rates of optimal foragers. Energy-intake rate [$f(n)v$] decreases with foraging time as resource density, 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). Competition increases the depletion rate of resources thereby reducing an individual's energy-intake rate and energetic state at any given foraging time. A. MOC decreases for individuals experiencing diminishing returns to fitness in energy. B. MOC increases for animals experiencing accelerating returns to fitness in energy. C. MOC remains constant for individuals experiencing linear returns to fitness in energy. For animals that experience accelerating returns to fitness (B), the net effect of competition on quitting-harvest rates depends on the relative magnitudes of changes in the marginal benefit and costs of foraging. Otherwise, competition reduces optimal quitting-harvest rate. Curvilinear functions would yield qualitatively similar conclusions.

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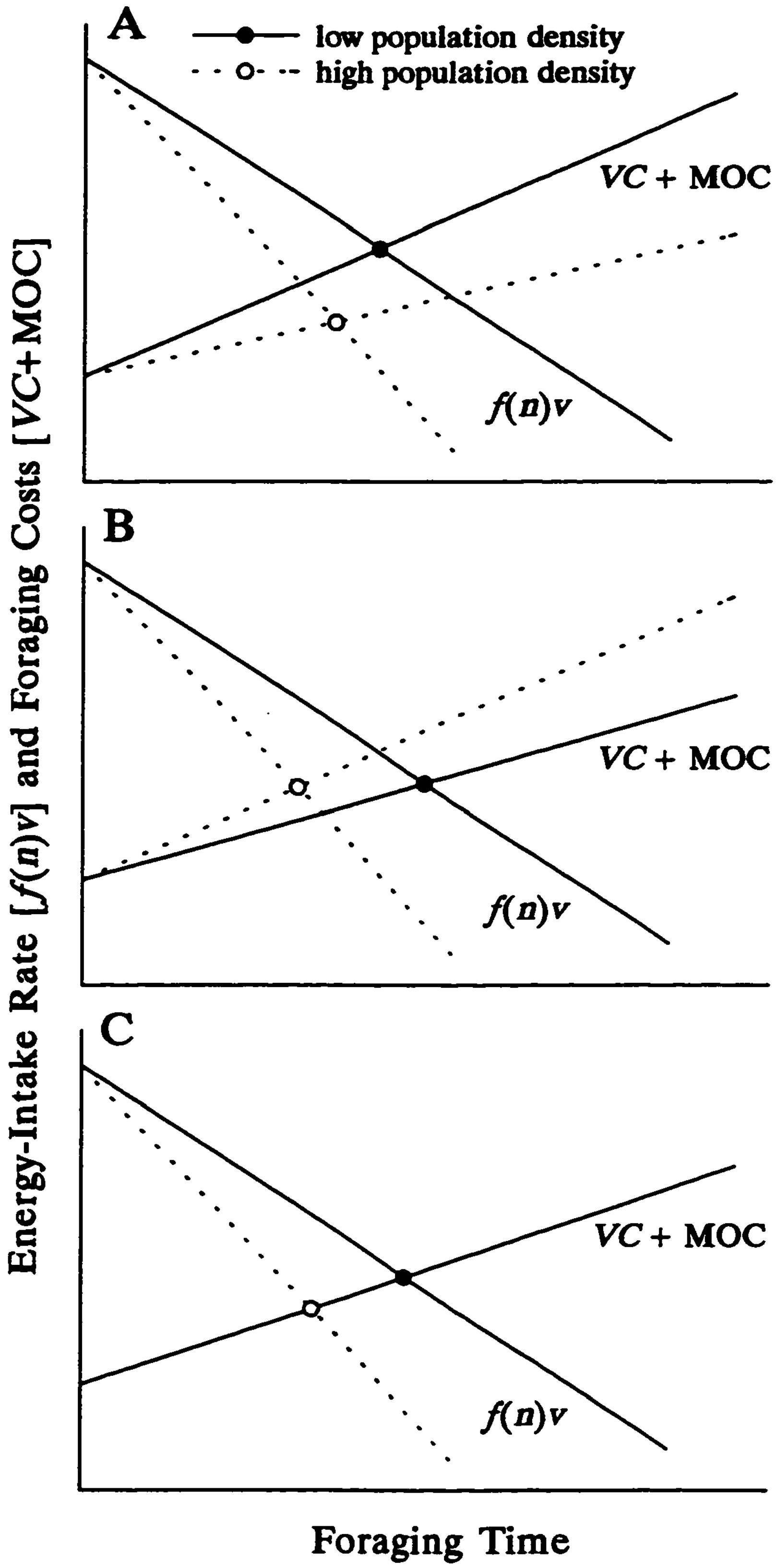

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increased competition depends on the relative reductions in the marginal benefit and costs (Fig. 1A). Because the energetic cost, *VC*, is unaffected by exploitation competition and sets a lower, positive bound on the marginal costs of foraging, increased competition will often reduce the marginal energy-intake rate more than the marginal costs (Mitchell et al. 1990). At the population scale quitting-harvest rate will decline even though foraging time is reduced (Fig. 1A).

The competition hypothesis is complicated if energy starved animals experience accelerating returns to fitness in energy (i.e., $\partial G/\partial x_1$ increases with x_1, Caraco et al. 1980). Increased competition, then, decreases the marginal value of energy thereby increasing MOC (Fig. 1B). The net density-dependent effect on quitting-harvest rate depends on the relative magnitudes of change in the marginal benefit and costs. The paradox of whether MOC should increase or decrease disappears if animals experience linear returns to fitness in energy. The marginal foraging costs, then, are independent of competition and quitting-harvest rate decreases with increased population density (Fig. 1C).

The social benefits hypothesis makes the contrary prediction that quitting-harvest rates should increase with population density (Fig. 2). Increased population density increases the value assigned to alternative activities such as finding or attracting mates, territorial defence, or other social interactions. The increased MOC will increase quitting-harvest rate (eq. 1). Note that the increase in quitting-harvest rate occurs with reduced foraging time (Fig. 2).

The two hypotheses are not mutually exclusive. Both predict a density-dependent decrease in the optimal foraging time (i.e., individuals should reduce foraging activity at increased population densities). The density-dependent change in the quitting-harvest rate

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Figure 2. The social benefits hypothesis for density-dependent quitting-harvest rates of optimal foragers. The increased value of engaging in social activities increases the missed opportunity costs of foraging (MOC) at higher population density. Quitting-harvest rate increases with increased population density. Curvilinear functions would yield qualitatively similar conclusions.

