

## CAN WE MEASURE CARRYING CAPACITY WITH FORAGING BEHAVIOR?

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**Abstract.** Carrying capacity is one of the most important, yet least understood and rarely estimated, parameters in population management and modeling. A simple behavioral metric of carrying capacity would advance theory, conservation, and management of biological populations. Such a metric should be possible because behavior is finely attuned to variation in environment including population density. We connect optimal foraging theory with population dynamics and life history to develop a simple model that predicts this sort of adaptive density-dependent change in food consumption. We then confirm the model's unexpected and manifold predictions with field experiments. The theory predicts reproductive thresholds that alter the marginal value of energy as well as the value of time. Both effects cause a pronounced discontinuity in quitting-harvest rate that we revealed with foraging experiments. Red-backed voles maintained across a range of high densities foraged at a lower density-dependent rate than the same animals exposed to low-density treatments. The change in harvest rate is diagnostic of populations that exceed their carrying capacity. Ecologists, conservation biologists, and wildlife managers may thus be able to use simple and efficient foraging experiments to estimate carrying capacity and habitat quality.

**Key words:** *Clethrionomys; habitat selection; life history; optimal foraging; population dynamics; quitting-harvest rate.*

### INTRODUCTION

*Thus in March, when the deer frequently browse white pines, the height of their browsing tells me how hungry they are. A deer full of corn is too lazy to nip branches more than four feet above the ground; a really hungry deer rises on his hind legs as high as eight feet.*

—Aldo Leopold (1949)

Leopold's prose tells us that foraging behavior can yield insight not only into whether animals are sated or hungry, but also into the causes of their hunger. Several models illustrate, for example, that animals should abandon foraging patches when their intake rate drops below that required to maintain an energetic balance (reviewed in van Gils et al. 2004). The theories suggest that we can use resource depletion to predict the number of animals obtaining sufficient food in a non-renewing

prey patch (energetic carrying capacity [Sutherland and Anderson 1993, van Gils et al. 2004]). Success has been somewhat variable, however, (e.g., Gill et al. 2001, Percival et al. 1998, Goss-Custard et al. 2003) because the models maximize the rate of energy gain rather than fitness (van Gils et al. 2004). The distinction between energy and fitness is crucial. Animals with higher fitness prospects are known to accept less risk while foraging, and possess higher quitting-harvest rates, than individuals with less fitness potential (Olsson et al. 2002).

Estimates of energetic carrying capacity are appropriate for many purposes, including management of migratory species (Goss-Custard et al. 2002). But estimates of demographic carrying capacity ( $K$ , equal birth and death rates) will often prove more useful to ecologists studying population dynamics. Thus we expand on the fitness-maximizing theme of food vs. safety trade-offs in foraging models by integrating them with elementary demographic theory. Our objective is an estimate of carrying capacity that is more in tune with its historical demographic definition.

All things being equal, resources will decline as populations increase, and individuals will work harder

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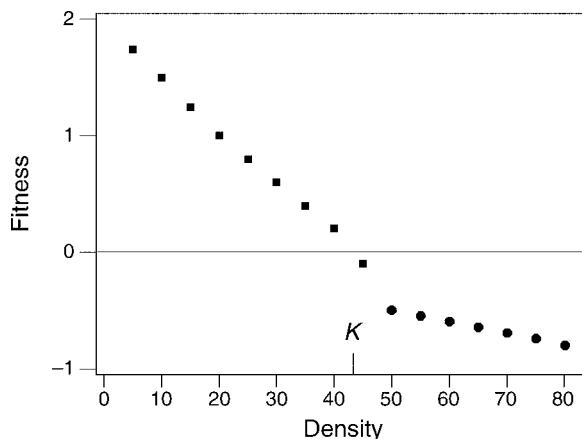


FIG. 1. An illustration of the discontinuity in the relationship between fitness (net geometric rate of population growth) and density for a model organism. The discontinuity is caused by an optimal life history that switches from reproduction to survival near carrying capacity ( $K$ ). To the left of the discontinuity (squares), fitness is determined by the density dependence of litter size, as well as both juvenile and adult survival. To the right of the discontinuity (circles), fitness is determined only by adult survival (data produced by simulations illustrated in Fig. 2; only data for optimal clutch sizes are displayed).

to secure energy from their environment. But all things are not equal. An organism's state varies with a population's density and demographic structure (Houston and McNamara 1999). The individual's state, and its state-dependent foraging behavior, is likely to vary continuously with population density if populations, and their demography, pass smoothly between periods of growth and decline. But consider the alternative. If state and demographic transitions around carrying capacity are not continuous functions, then we might be able to detect the discontinuous signal in foraging behavior. We develop a simple theory that predicts just such a discontinuity. We then test the theory with an experiment that measured foraging behavior of red-backed voles across a range of population densities.

