

## DENSITY DEPENDENCE, PREY DEPENDENCE, AND POPULATION DYNAMICS OF MARTENS IN ONTARIO

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**Abstract.** Ecological factors influencing demographic parameters of mammalian carnivores are poorly understood, due to the difficulty of simultaneously measuring predator and prey populations over an extended period. We used cohort analysis based on age-specific harvest data to estimate population densities over 20 yr for martens (*Martes americana*). Marten abundance increased threefold over the study period, probably due to relaxation in harvest intensity at the beginning of the study interval. Changes in rates of population growth by martens were positively correlated with population densities of three species of small mammals recorded over the same time span: deer mice (*Peromyscus maniculatus*), red squirrels (*Tamiasciurus hudsonicus*), and flying squirrels (*Glaucomys sabrinus*). We found no evidence of short-term cycles in marten abundance, nor were there significant cross-correlations at lags greater than 1 with prey population densities. Martens also showed evidence of density-dependent population growth. Such density dependence beyond the demographic effect of variation in prey density was possibly due to agonistic interactions among territory holders. Such mixtures of prey dependence and density dependence often have a stabilizing influence in theoretical models, which could contribute to the observed stability of deer mouse, red squirrel, and marten populations in Algonquin Park. Harvest intensity was negatively related to yearly variation in marten population growth. Mortality due to trapping averaged 37.9% over two decades, with no detectable relationship to changes in marten population density. Hence, harvesting acted as a stochastic external variable that was additive to density-dependent and prey-dependent effects.

**Key words:** cohort analysis; harvest; interference; *Martes americana*; numerical response; population dynamics; predator; prey; small mammal; stability; territoriality; time series.

### INTRODUCTION

It has long been appreciated that interactions between predators and their prey could destabilize community dynamics, inducing population oscillations over time (Lotka 1925, Volterra 1928, Rosenzweig 1971, Gilpin 1972, May 1972, Murdoch and Oaten 1975, Tanner 1975). Such mechanisms have been invoked to explain well-documented cycles in a variety of systems, including snowshoe hares and lynx in the Canadian arctic (Sinclair et al. 1993, Krebs et al. 1995), moose and wolves on Isle Royale (McLaren and Peterson 1994, Messier 1994), and communities of microtine mammals and mustelid predators in northern Europe (Hanski et al. 1991, 1993, Hanski and Korpi-mäki 1995).

These apparent examples of predator-prey cycles are especially intriguing because they involve carnivores with a territorial social structure. Theory suggests that

territoriality should itself lend a stabilizing influence (Rosenzweig and MacArthur 1963, DeAngelis et al. 1975, Schoener 1987, Fryxell and Lundberg 1997), if the rate of carnivore population growth is adversely affected by aggressive interactions among territory holders. This implies that the rate of carnivore population growth should be dependent on both the density of prey (hereafter termed prey dependence) as well as on the density of conspecifics (hereafter termed density dependence). Our ability to test this hypothesis is usually compromised, however, by scarcity of long-term demographic data on both predators and their prey. In this paper, we analyze 20 yr of time series data for a territorial carnivore, the marten (*Martes americana*), in relation to temporal fluctuations of small mammals in southern Ontario. We test whether the Algonquin marten population varies cyclically or unpredictably over time as well as test whether rates of marten population growth depend on densities of prey, predators, or both. This information provides the basis for simple models summarizing our current understanding of food chain dynamics of the Algonquin assemblage of small mammals.

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## METHODS

*Data*

Age data from a sample of the commercial marten harvest during 1972–1991 in the Bracebridge District adjoining Algonquin Provincial Park, Ontario (48°30' N, 78°40' W) were used to estimate population abundance via cohort analysis. Harvesting in this district is regulated by trapline quotas issued by the Ontario Ministry of Natural Resources and trappers were asked to voluntarily submit their marten carcasses. On average, 53% of the carcasses were turned in for aging each year, forming the age distribution used in cohort analysis. The sealing of marten fur was mandatory and the total harvest of marten in the Bracebridge District was obtained from the sealing records. We therefore corrected for the 47% of carcasses that were not turned in, by multiplying the proportion of each age group obtained from the carcass sample by the total harvest in each year. Trapline quotas fluctuated annually and were greatly reduced in the early 1970s, at the beginning of this study, following a long period of decline in trapping success in the Bracebridge District. Counts of cementum annuli in premolar teeth and/or radiographs of the canines were used to assess age (Dix and Strickland 1986, Strickland and Douglas 1987).

Marten population estimates were derived using cohort analysis (Ricker 1940, Fry 1949). The principle behind this population estimator is based on use of a backward recursion formula to reconstruct specific contemporaneous cohorts of harvested animals to estimate minimum population abundance at various points in time. When the harvest period is short, as was the case for the trapping data used in our study, one estimates the number of individuals ( $N$ ) of age  $i$  in year  $t$  by

$$N_{i,t} = \frac{N_{i+1,t+1}}{p} + K_{i,t} \quad (1)$$

where  $p$  = the annual survival rate and  $K_{i,t}$  = the number of animals of age  $i$  harvested in year  $t$ . This formula estimates the number of individuals present in the population immediately preceding the harvest period. Based on Hodgman et al.'s (1994) radiotelemetry data for an intensively trapped marten population in Maine, we estimated annual survival as 87%.

Application of cohort analysis to more recent cohorts that have not completely passed through the population requires estimation of age-specific abundance in the last year from harvest data only. We used Baranov's (1918) random catch equation to estimate age-specific abundance in the terminal year:

$$N_{i,t} = \frac{K_{i,t}}{1 - \exp(-q_i)} \quad (2)$$

with  $q_i$  estimated from completed cohorts (Fryxell et al. 1988, 1991). As with any population estimator, cohort analysis involves several assumptions, including an important assumption that trapping methods and

trapping effort have remained constant over time (Pope 1972, Ulltang 1977, Fryxell et al. 1988). There was little change in trapping technology or pelt prices over the study period, so we think that these assumptions are wellfounded.