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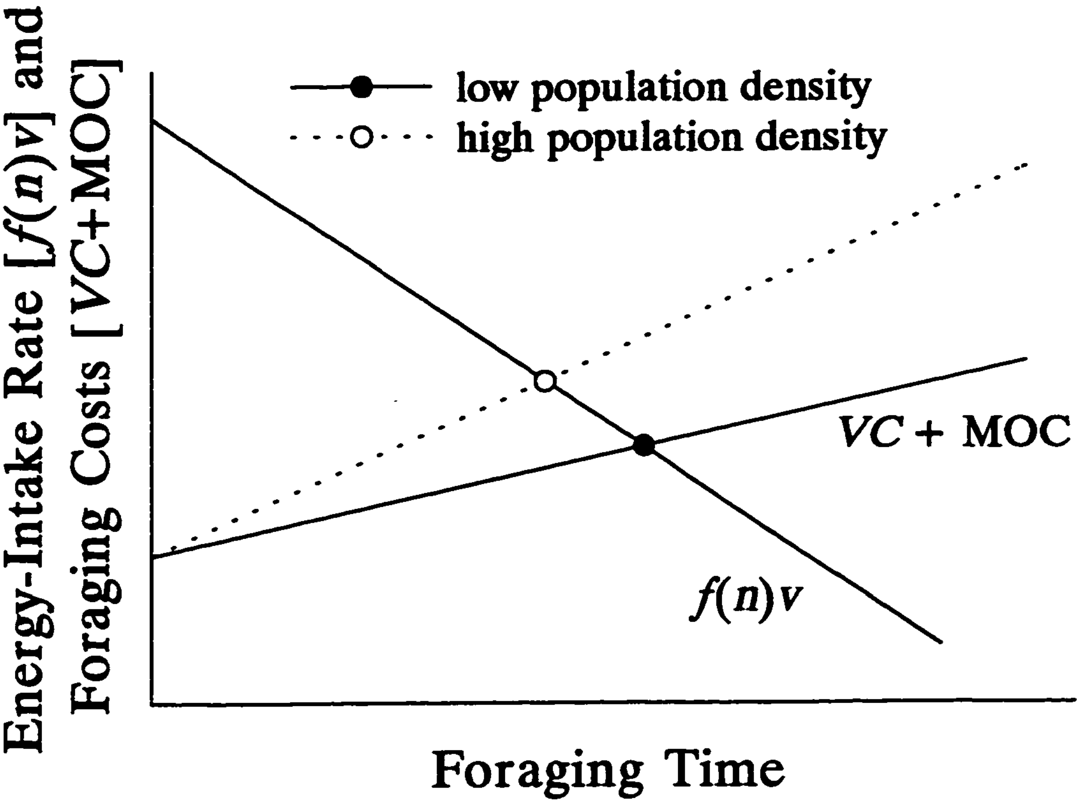

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depends only on the relative magnitudes of change in the marginal benefit and costs of foraging. While it would be interesting to evaluate the density dependence of both the benefit and costs of foraging, any population consequences depend on the net effect of density on quitting-harvest rates. A density-dependent reduction in quitting-harvest rate will always signify density-dependent competition for resources. The net result of any positive and negative density-dependent effects on quitting-harvest rates can be measured by manipulating population density and measuring the giving-up densities of resources in identical foraging patches.

Energy maximizers versus time minimizers

The foraging model represented by eq. 1 assumes that animals are "energy maximizers" (Schoener 1971). An energy maximizer always realises a fitness benefit from additional energy intake and quits foraging only when the costs equal this benefit (eq. 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. I can, however, differentiate between the two foraging goals from the density-dependent effect 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 at higher population densities (Fig. 1 and 2, Mitchell et al. 1990).

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METHODS

Study area and small mammal census

In July and August 1995, I measured the activity level and giving-up densities of deer mice under control and density-reduced conditions in boreal forest in northwestern Ontario. I established four study plots each consisting of 16 stations (4×4 grid) at 20-m intervals in a 30-ha stand of trembling aspen (*Populus tremuloides*) with a dense understorey of mountain maple (*Acer spicatum*) and beaked hazel (*Corylus cornuta*). Deer mice, red-backed voles (*Clethrionomys gapperi*), and yellownose voles (*Microtus chrotorrhinus*) 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 et al. 1976). Also present, but in low numbers, were woodland jumping mice (*Napaeozapus insignis*), meadow jumping mice (*Zapus hudsonius*), and mountain phenacomys (*Phenacomys intermedius*).

I estimated and manipulated deer-mouse density by live-trapping. I trapped each plot with a minimum of four bi-weekly trapping rounds before the start of the experiment and one trapping round six to ten days after the end of the experiment. A trapping round lasted two consecutive nights during which time three Tomahawk live-traps, baited with crushed oats, a slice of potato, and cotton nesting, were set at each station on a plot. Traps were checked each morning and the intervening evening. Each captured animal was identified to species and individually marked with a numbered eartag before being released at its point of capture. All captured deer mice were given the same unique toe clip to aid in identifying tracks for activity estimates (see below). Most deer mice on the plots had the unique toe-clip prior to activity measurements.

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Density-reduction experiments

I conducted six experimental trials to test for the effect of population density on foraging activity by deer mice and their quitting-harvest rates. I manipulated deer-mouse density in each trial by removing (and subsequently replacing) animals from a study plot. I estimated the foraging activity and quitting-harvest rate at both the high (control round, no animals removed) and low (density-reduction round) population densities. I conducted one experimental trial on each of the four plots (simultaneous trials on plots 1 and 2 followed by simultaneous trials on plots 3 and 4). I then conducted a second trial on each of plots 1 and 2 beginning nine days after the end of the first trial. The density reduction treatment was applied before control estimates in three trials and after control estimates in the other three trials.

Critics may be concerned that data from trials conducted on the same plot will not be independent. The problem of correlated responses is reduced in my design for three reasons. 1. Trials were separated in time. 2. A different set of individuals was removed from the plot in each trial. 3. There is no *a priori* reason to expect, at the scale of my study sites, that the functional relationship between density and quitting-harvest rates should vary among plots.

As a relative measure of the quitting-harvest rate, I measured GUDs in artificial foraging patches. A patch was a one-litre cardboard milk carton containing 2.0 g of pre-screened, unhusked millet seed (>2-mm diameter, mean mass = 7.3 mg·seed^{-1}) mixed into approximately 300 ml of screened sand (grain size < 0.5 mm). Deer mice readily dug to the full depth of the sand (~2 cm) making all seeds in a patch accessible. A 3-cm × 7-cm opening at one end of each carton served as an entrance to the patch. The number of millet seeds

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remaining in a patch after a night's foraging provided a measure of GUD. [In some experiments (see Experiments to test assumptions), I weighed the remaining millet; however, due to low GUDs, counting seeds proved to be an efficient method of determining GUDs in the field.] 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).

I did not attempt to prevent other small-mammal species from using the foraging patches. Captive red-backed voles, the second most abundant species on the study plots, 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±S.E.=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.