#### A THEORY OF DENSITY-DEPENDENT FORAGING

We begin by imagining a model organism with a simplified density-dependent life history. We use the model to illustrate that individuals should forego reproduction near carrying capacity because their own survival yields higher fitness than that of their offspring. We then interpret the switch to zero reproduction in the context of foraging theory to evaluate whether it yields a tell-tale sign in the way that animals harvest resources.

Our model life history is represented by an asexual species with discrete periods of reproduction and two distinct age classes. Juveniles do not reproduce. Juveniles that survive one time period become adults. Adults can reproduce or not. At any given population size, reproductive adults pay a basic "survival cost of reproduction" plus an incremental cost that increases

with the number of offspring. Juvenile mortality also increases with increasing clutch size (Charnov and Krebs 1974). Adults and juveniles face increasing mortality as populations grow, and maximum clutch size declines with increasing density. Then at any given population density,  $N$ ,

$$\lambda = P + B \times S \quad (1)$$

where  $\lambda$  is the geometric per capita population growth rate,  $P$  is the adult survival from one reproductive period to the next,  $S$  is the survival from juvenile to adult over the same interval, and  $B$  is clutch size ( $P = f_1(B)g_1(N)$ ,  $S = f_2(B)g_2(N)$ , and  $B_{\max(N)} = g_3(N)$ ). The optimum clutch size maximizes the net geometric per capita rate of growth  $R = \lambda - 1$  (where  $R = B \times S - M$ ;  $M = \text{adult mortality} = 1 - P$  [Charnov and Krebs 1974]).

Population size increases for any  $B > 0$  whenever reproduction yields more than enough recruits to exceed adult mortality ( $S \times B > M$ ). But there is a discontinuity. Individuals will cease reproduction at some density beyond the population's carrying capacity ( $\lambda = 1$ ). Reproduction will stop when the loss of fitness incurred through mortality of non-breeding adults is less than the fitness they would lose through reproduction (i.e., whenever  $R$  is negative and  $\{(M - S \times B): B \geq 1\} > \{M: B = 0\}$ ). Computer simulations (see *Methods: Fitness simulations*) confirm the density-dependent switch to zero reproduction that produces a sharp discontinuity in fitness (Fig. 1).

We wish to know how foraging behavior will respond to this discontinuity between reproduction vs. survival. Imagine that individuals live in a risky environment containing predators and that fitness obtained from foraging in a patch ( $F$ ) increases with net energy gain from that patch. Imagine further that fitness is maximized by the product of the fitness gained from the patch and the probability of surviving predation during the foraging interval ( $p$ ; Brown 1988, 1992). Two alternative foraging strategies are likely to emerge (Brown 1992, Brown and Kotler 2004). If foragers maximize the product  $p \times F$  (fitness gained by surviving for some interval of time), then  $F$  represents the cost of being killed by a predator while foraging (Olsson et al. 2002) and

$$\text{QHR} = C + \frac{\mu F}{\frac{\partial F}{\partial e}} + \frac{\Phi_t}{P \left( \frac{\partial F}{\partial e} \right)} \quad (2)$$

where QHR is quitting-harvest rate in the resource patch,  $C$  is the metabolic cost of foraging in the patch,  $\mu$  is the instantaneous rate of being killed by a predator while foraging in the patch,  $\Phi_t$  is the marginal fitness value of time that could be allocated to activities other than foraging, and  $\partial F / \partial e$  is the marginal value of energy in terms of fitness (Brown 1992, Brown and Kotler 2004). The second right-hand term thus represents the marginal cost of predation ( $P$ ) while the third is the marginal cost of missed opportunities (MOC) to

enhance fitness through activities other than foraging (Brown 1988, 1992). But if foragers are faced with a nonreproductive period, they might maximize their own survival ( $p$ ) subject to maintaining some minimum energetic state (Gilliam and Fraser 1987), then