Live-trapping of small mammals was conducted in a standardized manner over the same 20-yr period (1972–1991) at the Algonquin Park Wildlife Research Station (Fryxell et al. 1998), ~40 km from the border of the Bracebridge District from which marten data were obtained. Although we don't know whether rodent population dynamics are synchronized over such a broad spatial scale, there is evidence from Scandinavia that this can be the case (Steen et al. 1996). At each of 10–15 forested sites, a 90-m trapline was established with either one or two Sherman traps at stations 10 m apart. The physical dimensions of the Sherman traps were 7.5 × 7.5 × 30.5 cm, of sufficient size to catch even large rodents, such as red or flying squirrels. Single lines had 10 traps in total, whereas double lines had 20 traps. Lines were sampled either once or twice a month for three nights from mid-May until the end of August or September, yielding a maximum of 10 trapping periods per year. A few lines were abandoned or moved, but otherwise the trapping protocol was quite consistent from year-to-year.

Lines were set out in a variety of forest stands, ranging from pure deciduous hardwoods through mixed forest to pure coniferous stands. Small mammal traplines were at least 0.3 km apart and very few marked animals have been captured on more than one trapline. The total study area is ~8 × 2.5 km, comprising several stands in a continuously forested region of the park that has not been logged or burnt since the 1930s. Care was taken at the beginning of the study to locate traps in forest types typical of the region. Some of the most common tree species at our study sites include sugar maple (*Acer saccharum*), red maple (*A. rubrum*), speckled alder (*Alnus rugosa*), trembling aspen (*Populus tremuloides*), eastern hemlock (*Tsuga canadensis*), hop hornbeam (*Ostrya virginiana*), yellow birch (*Betula alleghaniensis*), white birch (*B. papyrifera*), balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), white spruce (*Picea glauca*), and black spruce (*P. mariana*).

Gross trapping effort was calculated by multiplying the number of lines by trap stations per line, trapping periods, and nights per trapping period. Comparative studies conducted by J. B. and E. A. Falls in the early part of the small mammal study showed that lines with two traps per station (hereafter termed double lines) yield ~1.5× the captures made by single lines. In one experiment conducted in the summer of 1959, five lines were trapped for three nights using single traps followed by three nights using double traps and five other lines had the opposite sequence (double followed by single). The ratio of total captures over 6 d on the double lines (107 individuals) compared to that on sin-

gle lines (74 individuals) was 1.45 for all species. Over the first 3 d the ratio was 1.35 compared to 1.61 over the last 3 d, with an equally weighted mean of 1.48. Rounding upwards, we accordingly multiplied the trapping effort from double lines by 1.5 to account for differences in the effectiveness of double vs. single lines. For example, a double line would have 45 trap nights of effective effort per 3-d sampling period whereas a single line would have 30 trap nights of effective effort. The effort correction factor should have little influence, however, on the temporal dynamics of trapped animals, the subject of this paper. The annual catch per unit effective effort was used as our index of small mammal population density. Further details on trapping procedures are provided in Fryxell et al. (1998).

There was a 1-yr data gap in our small mammal time series (1988). An uninterrupted time series is needed to use the PBLR test for both density- and prey-dependent effects (Dennis and Taper 1994). We therefore used average rodent abundance over the other 19 yr to estimate abundance in the missing year. We verified that this assumption did not bias our conclusions by using conventional regression tests of per capita rate of increase ( $r_t$ ) in relation to small mammal density for the 19 yr in which data were collected.

### Models

A common convention in the analysis of ecological time series is to consider population growth as a function of current or past densities of interacting species in the community (e.g., Royama 1992, Turchin and Taylor 1992, Ellner and Turchin 1995, Stenseth et al. 1996). Logarithmically transformed rates of population growth ( $\ln[P_t/P_{t-1}]$ ) often have more evenly distributed error terms and are therefore preferable for analysis than geometric growth terms ( $P_t/P_{t-1}$ ) (Turchin and Taylor 1992, Ellner and Turchin 1995). Our working hypothesis was that rates of predator population growth are a function of predator density (because of interference or territorial competition) as well as prey population density (due to effects on rates of energy gain by predators). We therefore estimated the relationship  $P_t = P_{t-1} \exp(r_t) = P_{t-1} f(P_{t-1}, N_t, \varepsilon_t)$ , where  $r_t = \ln(P_t/P_{t-1})$  is the per capita rate of predator population growth between years  $t - 1$  and  $t$ ,  $P_{t-1}$  is predator population density the previous year,  $N_t$  is prey population density in year  $t$ ,  $\varepsilon_t$  is stochastic variation in the rate of increase in year  $t$ , and  $f$  is some specified function of past and present population densities.

We first tested whether predator population growth was solely a function of its own population density, omitting the prey-dependent term, using the Ricker logistic model ( $r = a - bP_{t-1}$ ). Simple regression is often an inappropriate technique to test for density dependence because the null hypothesis need not be that mean  $r = 0$  (Dennis and Taper 1994). To solve this statistical problem, we used the parametric bootstrap

likelihood ratio (PBLR) test outlined by Dennis and Taper (1994) to evaluate the predictive power of a series of models of increasing complexity.