I estimated foraging activity of deer mice for two reasons; 1, to test for density dependence in the *per capita* foraging activity of deer mice and 2, to provide statistical control of deer-mouse activity at foraging patches when testing for an effect of population density on GUDs. A density-dependent reduction in GUDs could result from increased numbers of individuals visiting each patch at higher population densities. To see this, imagine

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that a patch has been exploited and abandoned at the optimal GUD. If each new visitor must sample the patch before rejecting it, then the measured GUD will decline as the number of visitors increases.

I based my estimate of foraging activity on rodent tracks accumulated overnight in 40-mm diameter x 30-cm plastic tubes. Each tube contained a 5-cm x 28-cm piece of paper with an ink blot (carbon powder mixed with mineral oil) in the centre (van Apeldoorn et al. 1993). An animal travelling through the tube in either direction leaves a set of ink tracks on the paper. The unique toe-clip given to all deer mice allowed me to distinguish their tracks from the similar tracks of other species present on the study plots. I estimated deer mouse activity at a tube as an activity score equal to the number of deer-mouse tracks left on the paper after a night's foraging.

Each experimental trial consisted of two trapping rounds spaced seven to nine days apart on the same plot. During one of the trapping rounds, I removed from the plot, and placed in holding cages, approximately half the deer-mouse population (no more than one individual was removed from any single station). No animals were removed during the control round. I estimated the population density of deer mice and voles for each plot and trapping round as the minimum number of animals known to be alive (MNA, Hilborn et al. 1976).

Jolly-Seber estimates of population size may be more accurate than MNA for open populations (Efford 1992), but MNA is comparable to Jolly-Seber estimates when trappability of animals is high (Efford 1992). My trapping effort per trapping round (48 traps x 2 nights per 0.36 ha study plot) effected a high trappability for deer mice and voles (on average, 92.6

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percent of animals known alive were captured during a trapping round, S.E.=1.71, N=12)

I measured the activity and GUD of deer mice at each station for two nights following each trapping round. At dusk, I placed one foraging patch at each station along with one tracking tube in line with and within 10 cm of the foraging patch entrance. I collected all patches and tubes the following morning. Activity scores and GUDs at each station were averaged over the two nights. I released all removed animals at their original capture points after the second night of measuring activity and GUD.

Experiments to test assumptions

Do harvest rates decline with resource density in a foraging patch?

I tested the assumption that harvest rate declines as a deer mouse reduces the amount of millet in an artificial foraging patch by monitoring foraging time and millet harvest of eight captive deer mice. Deer mice were housed in individual compartments (60 cm x 60 cm in area x 30 cm high) of two wooden observation arenas with hardware-cloth lids. Each compartment contained a substrate of wood chips and a nesting box with cotton nesting. I placed one foraging patch (top removed) containing 2.0 g of millet in each compartment each night during a minimum three-day acclimation period. I provided all animals with pelletized mouse food and water *ad libitum* throughout the experiment.

I observed foraging animals at night under two 40-W red lights. I assigned to each animal a random order of foraging times ranging from three to 36 minutes in intervals of three or five minutes. I monitored the cumulative time spent by an animal foraging in a patch and at the predetermined foraging time, or when the animal had quit foraging for more than ~45

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minutes, I removed the patch from the compartment. An observation included the foraging time and the mass (to the nearest 0.01 g) of millet harvested (2.0 g - mass of millet remaining in the patch). I recorded 26 observations on two animals in December 1994, and 55 observations on six animals in September 1995.

Is the deer-mouse patch-leaving rule based on harvest rate?

Foraging deer mice could use any of several different patch-leaving rules. Using GUDs to assess quitting-harvest rates carries the assumption that a forager's decision to abandon a patch is based on its marginal harvest rate in that patch. Animals could, however, choose to forage for a fixed time in each patch or harvest a fixed amount of resources from each patch. Each of these strategies can represent an optimal patch-leaving rule (Iwasa et al. 1981, McNair 1983). I tested among these three alternative strategies 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 and Brown 1989).

I established six foraging stations (2×3 grid) located at 60-m intervals in the same aspen stand used for density reduction experiments. On each of six consecutive nights in August 1994, I placed four foraging patches of equal initial millet density at the corners of a 10-m x 10-m square centred at each station. I assigned the six levels of initial millet density to the six stations and six nights using a Latin square design (Tabachnick and Fidell 1989). I collected all foraging patches each morning. The remaining millet in each patch was

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recovered and weighed to the nearest 0.01 g.

As a further test that the decision to abandon a foraging patch is based on harvest rate, I measured GUDs in adjacent patches each containing a different substrate (fine sand, grain size < 0.5mm, or coarse sand, 1.0mm < grain size < 1.4mm). I screened the fine and coarse sand from the same stock so that only grain size differed between the two substrates. A forager's search rate should, at least in part, depend on the substrate in the patch (Hughes et al. 1995, Ziv et al.1995, Price and Heinz 1984). GUDs will differ between foraging patches having different search rates if both patches are abandoned at the same quitting-harvest rate. Thus, GUD should vary with the substrate in a patch (Brown 1988).

I tested my assumption that search rate differs between fine and coarse sand by monitoring foraging time and the amount of millet harvested by deer mice foraging in each substrate. Of the 55 observations on the six deer mice recorded in 1995, 26 were on animals foraging in fine sand and 29 were on animals foraging in coarse sand. I randomly assigned fine or coarse sand to each observation. All animals were observed in both substrates.

Does quitting-harvest rate in a foraging patch increase with the marginal harvest rate for the habitat?

I tested the assumption that the quitting-harvest rate in a foraging patch increases with the marginal harvest rate for the habitat by measuring GUDs with and without habitat resource augmentation. I placed two foraging patches 60 cm apart at each of eight stations on each of the four study plots for one night in September 1995. One foraging patch at each station contained fine sand and the other contained coarse sand. I randomly selected one half of the

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stations for resource augmentation. Four stations were augmented on each plot. Control stations were located a minimum of 60 m from the nearest augmented station. I scattered 40 g of millet seed within a 1-m radius surrounding the patches at augmented stations. The remaining millet was recovered from each patch the following morning and the number of seeds counted. I reversed the augmentation (control stations became treatment stations and vice versa) three nights later and again measured GUDs in fine and coarse sand.

Statistical Analyses

All statistical analyses were performed using SPSS software (v. 6.1, SPSS Inc., Chicago). When necessary to stabilize variance and normalize the data, GUDs were transformed to natural logarithms.

Density-reduction experiments

I calculated *per capita* activity for each round by dividing the total activity score from all stations by the minimum number of deer mice known alive on the plot. I tested for a significant relationship between foraging activity and population density by regressing per capita activity on deer-mouse density.

To test for a difference in GUDs between the control and density-reduction treatments, I treated stations as subjects in a paired *t*-test for each trial. Separate tests were necessary because the actual treatments (numbers or proportions of animals removed) varied among the trials.