$$\text{QHR} = C + \frac{\mu p}{\Phi_F \frac{\partial F}{\partial e}} + \frac{\Phi_i}{\Phi_F \frac{\partial F}{\partial e}} \quad (3)$$

where  $\Phi_F$  represents the energetic constraint (marginal value of survival obtained by altering the amount of energy consumed [Brown 1992, Brown and Kotler 2004]). Individuals that require more energy will accept higher risks and spend less time on alternative activities in order to meet their energetic constraint. Regardless which model applies, quitting-harvest rates of a foraging individual exploiting identical resource patches (constant  $C$ ) will decline with reduced predation risk, with increased value of energy, and with reduced value of alternative fitness-enhancing activities (Brown 1988, 1992, Brown and Kotler 2004). In Eq. 2, QHR declines with any reduction in fitness. The cost of being killed by a predator while feeding is reduced. But QHR increases if the cumulative probability of survival is reduced. The longer a forager remains in the patch, the less chance it has to convert food into fitness. A reduction in  $p$  has the opposite outcome of reducing QHR in Eq. 3. An individual with a low chance of survival has less to lose by spending time foraging than does an individual with higher survival. Armed with these models, and assuming constant carrying capacity, we can assess how foraging behavior should react to the discontinuity in reproduction near  $K$ .

We make the following additional assumptions: (1) The marginal value of energy will be greater in high-density populations than in populations with low density. As food availability declines with increasing density, the forager's expected energetic state is reduced, and energy becomes more valuable. (2) Survival and fecundity decline with increased density and reduce the potential fitness obtained from foraging ( $F$ ). (3) A reduction in QHR can be achieved only through increased foraging time. (4) An increase in time spent foraging reduces the cumulative probability of survival ( $p$ ). The assumptions allow us to generate a series of hypotheses that we can evaluate with field experiments.

$H_1$ ) If per capita resource supply and fitness from foraging ( $F$ ) decline with density, then the quitting-harvest rate will be reduced (Eq. 2).

$H_2$ ) If quitting-harvest rates decline (increased foraging time, assumption 2 above), then the relative importance of missed opportunities to QHR will be inflated (directly in Eq. 2, indirectly through reduced predation risk in Eq. 3; this outcome will occur even if the only alternative activity is occupation of a safe refuge [MOC = resting metabolic rate]).

$H_3$ ) If the marginal value of energy is less for nonreproducing adults than it is for reproductive

individuals, then there will be a discontinuity in quitting-harvest rate at the density when reproduction stops, after which QHR will continue to decline with further increases in population size. This effect will be most pronounced when the foraging strategy switches from Eq. 2 to Eq. 3.

$H_4$ ) If, when the population ceases reproduction, a foraging strategy that maximizes reproductive value (Eq. 2) switches to a strategy maximizing survival (Eq. 3), then the relative value of missed opportunities will increase (even though it may be small and dominated by time spent in a safe refuge).

We conclude that the density-dependent foraging theory, and its ability to estimate  $K$ , will be confirmed if (1) there is a discontinuity in the relationship between QHR and density ( $H_3$ ); (2) quitting-harvest rate declines with increasing density on both sides of the discontinuity ( $H_1$  and  $H_3$ ); or (3) the discontinuity in QHR is associated with an increase in the relative importance of missed opportunities ( $H_2$  and  $H_4$ ).

The cost of missed opportunities, such as time devoted to courtship, other social activities, territorial defense, etc., may also increase with density irrespective of the discontinuity in QHR. Though there is scant support for such "social benefits" relative to competition for resources (Davidson and Morris 2001), they might nevertheless alter MOC with density. Social benefits should not, however, be associated with discontinuities in reproduction and QHR.

No clear density-dependent predictions emerge for predation rates that depend on the timing and value of predators' numerical and functional responses, as well as the role of conspecifics in reducing vigilance and apprehension. Even if instantaneous predation rates decline, the cost of predation could remain more-or-less constant if there is a similar reduction in the marginal value of energy. And additional complications arise if risk dilution at high density increases expected survival, and thereby causes an indirect increase in the marginal value of energy.

To test the theory we need first to demonstrate that the discontinuity in reproduction is legitimate. So we searched for the discontinuity with computer simulations of density-dependent fitness in which fecundity and survival declined linearly with population density.

Second, we need to measure quitting-harvest rates across a range of population densities spanning the reproductive discontinuity. The composite theory predicts a similar discontinuity in foraging. So we manipulated density in a controlled population of rodents while we measured their quitting-harvest rates.