The first stage in the PBLR test procedure is to estimate parameters for both random walk and density-dependent models. We used a Gauss-Jordan elimination algorithm to find these linear solutions, with least squares as a maximum likelihood estimator (Press et al. 1992:672–675). We then calculated the likelihood of the density-dependent model relative to the random walk model for the observed data. This is a measure of the improvement in predictive power obtained by assuming density dependence. We then generated 1000 new time series based on the parameters of the random walk model. For each simulated data set, we calculated the likelihood ratio ( $\Gamma = \sigma_1/\sigma_2$ , where  $\sigma_1$  and  $\sigma_2$  are the standard deviations of the residual variance of the density-dependent model and the random walk model). The proportion of simulated data sets with a likelihood ratio extreme as that recorded for the real data estimates the probability of making a Type I error (i.e., rejecting a true null hypothesis).

As the density-dependent terms proved significant, we then extended our PBLR test to consider prey-dependent effects, yielding a Ricker model augmented with prey dependence ( $r = a - bP_{t-1} + cN_t$ ). The PBLR test in this context determines whether prey dependence significantly improves demographic predictions relative to the pure Ricker logistic model. We also used nonlinear parameter estimation based on the quasi-Newton algorithm (Wilkinson 1990) to examine the fit to alternate prey-dependent models. These nonlinear models incorporated either a Michaelis-Menten numerical response term ( $r = aN_t/[b + N_t] - c - d \times P_{t-1}$ ) or a ratio-dependent numerical response term ( $r = aN_t/[b + N_t + d \times P_{t-1}] - c$ ). Both forms are consistent with the notion that carnivore feeding rates should saturate at high prey densities (Holling 1959), but that aggression among conspecifics might also affect rates of carnivore increase (Beddington 1975, DeAngelis et al. 1975, Getz 1993).

The logic of the Ricker logistic model is most compatible with univoltine species that have strict separation of generations (adults dying before the next generation is recruited). This is not true of martens, which have seasonal breeding and adults capable of surviving for up to 15 yr. By definition, moreover, predation is a continuous process. We accordingly view the density-dependent and prey-dependent models reported in this paper as statistical approximations for a mixture of seasonal and continuous population processes that were sampled at discrete intervals.

## RESULTS

### Population dynamics

Marten abundance increased roughly threefold over the course of the 20-yr study period (Fig. 1; mean  $r =$

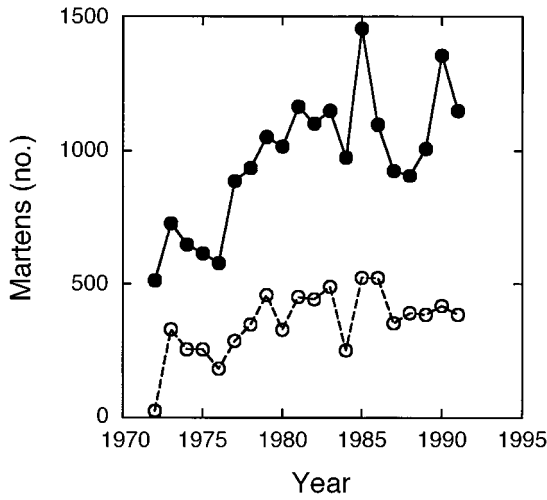


FIG. 1. Dynamics over time for the marten population in Bracebridge District and small mammals in southern Algonquin Provincial Park, Ontario. Marten population dynamics were based on cohort analysis of age-specific harvest data, whereas small mammal data derive from mark-recapture studies (Fryxell et al. 1998). ○, trapped; ●, abundance.

0.043 ± 0.047), although there were intervals of population decline interspersed with periods of increase. Autocorrelation functions showed no significant evidence of high-frequency periodicity in population abundance or the per capita instantaneous rate of increase ( $r$ ) over time (in both cases  $P > 0.05$ ). Hence the marten population was noncyclic, in the normal ecological sense of the term, even though it was growing for a large part of the study period.

The per capita rate of increase of marten was negatively related to marten density the previous year (Fig. 2;  $r_t = 0.45 - 0.00043P_{t-1}$ ,  $r^2 = 0.29$ ; PBLR test  $\Gamma =$

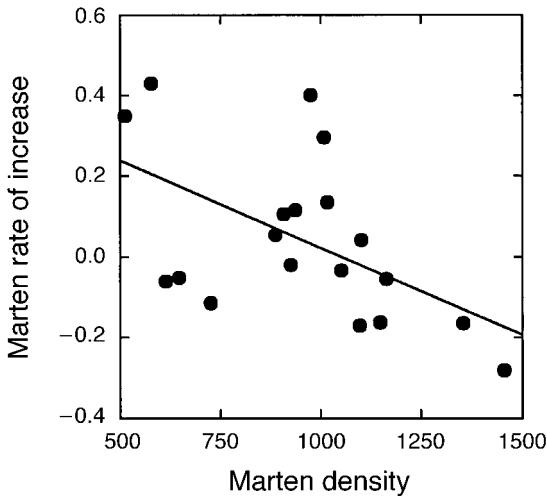


FIG. 2. The per capita rate of population growth by martens in relation to marten population density (no./Bracebridge district) the previous year.

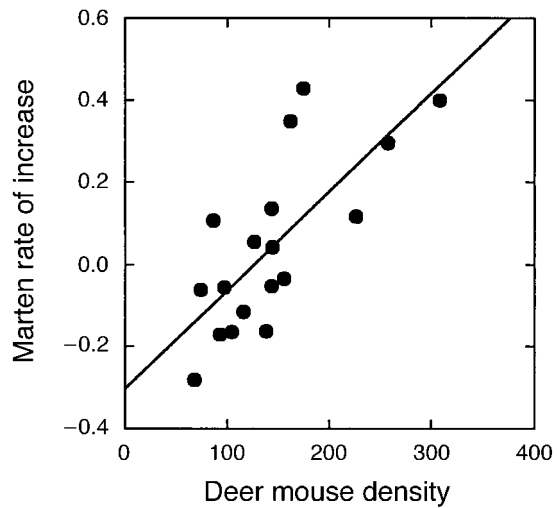


FIG. 3. The per capita rate of population growth by martens in relation to population density of deer mice.