I then pooled the data from all six trials in a hierarchical multiple regression

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(Tabachnick and Fidell 1989) to control statistically for vole density and deer-mouse activity while testing for an effect of deer-mouse density on GUD. Mean GUD from all stations following each trapping round (*N*=12) served as the dependent variable. I calculated vole density as the sum of MNA for red-backed and yellownose voles, and total activity score as the sum of deer-mouse tracks at all stations. I forced vole density and total activity score in the regression prior to the entry of deer-mouse density to remove variance in mean GUD accounted for by variance in vole density and activity. A significant increase in R^2 for deer-mouse density would thereby indicate that, when vole density is accounted for, deer-mouse density has a significant effect on GUD that is not mediated by any linear relationship with activity.

Diminishing returns in foraging patches

I tested for a diminishing harvest rate in foraging patches using polynomial regression (Neter et al. 1989) of the mass of millet harvested on foraging time. A significant and negative quadratic term would verify that harvest increased at a slower rate as foraging time increased.

Patch-leaving rule

I used polynomial contrasts in repeated measures ANOVAs (Norušis 1994) to test for differences in the proportion of millet harvested and GUD with increasing initial millet density in a foraging patch. I treated each of the six stations as a subject. GUD and the proportion of millet harvested for each station and night were averaged over the four patches. The proportion of millet harvested was square-root-arcsine transformed prior to analysis.

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I tested for a difference in GUDs between the two foraging substrates using a repeated measures ANOVA (Norušis 1994). Each station was treated as a subject in the analysis with substrate entered as a within-subjects factor. I tested for an effect of substrate on search rate by entering an indicator variable for substrate into the regression model for millet harvested versus foraging time.

Effect of the marginal harvest rate in the habitat

I tested for an effect of resource augmentation on GUDs by entering augmentation treatment as a second within-subjects factor in the repeated measures ANOVA (along with substrate). Study plot was entered as a between-subjects factor to remove variance in GUD associated with differences among plots (e.g., population density, resource levels, predation risk).

RESULTS

Experiments to test assumptions

Harvest rate declined as a forager depleted the resources in a patch

Of the eight animals observed, only one consistently consumed the millet seeds while in the patch. The harvest rate for this individual was notably low compared to the other seven animals that cached seeds (Fig. 3). I excluded the data for this animal from the analysis. 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. 3). 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.

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Figure 3. 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 cached seeds.

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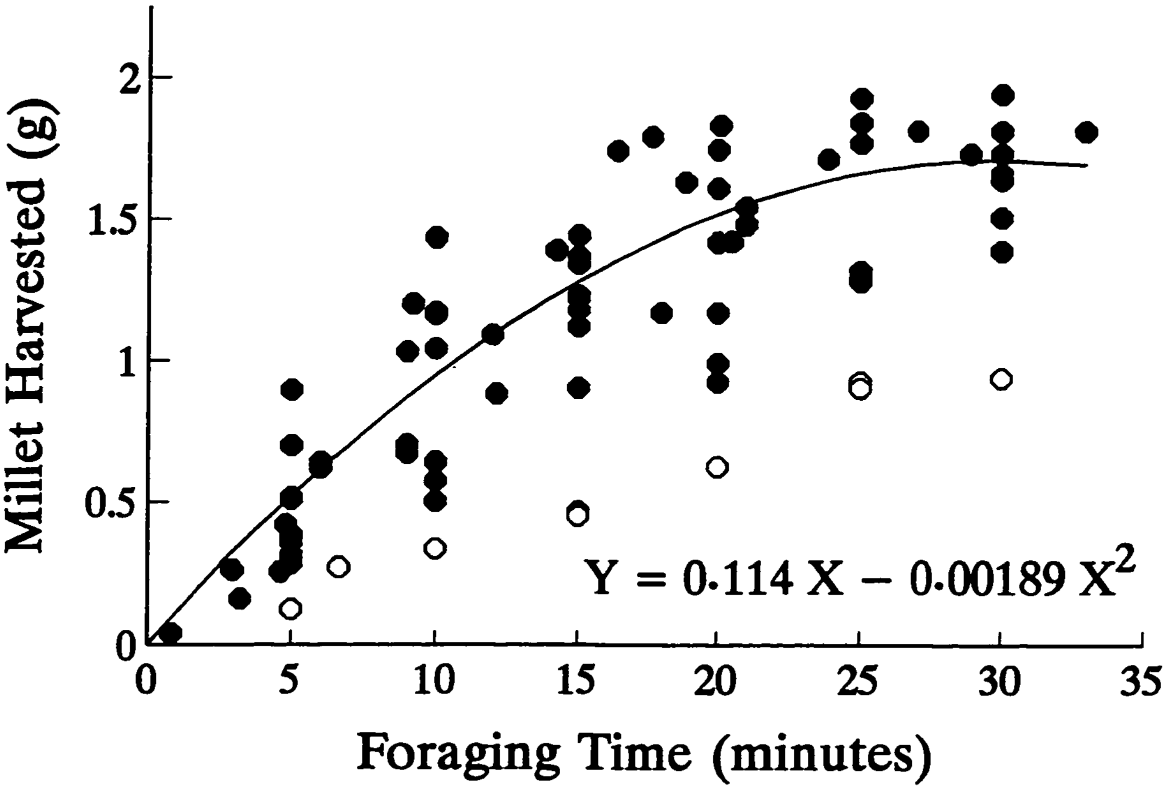

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The patch-leaving rule for deer mice appeared to be based on harvest rate

Mean GUD increased significantly with initial millet density (Fig. 4A, Table 1). Patches initially containing 32 g of millet were abandoned at relatively high millet densities with high variance (Fig. 4A) suggesting that some animals were satiated at this level of resource. These data were not included in the analyses. The increase in GUD with initial millet density for the remaining patches indicates that patches were abandoned at higher harvest rates as initial millet density increased. 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 increased with the initial millet density in patches because all patches at any one station contained the same initial millet density. 2. The increase in GUD with initial millet density could also mean that deer mice use a Bayesian foraging strategy that underestimates the resource level in rich patches while overestimating the resource level in poor patches (Valone and Brown 1989). Bayesian foragers will, like these deer mice, have higher GUDs in rich than they do in poor patches (Valone and Brown 1989).

The proportion of millet harvested also increased significantly with initial millet density but followed a more complex pattern ($P \leq 0.01$ for all polynomial contrasts, 32 g treatment excluded, Table 1, Fig. 4B). 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 is bound by an upper limit of one. The significant higher-order terms are likely a consequence of the flattening of the curve as the asymptote is approached. The salient point, however, is that the

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Figure 4. 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.