## METHODS

### *Fitness simulations*

We used simple computer simulations to illustrate how increased density changes the optimum clutch size by calculating fitness for various clutch sizes and population densities according to the following linear

models:  $B_{\max} = L - cN$ ,  $S = (1 - aB) - bN$ , and  $P = (1 - \alpha B) - \beta N$  where  $a$ ,  $b$ ,  $c$ ,  $\alpha$ ,  $\beta$ , and  $L$  are constants. We assume, for this example, that all adults are identical and capable of producing the optimum clutch size, and that evolution maximizes the number of recruits ( $S \times B$ ) minus adult mortality. Thus, a reproductive adult with low survival can, when  $N > K$ , have less fitness than an adult that does not reproduce. We realize that additional assumptions, incorporating such effects as differences in age- and stage-dependent survival, are likely to yield more complicated strategies. Our model is intended only to illustrate, at high density, that survival can yield more fitness than reproduction.

#### Field experiments

We searched for the foraging discontinuity in a population of red-backed voles (*Clethrionomys gapperi*) living at different densities in enclosed habitats. We manipulated density by moving animals from a high-density enclosure to an adjacent low-density treatment.

On 31 July 2005, we placed 20 ear-tagged adult red-backed voles (*Clethrionomys gapperi*) in one of two adjacent  $50 \times 50$  m galvanized metal enclosures (0.75 m high buried to a depth  $\geq 0.5$  m). Enclosures were located in natural second-growth forest vegetation near Lake Superior in northern Ontario, Canada (Lakehead University Habitron; Appendix B). Initial density was nearly three times greater than the maximum density of 30 animals/ha typically recorded on 1-ha study plots in nearby forests (Morris 2005). We placed two animals in the second enclosure at the same time. Voles were the only small mammals in the enclosures. We captured animals in these, and 10 adjacent enclosures used for different experiments, over a 24-hour time span every third day. Sherman live traps were set on a  $4 \times 4$  grid with 12.5-m intervals in late afternoon and were checked 12 and 18 hours later. We selected one animal at random during each trap rotation and moved it from the high- to low-density treatment. We maintained a sex ratio near 1:1 in each treatment by never moving more than one "extra" individual of the most common sex. The experiment lasted for 30 days (10 treatment densities) and was designed to create all possible densities between two and 20 animals. We counted and removed all remaining animals at the end of the experiment by trapping across several nights ( $\geq 3$ ) until no animals were captured.

Live-trapping revealed that a small subset of voles were able to move "through" the metal barrier separating enclosures. Three animals from this experiment moved to another enclosure, and one animal from another experiment moved into the "treatment enclosures." These animals were returned or removed as soon as they were encountered. Others died or were consumed by avian predators (Great-grey Owls [*Strix nebulosa*], Northern Harriers [*Circus cyaneus*], and Kestrels [*Falco sparverius*] were observed regularly during the study). Thus we used density estimates (minimum number

known alive) for our analyses in place of the actual density treatments applied to each enclosure. We assumed that any animal moving between pens did so in time to forage in that pen. We also assumed that disappearance of any animal placed in the enclosures at the beginning of the experiment, and not captured at the end, occurred during the three-day interval since its final capture, and before we collected the giving-up density (GUD) for that treatment (traps were set two hours later). The assumptions appear valid because recapture rates of animals known to be alive were consistently high throughout the experiment. We captured every vole known alive in an enclosure on nine out of 20 trapping opportunities (10 sessions  $\times$  2 enclosures), and we captured all but one rodent on eight occasions. On the remaining three opportunities, corresponding to the three highest densities, we captured all but three voles.

On the afternoon of the first day, and every third day thereafter, we placed four artificial food trays made from opaque plastic water bottles (9.5 L with a single 3-cm opening) in pairs at different trapping stations in each enclosure. Each pair consisted of a tray under the protective cover of a large alder (*Alnus viridis*), and another placed in the "open" approximately 1 m away. Each bottle contained 4.0 g of sized millet seed ( $>2$  mm diameter) mixed thoroughly in 1.5 L of screened (60–90 grain) silica sand. We collected bottles 48 hours later and used soil sieves to separate the sand from residual millet. We weighed the cleaned millet with an electronic balance to the nearest 0.01 g (the giving-up density, GUD). All trays were foraged by the red-backed voles that had been trained to use the trays over 14 days in a similar enclosure following their initial capture from the wild.