1.40,  $P < 0.001$ ). The per capita rate of increase was positively related to the ratio of young per adult ( $r_t = -0.42 + 0.50 \times \text{young per adult}$ ;  $r^2 = 0.60$ ,  $P < 0.001$ ), and there was marginal evidence that young per adult was negatively related to marten population density the previous year (young per adult =  $1.43 - 0.00053P_{t-1}$ ;  $r^2 = 0.18$ ,  $P = 0.07$ ).

The per capita rate of growth of marten was positively related to population densities of deer mice (Fig. 3;  $r_t = 0.0024N_t - 0.30$ ,  $r^2 = 0.54$ ,  $P < 0.001$ ), red squirrels (Fig. 4;  $r_t = 0.075N_t - 0.15$ ,  $r^2 = 0.44$ ,  $P = 0.003$ ), and flying squirrels (Fig. 5;  $r_t = 0.18N_t - 0.12$ ,  $r^2 = 0.45$ ,  $P = 0.002$ ). In each case, the explanatory power of the prey-dependent term was greater than that of pure density dependence. We therefore proceeded to

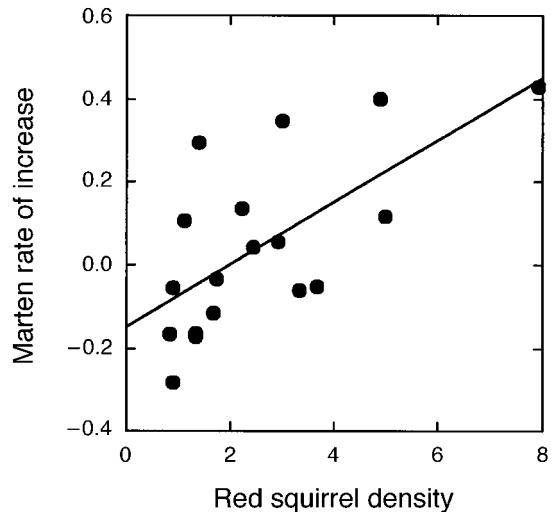


FIG. 4. The per capita rate of population growth by martens in relation to the population density of red squirrels.

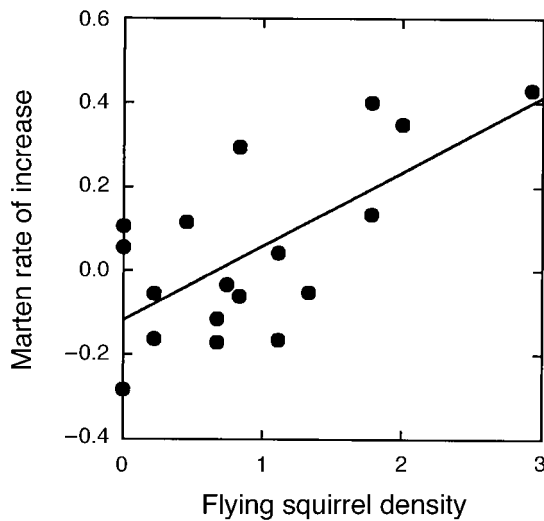


FIG. 5. The per capita rate of population growth by martens in relation to population density of flying squirrels.

use the PBLR test to evaluate whether a mix of prey-dependent and density-dependent processes significantly improved on predictions of instantaneous per capita rates of increase obtained from the Ricker logistic equation. The per capita growth rate of marten was negatively related to marten density, but positively related to deer mouse density ( $r_t = 0.059 - 0.00034P_{t-1} + 0.0022N_t$ ,  $r^2 = 0.72$ , PBLR test  $\Gamma = 2.45$ ,  $P < 0.001$ ). The per capita growth rate of marten similarly related to population densities of martens and red squirrels ( $r_t = 0.056 - 0.00017P_{t-1} + 0.060N_t$ ,  $r^2 = 0.47$ , PBLR test  $\Gamma = 1.33$ ,  $P = 0.026$ ) or martens and flying squirrels ( $r_t = 0.12 - 0.00022P_{t-1} + 0.14N_t$ ,  $r^2 = 0.51$ , PBLR test  $\Gamma = 1.43$ ,  $P = 0.014$ ). In all three cases, the mixed model yielded significant improvement in predictive power over the pure Ricker logistic model. These results suggest that population dynamics of Algonquin martens are influenced by both prey availability and the density of martens.

There are strong theoretical reasons to expect that the numerical response to prey abundance should tend to saturate at high prey densities, due to the effect of a finite handling time in killing and processing each prey item (Holling 1959). Curvilinear numerical responses have been previously documented for other terrestrial mammals (Bayliss 1985, Messier 1994). On the grounds that we had already rigorously tested for both prey and density dependence, we fitted two different density-dependent functions: a Michaelis-Menten function with an additional density-dependent term and a ratio-dependent function with predator density in the denominator of the numerical response. The Michaelis-Menten function for marten preying on deer mice ( $r_t = 6.96N_t/[6.36 + N_t] - 6.29 - 0.00030P_{t-1}$ ) explained 64% of the temporal variation in marten growth rates. The ratio-dependent numerical response

for marten preying on deer mice ( $r_t = 2.07N_t/[0.14 + N_t + 0.55 \times P_{t-1}] - 0.42$ ) explained 74% of the temporal variation in marten growth rates. Both nonlinear models had similar explanatory power as the linear model, but the ratio-dependent model performed marginally better than the Michaelis-Menten model. The lack of improvement in predictive power using nonlinear formulations probably stems from the fact that there is only slight curvature in the relationship between marten rates of increase and prey population density (Figs. 3-5).