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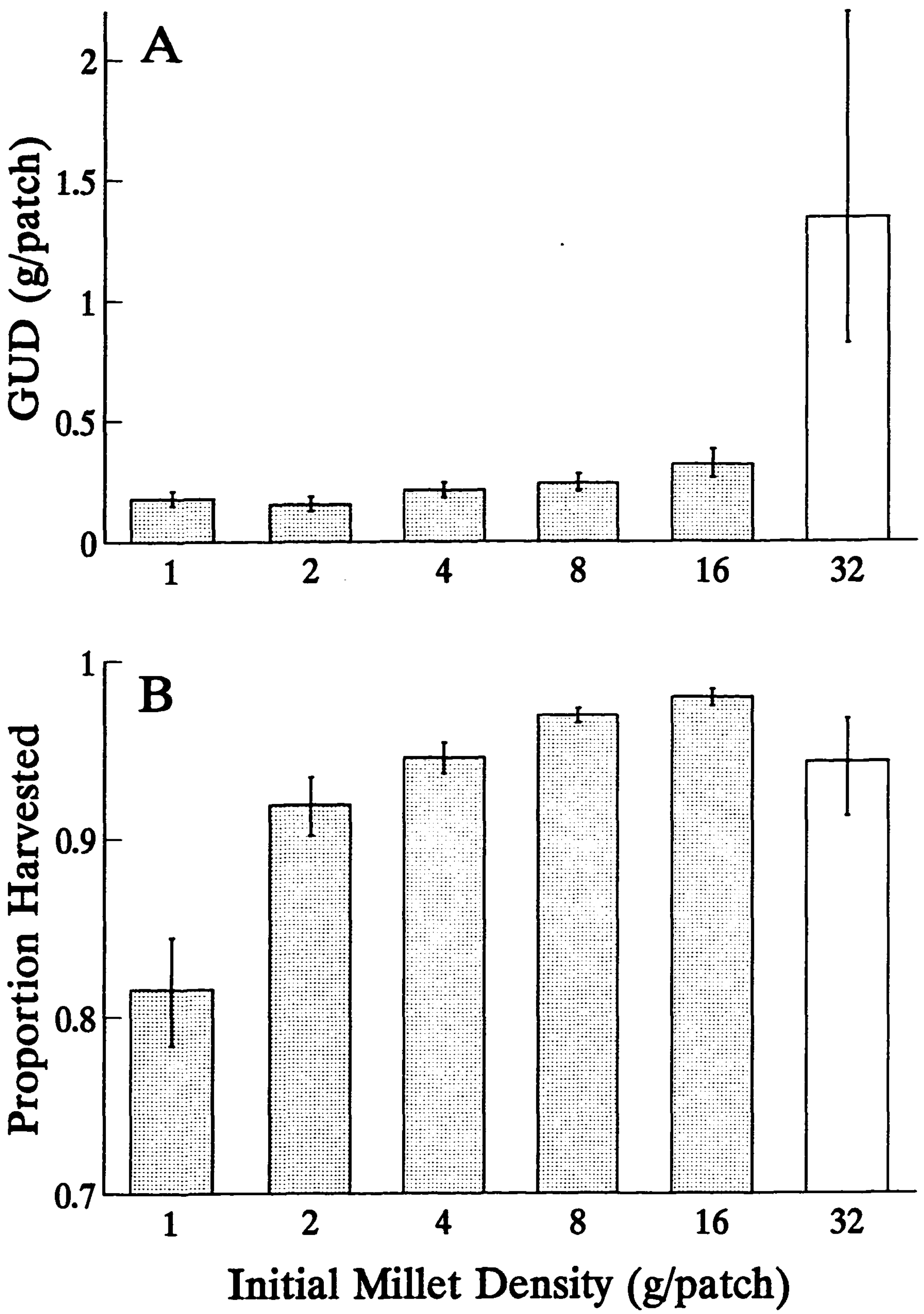

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Table 1. The effect of initial millet density in a foraging patch on giving-up density ($\log_e$ transformed) and on the proportion of millet harvested (square-root-arcsine transformed) by deer mice foraging in boreal forest in northwestern Ontario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

Giving-up density

Source	df	*F*	*P*
Constant	1,5	1990.41	<0.001
Polynomial contrasts			
linear component	1,5	7.83	0.04
quadratic component	1,5	0.59	0.48
cubic component	1,5	0.01	0.91
fourth power component	1,5	2.57	0.17

Proportion of millet harvested

Source	df	*F*	*P*
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

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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.

Mean GUDs were significantly higher in fine than in coarse sand (13.4 and 10.3 seeds·patch^{-1} respectively, Fig. 5, 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 I re-analysed the data excluding these outliers; no other terms changed in significance.

Higher GUDs in fine sand are consistent with a lower search rate in fine compared to coarse sand. I did not detect, however, a significant effect of substrate on search rate. The addition of an indicator variable for substrate into the quadratic model for millet harvested versus foraging time did not significantly improve the model (R^2 change=0.01, P=0.31; repeating the analysis using only data from 1995 when all animals were observed in both substrates yielded similar results).

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 compared to coarse sand. Deer mice may, therefore, 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.

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Figure 5. 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.

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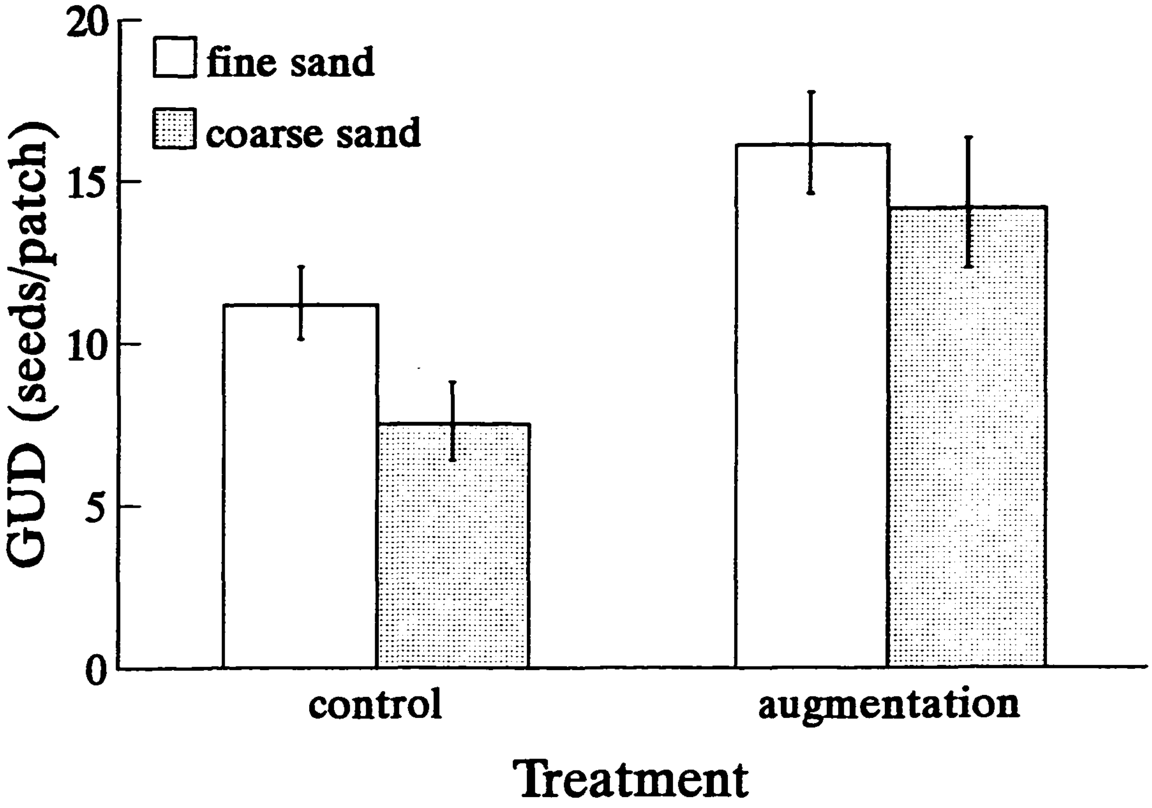