We calculated the mean GUD for the two open trays, and separately for the two shrub-covered trays in each pen, and calculated the difference between them. We used the log-transformed mean GUD ( $\log_{10}[\text{GUD} + 1]$ ) to estimate the quitting-harvest rate of the final animal using the tray. The transformation linearizes the relationship between GUD and QHR and is effective provided that animals forage in patches with diminishing returns (Brown and Kotler 2004). The diminishing-returns assumption fits gain curves for other northern small mammals foraging for millet in similar trays (Morris 2001, Morris and Davidson 2000, Davidson and Morris 2001).

#### Statistical analysis

We searched for the expected discontinuity in QHR by regression, then assessed whether the density-dependent decline was different at high, vs. low, density. We confirmed the cost of predation by comparing QHRs of voles using risky (open) vs. safe (under shrubs) foraging patches. We then tested whether we could account for the increase in QHR at high density through an elevated risk of predation. If not, the discontinuity must have been caused by an increase in the value of missed opportunities.

Theory predicts a sharp discontinuity in the relationship between quitting-harvest rate (log-transformed GUD) and population density, a prediction our experimental data appear to confirm (Fig. 4). Accordingly, we removed outliers (two points of very low GUD from the first treatment interval in the low-density enclosure that may represent chance occurrence of two animals in a low energy state), then created a moving window composed of 10 sequential densities to objectively assess “breaks” in the QHR  $\times$  density relationship. We regressed log-transformed GUD against density for each window (Appendix A), calculated the coefficient of determination (adjusted for bias), and plotted these values sequentially to detect any discontinuity in the overall relationship. Adjusted  $R^2$  should decline toward zero at both ends of the discontinuity. The data revealed a clear discontinuity at a density of 10 animals per enclosure. We broke the data in two at this point, then analyzed for differences in the relationship between our estimate of QHR and density with ANCOVA.

We used paired  $t$  tests to evaluate differences in log-transformed GUD calculated between trays in open and shrub-covered microhabitats. We then used regression to assess whether these differences were related to density, followed by a one-way ANOVA to evaluate whether the differences were distinct between densities  $<10$ , vs. those  $\geq 10$ . All analyses were performed in either MINITAB (Version 12; Minitab, Inc., State College, Pennsylvania, USA) or SPSS (Version 13; SPSS, Inc., Chicago, Illinois, USA).

RESULTS

*Fitness simulations*

The simulated fitness values illustrate how the maximum clutch size, optimum clutch size, and population growth rate (recruits) all decline with increasing population size (Fig. 2). At low density ( $N = 10$ ,  $N = 30$ ), individuals maximizing profit (recruitment [benefit] minus adult mortality [cost]) produced an optimum clutch size that is the smallest of the two most productive clutch sizes. At high density ( $N = 50$ ), individuals minimizing losses (adult mortality exceeds recruitment for all clutches) do not reproduce. There is a threshold density above which optimal individuals curtail reproduction.

*Field experiments*

Analysis of our field experiments confirmed each prediction. (1) There was a pronounced discontinuity between quitting-harvest rate and density at 10 animals (Figs. 3 and 4). (2) QHR increased at the discontinuity to yield a higher QHR (controlled by the number of foragers) at high density than at low density ( $F_{1,35} = 11.85$ ,  $P = 0.002$  for low- vs. high-density treatment while controlling for the covariate of density [ $F_{1,35} = 100.06$ ,  $P < 0.001$ ]).

We designed our experiment to detect additional predation costs associated with foraging away from