There was a significant negative effect of harvest intensity (i.e., the proportion of martens harvested each year) on the per capita rate of increase by martens (Fig. 6;  $r_t = 0.50 - 1.26 \times \text{harvest intensity}$ ,  $r^2 = 0.34$ ,  $P = 0.009$ ). This negative effect of harvest intensity was detectable in addition to density-dependent effects on the rate of population growth ( $r_t = 0.72 - 0.00032P_{t-1} - 1.01 \times \text{harvest intensity}$ ,  $r^2 = 0.49$ ,  $P = 0.024$  for harvest coefficient), or a mixture of density-dependent and prey-dependent effects imposed by deer mice ( $r_t = 0.27 - 0.00029P_{t-1} + 0.0019N_t - 0.63 \times \text{harvest intensity}$ ,  $r^2 = 0.78$ ,  $P = 0.045$  for harvest coefficient). Harvest intensity was unrelated, however, to marten population density ( $P = 0.23$ ) or time ( $P = 0.29$ ). Marten pelt prices were fairly static during this period (Strickland and Douglas 1987), so it is perhaps not surprising that there was no detectable long-term trend in harvesting pressure. These patterns suggest that harvest acted as a stochastic external variable in addition to density-dependent and prey-dependent processes occurring within the small mammal assemblage.

#### Local stability

Our previous work has shown that deer mice, red squirrels, and flying squirrels have density-dependent population growth (Fryxell et al. 1998). Trophic models

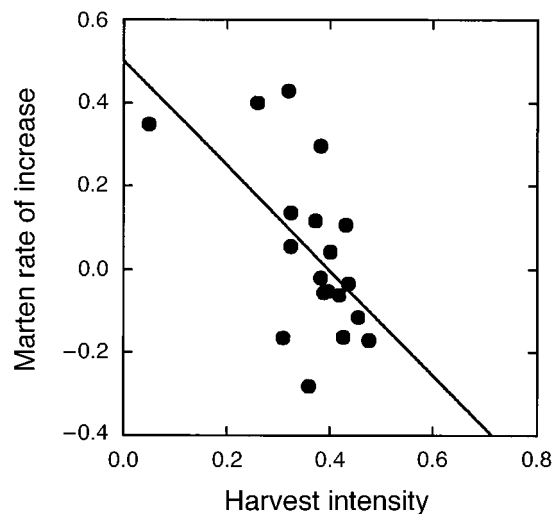


FIG. 6. The per capita rate of population growth by martens in relation to harvest intensity.

in which prey are density dependent and predators have linear functional and numerical responses are often locally stable, so we concentrate here on the nonlinear forms (with Michaelis-Menten or ratio-dependent functional and numerical responses). A simple dynamical description of a Michaelis-Menten system that exhibits density-dependent and prey-dependent demographic processes is as follows:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - \frac{eNP}{b + N}$$

$$\frac{dP}{dt} = \frac{aN}{b + N} - cP - dP^2$$

where  $r$  = the maximum per capita rate of increase by prey,  $K$  = prey carrying capacity,  $e$  = maximum rate of consumption by predators,  $a - c$  = maximum per capita rate of predator increase, including the effects of trapping,  $b$  = prey population density at which the per capita rate of predator growth is one-half maximum and  $d$  = per capita negative effect of conspecifics on the predator rate of increase. All other parameters were defined earlier.

One can approach such systems by analyzing local stability conditions: parameter combinations that yield point equilibria vs. those that produce perpetual population cycles. For the simple predator-prey systems we are considering, local stability depends on the magnitudes of the community matrix coefficients  $\alpha_{NN}$ ,  $\alpha_{NP}$ ,  $\alpha_{PN}$ , and  $\alpha_{PP}$ , where  $\alpha_{NN} = \partial(dN/dt)/\partial N|_{N^*,P^*}$ ,  $\alpha_{NP} = \partial(dN/dt)/\partial P|_{N^*,P^*}$ ,  $\alpha_{PN} = \partial(dP/dt)/\partial N|_{N^*,P^*}$ , and  $\alpha_{PP} = \partial(dP/dt)/\partial P|_{N^*,P^*}$  (May 1973, Pimm 1982, Yodzis 1989). These coefficients represent the effect of a slight change in population densities of prey and predator on their respective rates of increase near points of equilibrium ( $N^*$  and  $P^*$ ). When  $\alpha_{NN} + \alpha_{PP} < 0$  and  $\alpha_{NN}\alpha_{PP} - \alpha_{NP}\alpha_{PN} > 0$ , then this implies that the negative feedbacks supercede the positive feedbacks and the community will approach a stable point equilibrium. On the other hand, when these conditions do not hold, then this implies that the positive feedbacks near equilibrium supercede the negative feedbacks and the populations will exhibit stable limit cycles rather than a stable point.

For a carnivore that is purely prey dependent, there is no direct density-dependent mortality ( $d = 0$ ), so the community matrix coefficients are calculated in the following way:

$$\alpha_{NN} = r - \frac{2rN^*}{K} - \frac{eP^*}{(b + N^*)^2} \quad \alpha_{NP} = -\frac{eN^*}{b + N^*}$$

$$\alpha_{PN} = \frac{abP^*}{(b + N^*)^2} \quad \alpha_{PP} = 0.$$

There are only two parameters for this dynamical system that we cannot estimate for the Algonquin populations of predators and prey:  $e$  (the maximum rate of consumption by the predator) and  $K$  (the intrinsic carrying capacity of the prey).