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Table 2. Summary of repeated measures ANOVA on giving-up densities ($\log_e$ transformed) for deer mice foraging in artificial resource patches containing fine and coarse sand substrate, with and without resource augmentation (32 stations on four study plots).

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
Augmentation × Plot	3,28	0.05	0.98
Substrate × Plot	3,28	3.11	0.04
Augmentation × Substrate	1,28	1.52	0.23
Augmentation × Substrate × Plot	3,28	0.13	0.94

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Quitting-harvest rates in patches increased with the marginal harvest rate for the habitat

Mean GUDs were significantly higher with resource augmentation than without (15.1 and 9.1 seeds·patch^{-1} respectively, Fig. 5, Table 2). 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 predation risk, level of resources, or other factors that influence GUDs.

Density-reduction experiments

Population reduction treatments reduced deer-mouse density by up to 70 percent compared to controls

The observed reduction in deer-mouse density relative to controls ranged from 0 to 70 percent among the six trials (Table 3). Deviations from the attempted 50 percent reduction were caused mainly by natural changes in the population densities between control and density reduction trapping rounds. In trial 3, the increase in the number of deer mice on the plot (caused by the emergence of juveniles) was equal to the number of animals removed during the density reduction treatment. 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 (Fig. 6). Deer mice decreased their foraging activity as population

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Table 3. Population densities (MNA) of deer mice in control and density-reduction treatments for six experimental trials. One half of all density reductions were conducted during the first census (trials 2, 4, 6). The other half were conducted 7–9 days later during the second census.

Trial	MNA		Percent reduction in MNA
	Control	Treatment	
1	29	19	34.5
2	22	14	36.4
3	9	9	0
4	23	7	69.6
5	33	14	57.6
6	18	7	61.1

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Figure 6. *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.

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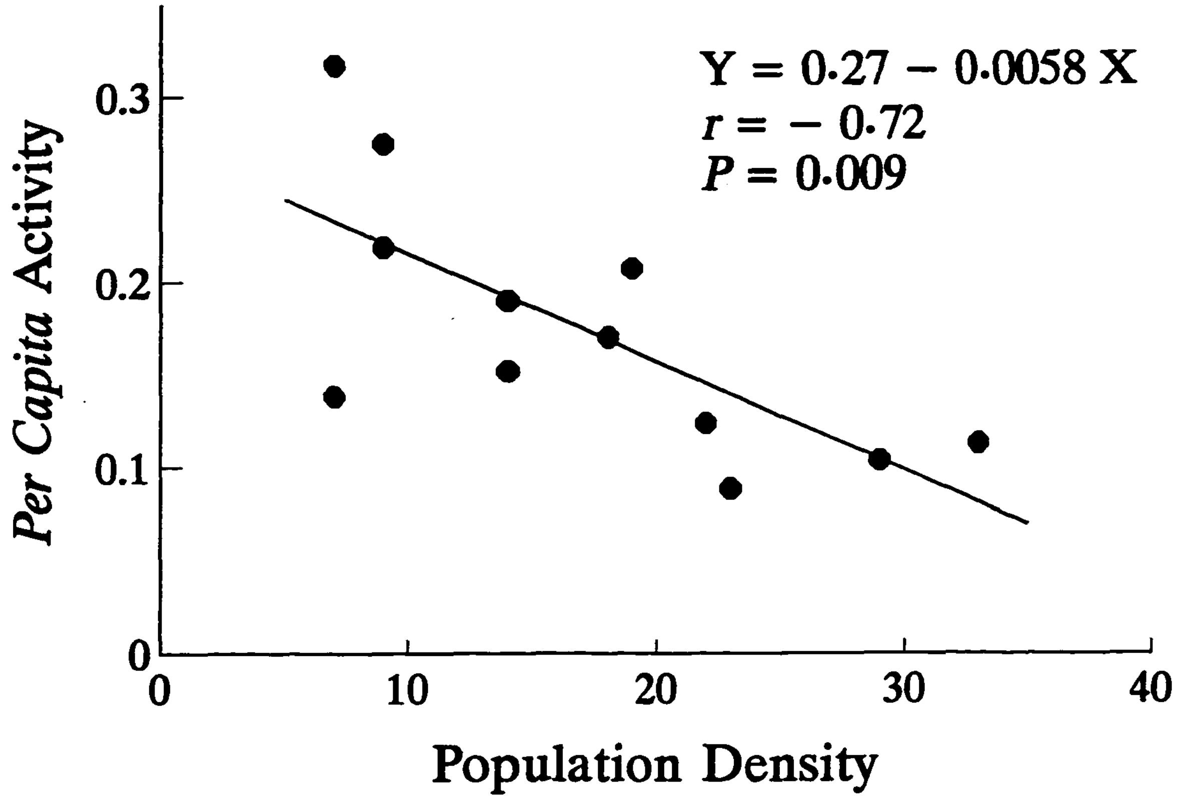

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density increased. The result is inconsistent with the hypothesis that deer mice are time minimizers.

Density-reduction treatments resulted in higher giving-up densities compared to controls

In four trials, mean GUD was higher in deer-mouse density-reduction treatments than in controls (P=0.005, 0.06, 0.04, 0.001 respectively; Fig. 7). As expected, there was virtually no difference in mean GUD in trial 3 (P=0.97, Fig. 7) 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). This may have been caused by a relatively large increase in vole density between control and treatment rounds in trial 5 compare to the other trials. Nonetheless, the density-reduction treatments tended to increased GUDs for foraging deer mice.

Quitting-harvest rates declined with increased deer-mouse density

The higher GUDs in density-reduction treatments compared to controls may have been caused by decreased deer-mouse density, activity, or vole density. Mean GUD on a plot was negatively correlated with total activity score (r=-0.56, n=12, P=0.06) and vole density (r=-0.58, n=12, P=0.05). Total activity score was positively correlated with deer-mouse density (r=0.66, n=12, P=0.02). When vole density and activity were controlled for in a hierarchical regression, deer-mouse density had a significant and negative effect on the mean GUD on a plot (mean GUD = 52.2 - 0.77 vole density - 0.10 total activity score - 0.63

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Figure 7. 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 percent 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).