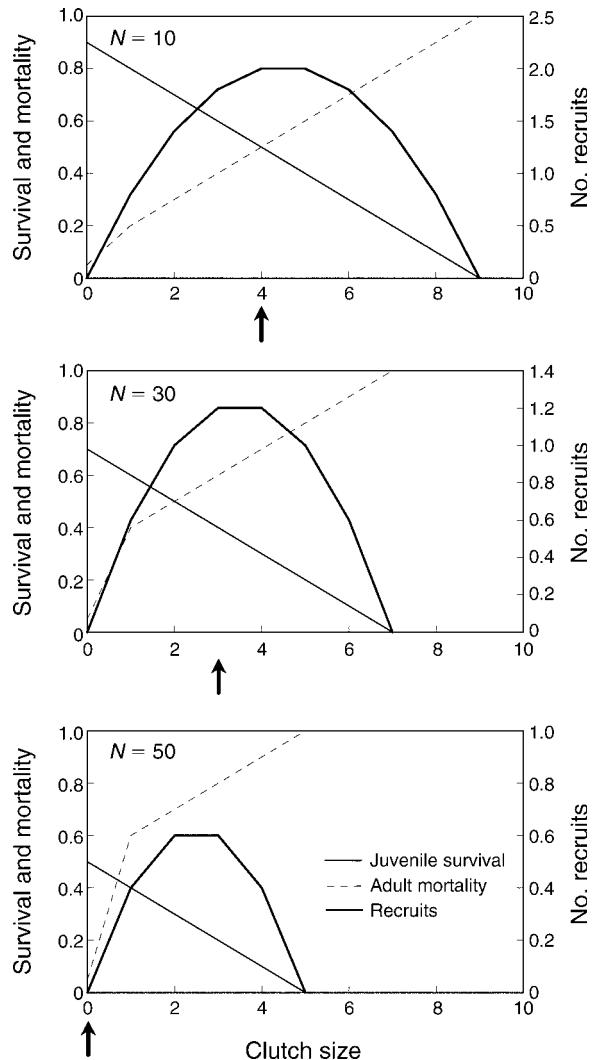


FIG. 2. An illustration demonstrating changes in optimum clutch sizes (arrows) produced at different population densities ( $N$ ) when juvenile and adult survival ( $1 - \text{adult mortality}$ ; light lines) decline linearly with clutch size and when survival and maximum clutch size decline linearly with increasing population density. Adult mortality is piecewise linear because it is composed of a basic density-dependent rate (whether individuals reproduce or not) plus an additional linear rate associated with increasing clutch size (clutches of size 1 and greater). The optimum clutch size maximizes fitness (the difference between adult mortality [dashed line] and the hump-shaped recruitment curve; this difference is negative when the adult mortality curve lies above the recruitment curve [heavy lines]). Note that the scale for the number of recruits varies among panels. Parameter values are  $a = 0.1$ ,  $b = 0.01$ ,  $c = 0.2$ ,  $\alpha = 0.1$ ,  $\beta = 0.01$ ,  $L = 10$ .

cover. We placed pairs of otherwise identical bottles in the open and under shrubs. Foraging costs ( $C$ ) and the value of missed opportunities (MOC) were the same for each bottle because MOC is a property of the individual and the environment it exploits, not the foraging patch (Brown et al. 1992). So any difference in QHR must reflect the cost of predation (Brown 1988). Quitting-harvest rates were higher in the open than under shrubs

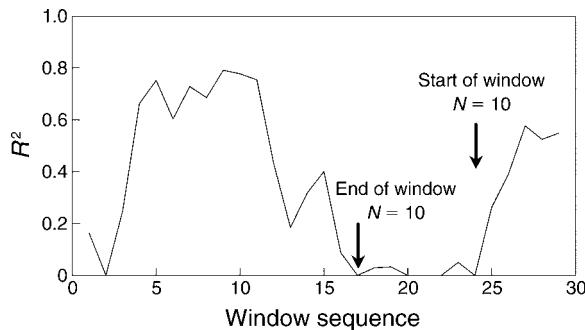


FIG. 3. A test to locate discontinuities in quitting-harvest rates with the density of red-backed voles. Values on the ordinate are adjusted coefficients of determination obtained from sequential linear regressions along a moving window with 10 observations of density. Values on the abscissa correspond to each successive window. Arrows indicate the final and beginning observations of windows with  $R^2 = 0$ . All windows between these limits were nonsignificant with very small coefficients of variation.

(paired  $t$  test,  $n = 40$ ,  $t = 3.36$ ,  $P = 0.002$ ). The difference was not related to density ( $r = -0.08$ ,  $P = 0.62$ ; Fig. 5), or to the discontinuity in QHR (one-way ANOVA,  $F_{1,38} = 0.27$ ,  $P = 0.61$ ). We conclude that the relatively greater QHR at high density was caused by increased importance of MOC.