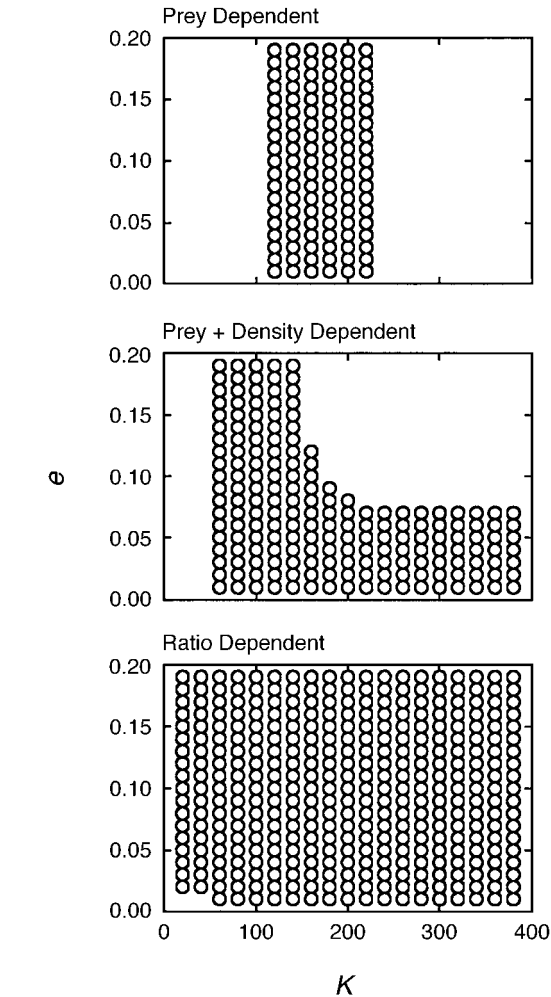


FIG. 7. Locally stable parameter combinations for a continuous model of predator-prey dynamics with only prey dependence (top), with both density dependence and prey dependence based on a Michaelis-Menten formulation (middle), and with ratio-dependent predation (bottom). All parameters were estimated from the Algonquin populations of deer mice and martens, with the exception of  $e$  (the maximum consumption rate by marten) and  $K$  (the carrying capacity of deer mice).

rying capacity of the prey). The range of stable parameter combinations for the pure prey-dependent system is quite narrow (Fig. 7).

For a carnivore that is both prey dependent as well as density dependent,  $\alpha_{NN}$ ,  $\alpha_{NP}$ , and  $\alpha_{PN}$  are calculated in exactly the same ways as for a pure prey-dependent system, but the carnivore coefficient takes on a nonzero value:

$$\alpha_{NN} = r - \frac{2rN^*}{K} - \frac{eP^*}{(b + N^*)^2} \quad \alpha_{NP} = -\frac{eN^*}{b + N^*}$$

$$\alpha_{PN} = \frac{abP^*}{(b + N^*)^2} \quad \alpha_{PP} = \frac{aN^*}{b + N^*} - c - 2dP^*.$$

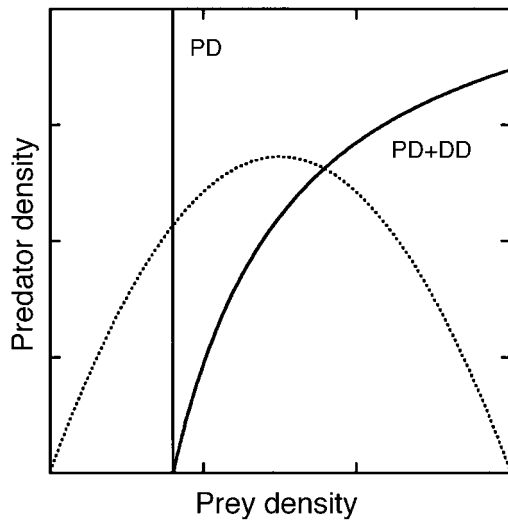


FIG. 8. Zero growth isoclines for prey-dependent (PD) vs. prey-dependent plus density-dependent (PD + DD) models. Note how density dependence can cause the intersection of the prey and predator isoclines to occur to the right of the hump in the prey isocline, conferring local stability.

The range of stable parameter combinations can be larger for the system with a predator that is both prey dependent and density dependent than it is for the system with a predator that exhibits no density dependence (Fig. 7), particularly when maximum consumption rates are low (small  $e$ ).

A useful way of understanding this stabilizing effect is to examine the zero growth isoclines, i.e., the combinations of predators and prey at which either population is unchanging. Regardless of model, the prey zero isocline is a hump-shaped curve in the predator-prey phase plane (Fig. 8). Pure prey dependence produces a vertical isocline (labeled PD in Fig. 8), implying that the rate of predator population growth depends on the quantity of prey available. When the predator isocline intersects the prey isocline to the left of the hump, the system is intrinsically unstable (Rosenzweig and MacArthur 1963, Rosenzweig 1971, Gilpin 1972, May 1972, Murdoch and Oaten 1975, Tanner 1975). That is because the positive feedback effect of predation (due to the saturating functional response) is stronger than the negative feedback effect of intraspecific competition among prey. Hence, prey tend to increase faster than can their predators, at least at low levels of predator abundance. As the prey population gets large, its own density dependence slows the rate of prey increase, whereas predators continue to increase. Eventually the sheer abundance of predators is such that they decimate the prey population. Predators soon decline, completing the demographic cycle.

In contrast, predators exhibiting both density dependence and prey dependence (labeled PD + DD in Fig. 8) have a saturating zero isocline, intersecting the horizontal axis at the same point as for the pure prey-

dependent system, but becoming increasingly bent as predator density increases (Rosenzweig and MacArthur 1963, Fryxell and Lundberg 1997). This density-dependent displacement of the predator isocline can be sufficient to cause an intersection to the right of the hump in the prey zero isocline, conferring stability, where the negative feedback of prey competition is stronger than the positive feedback of a decelerating functional response (Fig. 8). Trophic models incorporating both prey dependence and density dependence are accordingly more stable than their prey-dependent counterparts (Rosenzweig and MacArthur 1963, May 1973, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989, Ruxton et al. 1992, Fryxell and Lundberg 1997), due to depression in predator growth rates as the predator population gets large. Hence, many parameter combinations that would be unstable for a purely prey-dependent predator are stable for a predator exhibiting both density dependence and prey dependence.