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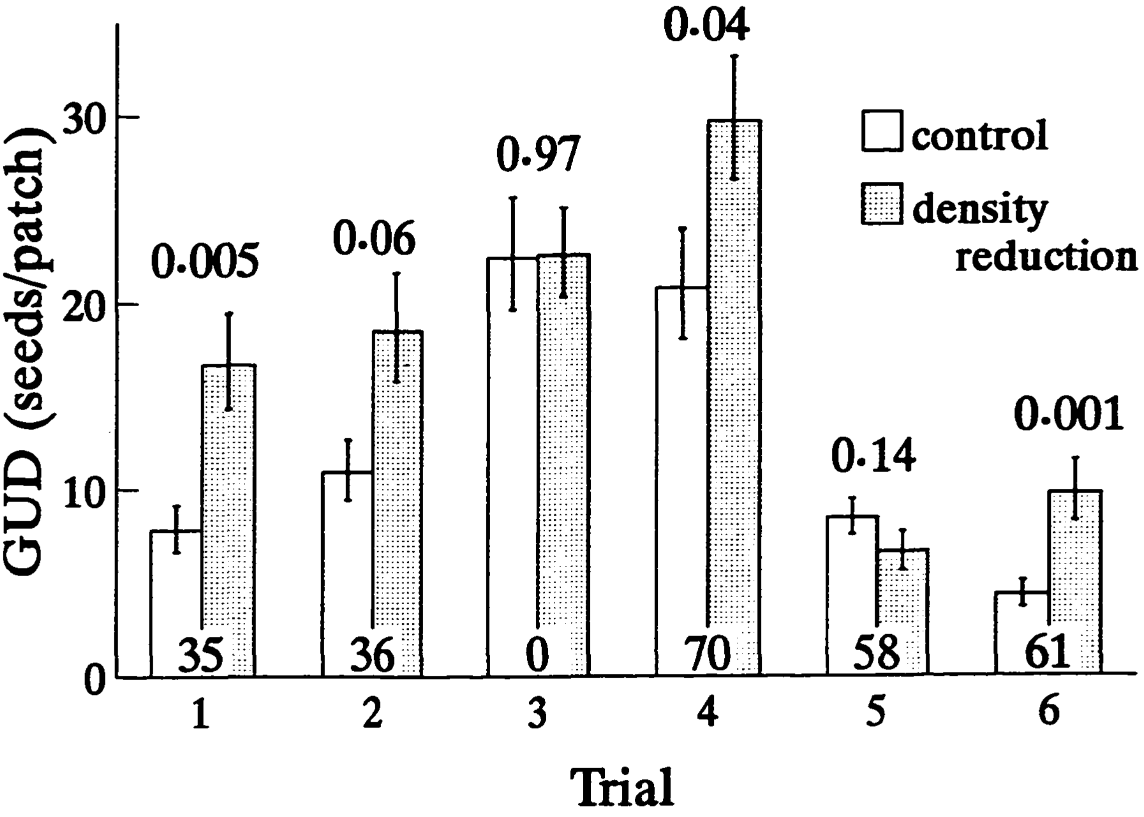

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deer-mouse density, $R^2=0.83$, $F_{3,8}=13.4$, $P=0.002$, Table 4). The decrease in GUD with increased deer-mouse density cannot be attributed solely to an increase in the deer-mouse activity at foraging patches. Quitting-harvest rates for deer mice were negatively density dependent.

DISCUSSION

Deer-mouse foraging is markedly density dependent. *Per capita* foraging activity 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 I 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. I suspect that the density-dependent reductions in the foraging activity of gerbils (Abramsky and Pinshow 1989, Mitchell et al. 1990, Hughes et al. 1994) also reflect density-dependent competition for resources.

The competition hypothesis is also supported by the well documented effect of interspecific competition on foraging behaviour (eg. Abramsky and 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 interpret vole/deer mouse coexistence to be non-competitive (e.g., Grant 1972, Morris 1983, 1996, Wolff and Dueser 1986, Barry et al. 1990). My use of artificial foraging patches may have presented an unnatural medium for competition

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Table 4. Summary of hierarchical regression analysis of mean giving-up density on a plot versus 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).

Step	Variable entered	R^2 change	df	*F*	*P*
1	Vole density	0.34	1,10	5.13	0.05
2	Activity score	0.31	1,9	8.08	0.02
3	Mouse density	0.18	1,8	8.84	0.02
Model		0.83	3,8	13.4	0.002

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between these apparently non-competitive species. Although red-backed voles harvest few seeds, they may consume enough to significantly influence the energy state of deer mice. Alternatively, vole density, which increased over time, may have been associated with unmeasured factors that influenced the GUDs of deer mice. The correlated decrease in deer-mouse GUDs may simply have been a response to temporal changes in habitat resource densities. It is also possible that deer mice became more efficient in the artificial foraging patches over time. I have no independent data to test these hypotheses, but it is crucial to reiterate that, regardless of any influence by voles, the quitting-harvest rates of deer mice were negatively density dependent.

I assumed that tracks left in tracking tubes represented foraging activity. This seems reasonable because tracking tubes were placed adjacent to foraging patches. A possible complication lies in the determination of *per capita* foraging activity. The populations on the study plots were not 'closed'. My density estimates would not have accounted for any deer mice that may have moved onto the plots while densities were supposed to have been depressed by the density-reduction treatment. If immigrating mice did not have the unique toe-clip used to identify tracks, then my estimates of *per capita* activity were unbiased. It is possible, however, that some marked mice immigrated from nearby plots and inflated my estimates of *per capita* activity. Thus, underestimation of depressed population densities may have accounted for a proportion of the observed density-dependent reduction in *per capita* foraging activity. Regardless, the possible immigration of mice onto the plots has no effect on my general interpretation of density-dependent foraging because, if anything, it would have made negatively density-dependent quitting-harvest rates even more difficult to detect.

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The reduction in GUDs with increased population density is consistent with the results of Morris (1997). Mean GUD for deer mice foraging in millet-in-sand patches along transects crossing prairie-badland boundaries in western Canada was negatively correlated with deer-mouse density on the transect (Morris 1997). Density-dependent GUDs of deer mice in the boreal forest confirm Morris' interpretation that the density-dependent GUDs reflected competition among prairie deer mice. We now see, for deer mice in the boreal forest, that the density-dependent reduction in GUD is apparently caused by a reduction in the energetic state of individuals.