Though history, aspect, soil, drainage, vegetation, and habitat structure in the two enclosures was similar, our design may have confounded density with space. One enclosure represented low density while the other maintained high density. We can discount the criticism

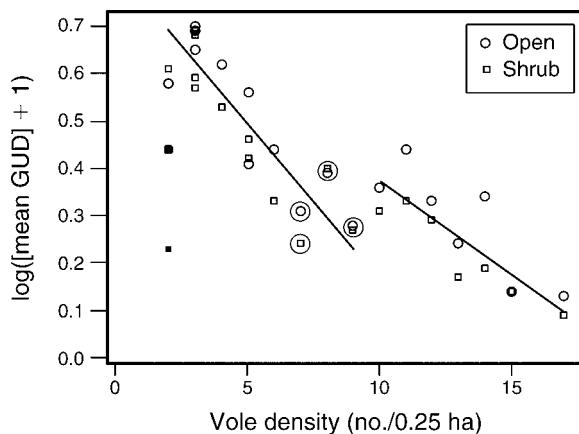


FIG. 4. A scatter plot of quitting-harvest rates (log-transformed mean GUDs) plotted against the population density of red-backed voles living in a 0.25-ha enclosure in northern Ontario, Canada. Data are mean values of the two identical artificial foraging trays located in a single enclosure. Circles correspond to data obtained from trays in the open; squares represent data collected under shrubs. Outliers eliminated from analysis are indicated by filled symbols. Large circles surround data points from the "high-density treatment" that fit the data from the low-density regression. Lines represent the least-squares fit of separate regressions calculated on either side of the discontinuity revealed at a density of 10 animals.

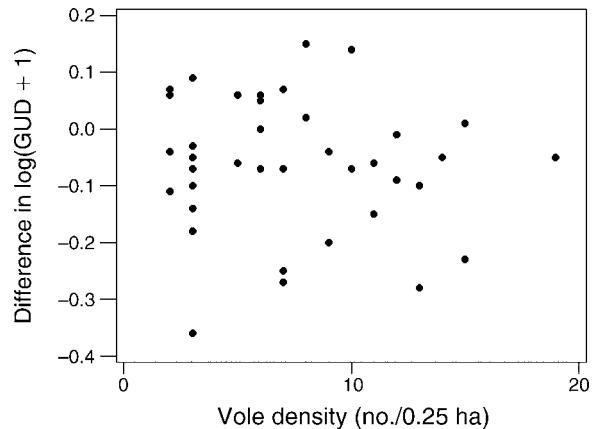


FIG. 5. A scatter plot illustrating that the difference between quitting-harvest rates in shrub-covered and open microhabitats did not vary with the population density of voles.

in two ways. First, animals that we moved from the high-density treatment were accustomed to foraging at a different density-dependent rate than animals in the low-density treatment. Even so, they quickly altered behavior to forage at a different rate. Second, the high-density treatment included data on both sides of the discontinuity. Data on the high side fit the high-density regression. Data on the low side fit the low-density regression (Fig. 4).

#### DISCUSSION

Our simple expansion of Charnov and Krebs' theory for an optimal clutch size demonstrates, when populations exceed their carrying capacities, that individuals should switch from maximizing reproduction to maximizing survival. When they do so, their foraging behavior also switches from a strategy dominated by food-safety trade-offs that maximize net reproductive value (Brown 1992, Brown and Kotler 2004) to one dominated by a nonreproductive period where individuals maximize their own survival (Gilliam and Fraser 1987). The discontinuity in life history should thus be reflected by a similar discontinuity in quitting-harvest rates. The combined theory yields three predictions confirmed by experiments on the foraging behavior of red-backed voles living at different densities. There was a discontinuity in the relationship between QHR and density (at 10 animals per enclosure). Quitting harvest rates declined with density on both sides of the discontinuity. The discontinuity in QHR was associated with a relative increase in missed opportunities.

Thus, we calculate that the carrying capacity for red-backed voles in our experimental enclosures was  $\leq 10$  animals (40 animals/ha). This value compares very favorably with maximum density estimates of 30 animals/ha typically recorded in late summer on 1-ha study plots in nearby forests (Morris 2005).

The discontinuity in reproduction and foraging depends critically on the trade-offs between adult and juvenile survival with clutch and population size. Reproduction is the preferred option, even in declining populations, whenever the mean fitness of recruits exceeds the fitness obtained through parental survival. Foraging theory based on reproductive patterns may thus yield biased predictions of demographic carrying capacity. But it is difficult to imagine scenarios in populations above carrying capacity where parents can successfully rear offspring of sufficient quality to replace their own fitness value. Even in territorial or hierarchical social systems, dominant individuals may be forced to forego reproduction because “surplus” resources are exhausted on defense. The ability of reproduction to yield greater fitness than survival at high population densities becomes even more difficult to attain in sexually reproducing species. Female parents in such species must produce, on average, twice as many descendants as asexually reproducing individuals to compensate for their mortality risk.