A simple dynamical description of a ratio-dependent system that exhibits density-dependent and prey-dependent demographic processes is as follows:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - \frac{eNP}{b + N + dP}$$

$$\frac{dP}{dt} = \frac{aN P}{b + N + dP} - cP.$$

The community matrix coefficients for the ratio-dependent system are calculated in the following way:

$$\alpha_{NN} = r - \frac{2rN^*}{K} - \frac{eP^*(b + dP^*)}{(b + N^* + dP^*)^2}$$

$$\alpha_{NP} = -\frac{eN^*(b + N^*)}{(b + N^* + dP^*)^2}$$

$$\alpha_{PN} = \frac{aP^*(b + dP^*)}{(b + N^* + dP^*)^2}$$

$$\alpha_{PP} = \frac{aN^*(b + N^*)}{(b + N^* + dP^*)^2} - c.$$

The range of stable parameter combinations is also much larger for the ratio-dependent system than it is for the system with a predator that exhibits no density dependence (Fig. 7). Hence, combinations of prey dependence and density dependence in the predator numerical response tend to have a stabilizing influence on population dynamics, irrespective of whether those effects are represented by Michaelis-Menten or ratio-dependent formulations.

These food chain equations represent a minimalist representation of the dynamics of the Algonquin mammal assemblage. We have left out terms for stochastic variation in weather conditions or seed crops, thought to have a strong influence on forest rodent populations (Pucek et al. 1993, Wolff 1996, Elkinton et al. 1997, J. B. Falls and E. A. Falls, unpublished data). Perhaps

most importantly, we have left out any representation of harvest dynamics, in order to focus on the biological interactions among the Algonquin mammal assemblage. Although our work shows that harvest intensity is an important stochastic factor for martens, it is readily accommodated by the density-independent growth terms.

#### DISCUSSION

Our results indicate that population growth rates of Algonquin martens are affected by both marten density as well as the density of their small mammal prey. Previous studies have shown that martens have catholic feeding habits, including small mammals, insects, and berries, but small mammals form a sizeable component of the marten's diet (Weckworth and Hawley 1962, Francis and Stephenson 1972). So it is not surprising that we found demographic links between population changes of small mammals and the dynamics of mustelid predators, as documented over shorter time spans in Ontario (Thompson and Colgan 1987) and elsewhere (Tapper 1979, King 1983). In much of Canada, snowshoe hares form a large part of the diet of martens (Strickland and Douglas 1987) and marten harvest totals in Canada are historically well synchronized with those of snowshoe hares (Bulmer 1974, 1975). We have no population data for snowshoe hares in our study area, so we cannot comment on whether they influence marten dynamics as strongly as do other small mammals in Algonquin. We certainly found no suggestion of a 10-yr cycle in marten abundance in our study area that would be reminiscent of that of snowshoe hares.

Evidence of strong linkage between prey density and the per capita rate of increase by marten is exciting from a practical perspective. Wildlife managers are often challenged with setting harvest quotas without knowing current population densities. Our results suggest that >70% of the variability in annual rates of marten increase can be predicted on the basis of past marten densities and current densities of deer mice. This suggests that monitoring of small mammal population dynamics could be useful in setting harvest levels appropriate to the biotic potential for marten population growth.

There are many ways one could algebraically represent such trophic interactions, and we showed three such depictions: linear, Michaelis-Menten, and ratio-dependent formulations. The predictive power of the nonlinear Michaelis-Menten and ratio-dependent models were not substantially better or worse than that of the linear numerical response model, suggesting that none of the algebraic formulations was demonstrably more useful than the others. On the grounds of mathematical simplicity, one might argue for primacy of the linear formulation. On the other hand, biological considerations favor the nonlinear formulations.

The evidence currently available for the Algonquin marten population is inadequate to discriminate among

these alternate mathematical "hypotheses." For one thing, there may be too little variability in our small mammal or marten populations to detect nonlinear growth terms. Moreover, simulation models indicate that imprecise population estimates of both predators and prey (the so-called error in variables problem) can affect model fitting in such a way that leads to a statistical bias favoring incorrect linear models over the correct nonlinear models (Carpenter et al. 1994). This suggests we should use caution in dismissing nonlinear trophic models in favor of simpler models purely on the basis of their statistical explanatory power.

The combination of prey dependence and density dependence could explain the demonstrated stability of Algonquin martens as well as their small mammalian prey (Fryxell et al. 1998). A truly rigorous test of this hypothesis can only come from direct experimentation, but it is encouraging that the empirical dynamical characteristics of the Algonquin mammal assemblage are consistent with the documented patterns of density dependence and prey dependence. Similar stability properties have been demonstrated in other small mammal populations in which territoriality plays an important regulatory role (Saitoh 1987, 1991, Stenseth et al. 1996, Saitoh et al. 1997). On the other hand there are many examples of cyclic territorial species (Hanski et al. 1991, 1993, Sinclair et al. 1993, McLaren and Peterson 1994, Messier 1994, Hanski and Korpimäki 1995, Krebs et al. 1995), so territoriality per se is not sufficient to guarantee community stability.