Very importantly, the density-dependence in GUD reported by Morris (1997) disappeared at the foraging scale of deer mice (within transects) even though density varied. The lack of density-dependence of GUD at the foraging scale is consistent with the hypothesis that density-dependent habitat selection equalizes individuals' energetic profits among habitats (Morris 1997). Thus, the deer-mouse studies, and those on gerbils and other foragers (e.g., Brown 1989, Abramsky and Pinshow 1989, Brown et al. 1992a, 1994, Kotler et al. 1993, Hughes et al. 1994, Ziv et al. 1995), demonstrate an impressive ability to use optimally behaving individuals to understand their emergent effects on distribution and abundance.

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APPENDIX

I present here a brief derivation of the optimal foraging model proposed by Mitchell et al. (1990) following Brown (1988). I refer the reader to Mitchell et al. (1990) for details.

Let x_l and x_a represent the inputs to fitness from foraging and alternative activities respectively. x_l is the energy state of the forager and is a function of time spent foraging, t_f. x_a is a function of time spent engaged in alternative activities, t_a. Fitness is represented by a function of the inputs, $G[x_l(t_f),x_a(t_a)]$. Fitness is assumed to be a strictly increasing function of both inputs, i.e.,

$$\partial G/\partial x_l > 0 \ , \qquad \partial G/\partial x_a > 0$$

Finally, let T represent the total time that can be allocated among activities, i.e.,

$$t_f + t_a = T \tag{A1}$$

Under the constraint of (A1), $G[x_l(t_f),x_a(t_a)]$ is maximized when the following two equalities are met,

$$(\partial G/\partial x_l)(\partial x_l/\partial t_f) = \lambda \tag{A2}$$

$$(\partial G/\partial x_a)(\partial x_a/\partial t_a) = \lambda \tag{A3}$$

where λ is the Lagrangean multiplier (Ellis and Gulick 1991). Substituting (A3) into (A2) and rearranging gives,

$$\partial x_l/\partial t_f = (\partial G/\partial x_a)(\partial x_a/\partial t_a)/(\partial G/\partial x_l) \tag{A4}$$

The left-hand side of (A4) is the marginal net energy-intake rate. Assuming resource-harvest rate is an increasing function, f, of resource density, n, and letting v be the per unit energy value of the resource, the net energy-intake rate is given by,

$$\partial x_l/\partial t_f = f(n)v - VC \tag{A5}$$

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where VC is the energy expenditure per unit time spent foraging. Substituting (A5) into (A4) and rearranging gives the model,

$$f(n)v = VC + (\partial G/\partial t_a)/(\partial G/\partial x_1)$$

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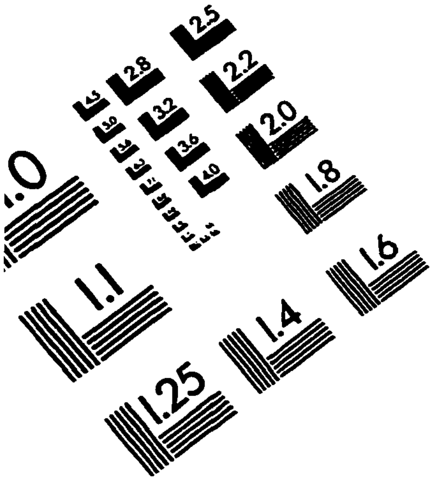

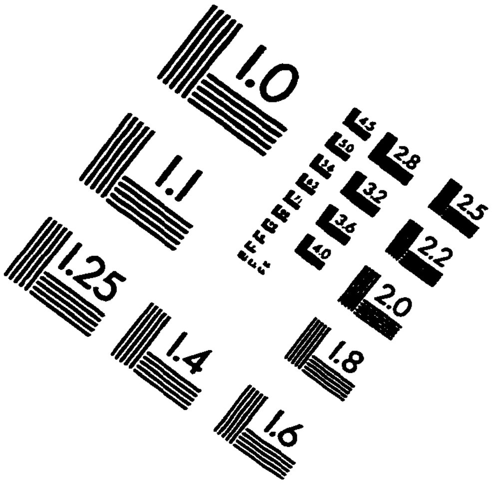

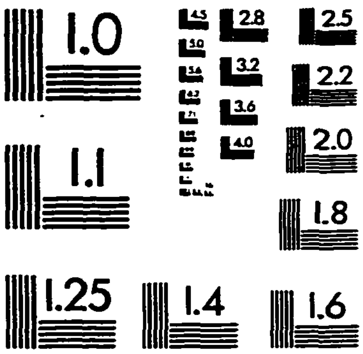

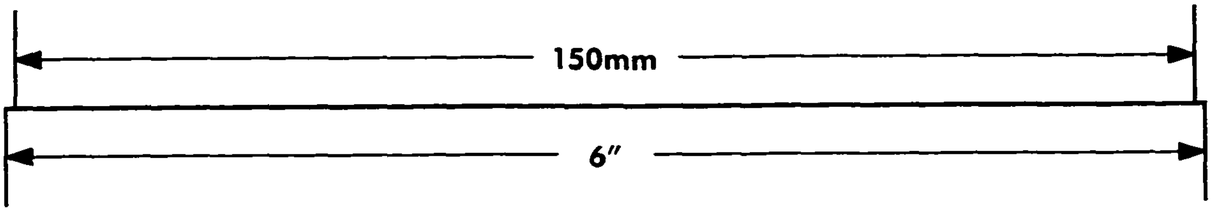

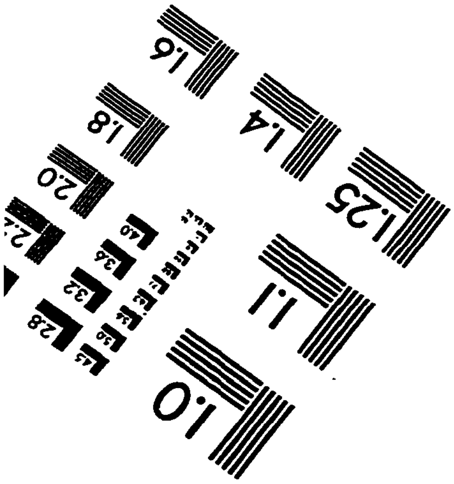

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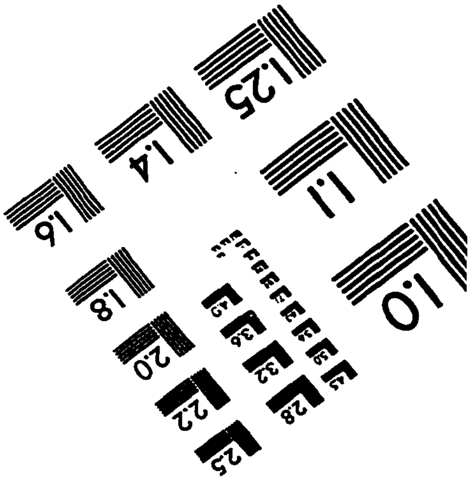

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