The discontinuity's dependence on density and clutch-size trade-offs with survival implies, nevertheless, that the “carrying capacity” detected by foraging experiments will tend to overestimate the density where population growth is exactly zero. Reproduction can yield higher fitness than survival at densities above, but near,  $K$ . And, when no other individuals are reproducing, the first parents to do so successfully should normally produce more descendants than their nonreproductive neighbors. The disconnect between estimated and true carrying capacity will be most pronounced if (1), clutch-size-dependent adult mortality increases much more slowly with population density than does that for juvenile mortality, or (2), if reproducing adults have higher survival than those that do not reproduce (a concave downward mortality function with clutch size). Even so, the discontinuity should be a reliable indicator to identify differences in  $K$  between habitats.

There are at least four important corollaries. (1) The discontinuity, measured in different habitats, should be a useful metric of habitat quality. Habitat sinks, for example, will have a higher QHR for their density than source habitat. (2) The density-dependent decline in QHR should mirror habitat differences in fitness. Thus graphs such as Fig. 4 reveal how rapidly fitness falls with increasing population size. (3) Once we know the location of the discontinuity, we may be able to use repeated estimates of QHR as a quick and efficient assay to detect changes in population density. (4) After we estimate the carrying capacity in one habitat, we should be able to use the pattern of relative densities to calibrate carrying capacity in other habitats (e.g., isodars [Morris 1988]).

Our test would be more convincing if we had demonstrated that red-backed voles ceased reproduction at densities exceeding 10 individuals in an enclosure. The time scale and design of our experiment did not allow us

to conduct this test. We caution readers, even if we had attempted such a test, that its results would be complicated by the past state of individuals, as well as the recent dynamics of the population.

Voies in our training enclosures, for example, had free access to laboratory rodent chow and both male and female voles were in breeding condition at the start of the experiment. It is reasonable to expect that some of these animals may have mated, even at high population densities. Some readers might wonder whether reproduction by these individuals invalidates our tests. We counter by reminding those readers that the theory predicts a set of novel and dramatic effects confirmed by experiment. There was a discontinuity between QHR and density, when controlled for the number of foragers, the QHR of animals living at high density was greater than that of similar animals at low density, and there was an increase in relative MOC at the discontinuity.

We can speculate, nevertheless, whether the immediate advantages of optimal foraging decisions should be based on time-lagged reproductive cues. Imagine a pregnant vole confronted with a habitat of rapidly declining quality in which she will not be able to provision her young. The change in habitat quality could be caused by the female moving into a new habitat, by invasion of other individuals into the female's habitat, or by seasonal, climatic, or disturbance events. Regardless whether the female is pregnant or not, her only viable strategy is to maximize her own survival. The pregnant female's offspring will not survive. Since she cannot simply discard her young (though abortion and resorption are possible alternatives), we can assume that the female's developing offspring will increase her marginal value of energy. But if she attempts to forage at a high rate she will compromise her own survival and reduce the opportunity for future reproduction. So she will forage at a rate that maintains the minimum energetic state guaranteeing her own survival. This rate will likely be higher than for non-pregnant females living in the same habitat, but will be less than pregnant females living in a similar habitat at low density. The example tells us that though animals can respond to physiological changes associated with reproduction, they are likely to base their adaptive foraging decisions on any reliable cue that minimizes time-lagged responses to changing conditions. It may be naive to search for a lock-step mechanism between breeding behavior and changes in density-dependent foraging.

The astonishing agreement between data and predictions informs us that there is indeed an underlying unity among otherwise disparate theories in demography, life history, population dynamics, and optimal foraging. The value and insight of those unifying principles is shown clearly in the discontinuous pattern of density-dependent foraging by red-backed voles. Our future challenge is to gain as much value from that foraging pattern as do the animals that create it.

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## APPENDIX A

Justification for using both open and shrub-covered foraging sites to determine the relationship between quitting-harvest rates and population densities (*Ecological Archives* E088-038-A1).

## APPENDIX B

A photograph of enclosures at the Lakehead University Habitron where foraging behavior was used to estimate carrying capacity of red-backed voles (*Ecological Archives* E088-038-A2).