The biological explanation for prey dependence is obvious: predators encounter prey more frequently when prey are abundant than when prey are rare. This is simply another way of saying that Algonquin martens have positive functional and numerical responses to increased prey density. It is also possible, however, that the positive association between marten rates of growth and prey density reflects common responses to stochastic environmental variation. According to this alternate hypothesis, years with favorable climatic conditions produce abundant deer mouse and squirrel populations that simply happen to coincide with above-average population growth by martens. The trophic and climatic hypotheses can be best discriminated by further manipulative experiments, which are currently underway.

It seems likely that direct density dependence in the Algonquin marten population stems from aggressive interactions. This could arise from interference with search due to agonistic interactions with conspecifics (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Sutherland and Parker 1985, 1992, Ruxton et al. 1992, Holmgren 1995, Moody and Houston 1995). The frequency of agonistic encounters should covary positively with carnivore density but negatively with prey density (the latter because feeding predators are unlikely to be interfering predators). As a consequence, interference can lead to a stabilizing combi-

nation of both prey dependence and predator density dependence (Beddington 1975, DeAngelis et al. 1975, Ruxton et al. 1992, Fryxell and Lundberg 1997).

Territorial strife could also explain the observed numerical response by martens. If one assumes that the frequency of territorial disputes increases with the number of territory holders, a particularly likely proposition if territory size is linked to both resource and predator density (Dill 1978, Schoener 1983, 1987, Stephens and Dunbar 1993, Schneider and Yodzis 1994, Fryxell and Lundberg 1997), then one might reasonably expect the frequency of territorial aggression to scale proportionately with predator density. If one assumes furthermore that there is an inherent risk of mortality during aggressive encounters with conspecifics, then this should contribute a strong stabilizing density dependence to the predator numerical response (DeAngelis et al. 1975, Fryxell and Lundberg 1997).

Several previous behavioral studies have concluded that martens, like most mustelids (Powell 1979), are indeed territorial. Marten of both sexes are territorial, with individuals apparently avoiding members of the same sex and foraging in different locations, with extensive overlap in territories across sexes (Francis and Stephenson 1972, Taylor and Abrey 1982, Balharry 1993). Studies in Great Britain show that home range size is linked to population density, which is consistent with either resource-based territorial defense or simply intolerance of infanticide by neighboring conspecifics (Balharry 1993). Ontario studies have shown that marten respond to declining prey abundance by home range expansion, reduced offspring recruitment, increased cannibalism, increased dispersal from the natal range, and eventually reduction in marten population density (Thompson and Colgan 1987). Similar numerical responses to changes in prey abundance have also been recorded in stoats in New Zealand (King 1983). These previous studies suggest (1) that martens are probably territorial, (2) that territory size and local population density of martens are possibly linked to food density, and (3) that intraspecific aggression has the potential to increase marten mortality rates.

If territoriality and other agonistic interactions have such a powerful stabilizing influence, then one might well wonder why other populations of territorial predators cycle (Hanski et al. 1991, 1993, Sinclair et al. 1993, McLaren and Peterson 1994, Messier 1994, Hanski and Korpimäki 1995, Krebs et al. 1995). The answer perhaps depends on the magnitude of other ecological parameters. Like most other forms of trophic interactions, predators whose rate of population growth depends on densities of both prey and other carnivores will only be stabilized for some parameter combinations (Fig. 7). Prediction of cyclic vs. noncyclic systems on the basis of ecological parameters should in principle be possible, providing a far more rigorous test of predator-prey theory than simple goodness of

fit. Unfortunately, we are probably still rather far from such ecological predictions.

Recent years have witnessed a fierce ecological debate about whether the rate of predator increase should be proportionate to the ratio of predators to prey rather than prey density alone, as has been proposed numerous times (Leslie 1948, May 1973, Powell 1980, Getz 1984, Arditi and Ginzburg 1989, Hanski et al. 1991, 1993, Akçakaya 1992, Gutierrez et al. 1994, Hanski and Korpimäki 1995). Several biological characteristics leading to ratio dependence have been postulated, including prey spatial heterogeneity, interference between consumers, and differences in the time scales that are demographically relevant at different trophic levels. Ratio-dependent models have peculiar mathematical properties, however, that are somewhat difficult to reconcile with the biology of real predators (Abrams 1994, Gleeson 1994). Although this is scarcely an appropriate place to thoroughly review the debate over ratio dependence, it is intriguing that ratio-dependent trophic models would lead to patterns of prey dependence and density dependence consistent with those recorded in our Algonquin marten population. We hasten to add, however, that such patterns are also well explained by conventional trophic models with density-dependent and prey-dependent terms.

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#### APPENDIX

Annual population estimates during 1972–1991 for three species of prey in Algonquin Provincial Park and martens in the Bracebridge District, Ontario. Symbols for each species are as follows: P.m. = *Peromyscus maniculatus* (deer mouse), T.h. = *Tamiasciurus hudsonicus* (red squirrel), G.s. = *Glaucomys sabrinus* (flying squirrel), and M.a. = *Martes americana* (marten).

Year	P.m.	T.h.	G.s.	M.a.
1972	320.00	6.67	0.33	512
1973	161.67	3.00	2.00	725
1974	115.67	1.67	0.67	646
1975	143.33	3.67	1.33	613
1976	73.75	3.33	0.83	577
1977	174.58	7.92	2.92	886
1978	126.25	2.92	0.00	936
1979	226.30	4.99	0.45	1051
1980	155.56	1.73	0.74	1016
1981	143.33	2.22	1.78	1163
1982	96.89	0.89	0.22	1101
1983	144.22	2.44	1.11	1148
1984	138.00	1.33	0.22	975
1985	308.22	4.89	1.78	1455
1986	67.56	0.89	0.00	1097
1987	92.67	1.33	0.67	925
1988	...	...	...	907
1989	86.00	1.11	0.00	1008
1990	257.50	1.39	0.83	1354
1991	104.17	0.83	1.11	1148