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Virtual population analysis (cohort analysis) was used to reconstruct past dynamics of a harvested population of martens *Martes americana* in the Bracebridge District of southern Ontario. Harvests in the Bracebridge District were managed using a quota system set by regional authorities. Quotas changed from year to year, apparently on the basis of past trapping success and variation in the proportion of young-of-the-year among harvested animals. The proportion of young in the harvest was a sensitive indicator of the annual rate of increase, whereas trapping success tended to be linked most strongly, in inverse fashion, with marten harvesting quotas. The proportion of martens harvested each year was constant, averaging 34%, despite 3-fold variation in marten abundance. This proportion was very close to the maximum sustainable yield (36%) for the population, suggesting that the management policy in the administrative unit was effective in the past in sustaining the source population as well as yielding high trapping returns. Monte Carlo simulation showed that proportionate harvesting, such as the policy in the Bracebridge District during 1972-1991, should be considerably less likely to lead to overharvesting than a constant quota policy, particularly at high average yields.

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One of the most challenging issues in wildlife management is developing robust methods for managing harvests to maintain long-term sustainability. Some wildlife species are simply too costly and difficult to census directly, particularly cryptic forest-living species. In such cases, population managers rarely have estimates of stock abundance upon which to base recruitment projections or harvest controls. As a consequence, management of such species is often reduced to informed guesswork. Moreover, wildlife managers often lack robust, yet simple, strategies for responding to year-to-year variation in resources.

Faced with similar challenges, fishery scientists have developed a variety of techniques for estimating abundance from catch-at-age data obtained from survey vessels or from harvesters themselves. One of the most simple of these techniques is known as virtual population or cohort analysis (Ricker 1940, Fry 1949, Quinn & Deriso 1999). Using a series of catches of known age composition, one uses a backward recursion formula to estimate the minimum number of individuals alive at a given point in time. Such catch-at-age estimators have been employed rarely by wildlife managers (McCullough 1979, Fryxell, Mercer & Gellately 1988, Fryxell, Hussell, Lambert & Smith 1991, Peterson 1999, Solberg, Sæther, Strand & Loison 1999) yet these techniques are just as appropriate for wildlife species as they are for fisheries.

In this paper, we report a 20-year time series of harvests of a mustelid carnivore, the American marten *Martes americana*, in mixed forests of southern Ontario. We first demonstrate how catch-at-age information may be applied to estimate population abundance. We show how changes in age ratios and harvesting success were related to changes in resource abundance. We then show how facultative responses to changing age distribution and trapping success allowed managers to maintain a constant level of harvesting mortality near the biological optimum for the population. This indicates that age-specific harvest data can be of considerable utility in managing harvests in a stochastic environment.

Methods

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 virtual population or cohort analysis. Harvesting in the Bracebridge District was regulated by trap-line 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 ageing 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. Trap-line 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 (Strickland & Douglas 1987, Dix & Strickland 1986).

Marten population estimates were derived using virtual population analysis, following the methodology outlined in Fryxell et al. (1988). The principle behind this population estimator is based on the use of a backward recursion formula to reconstruct specific contemporaneous cohorts of harvested animals to estimate minimum population abundance at various points in time. One estimates the number of individuals of age i in year t by $N_{i,t} = K_{i,t} + (N_{i+1,t+1}/p)$, 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, Harrison, Katnik & Elowe's (1994) radio-telemetry 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 $N_{i,t} = K_{i,t} /(1\text{-}\exp[-q_i])$ to estimate age-specific abundance in the terminal year, with the catchability coefficient q_i estimated from completed cohorts (Fryxell et al. 1988).

The cohort analysis population estimator relates to marten abundance at the beginning of the annual trapping period. Trapping is regulated by a quota system in Ontario, spanning several months in the autumn and winter. We subtracted the annual harvest in year t (H_t) from the abundance (N_t) recorded at the beginning of the trapping season to estimate post-harvest abundance ($\tilde{N}_t = N_t - H_t$), often termed escapement in the harvesting literature. We then calculated the exponential rate of population growth from the pre-harvest abundance in year t relative to the post-harvest escapement the previous year, according to $r_t = \ln(N_t/\tilde{N}_{t-1})$.

Results

The age distribution of martens harvested in the Bracebridge district is shown in Table 1 for males and in Table 2 for females. The vast majority of animals sampled were young individuals (1-3 years old), as is often recorded in harvested mustelid populations (Fortin & Cantin 1994, Krohn, Arthur & Paragi 1994, Strickland 1994). Males outnumbered females in the total carcass sample by a ratio of 2:1 (total males = 4,746, total females = 2,339), and a similar sex-ratio bias occurred in most years. Such a preponderance of males is typical in harvested mustelid populations (Strickland 1994).

We used cohort or virtual population analysis to reconstruct abundance in the live population. Our results indicate that younger individuals dominated the standing distributions in most years (Table 3 for males and Table 4 for females). Although martens had a potential life-span of at least 13 years in our study area, based on the oldest animal appearing in our trapped sample, it is apparent that remarkably few individuals survived even half that long, no doubt due to intense harvesting. We used 13 years as our terminal age in the cohort analy-

Table 1. Age composition of harvested male martens in the Bracebridge District during 1972-1991.

	Males harvested per age class (years)								
Year	0	1	2	3	4	5	6	7	Total
1972	13	5	1	0	0	0	0	0	19
1973	109	45	34	13	0	4	0	6	212
1974	100	27	27	8	8	0	2	0	174
1975	102	38	20	5	2	0	2	0	174
1976	53	35	14	4	4	1	0	0	118
1977	144	20	16	4	5	4	0	0	198
1978	115	56	27	8	5	2	2	2	215
1979	159	51	64	13	11	4	4	0	316
1980	110	70	17	9	5	2	2	0	214
1981	147	84	29	20	4	2	4	2	302
1982	139	84	35	18	2	2	0	2	284
1983	230	54	21	17	6	2	6	4	338
1984	82	53	27	4	4	0	0	0	173
1985	233	47	44	5	10	0	7	0	351
1986	104	151	45	6	4	6	0	2	324
1987	141	25	44	5	0	12	0	5	237
1988	156	61	11	26	4	5	4	2	275
1989	176	45	12	13	13	3	3	0	271
1990	175	76	9	5	2	2	0	4	285
1991	95	103	41	7	9	3	1	3	266

Table 3. Age composition of the male marten population prior to harvest in the Bracebridge District during 1972-1991.

	Estimated living males per age class (years)								
Year	0	1	2	3	4	5	6	7	Total
1972	133	85	34	20	14	12	18	3	325
1973	196	104	70	28	17	12	10	16	462
1974	213	76	51	31	14	15	7	9	430
1975	220	98	43	21	20	5	13	4	442
1976	161	103	51	19	15	15	4	10	394
1977	379	94	59	33	13	9	12	4	619
1978	242	205	64	37	25	7	5	10	608
1979	365	110	130	32	25	18	4	3	707
1980	323	179	52	57	16	12	12	0	662
1981	311	185	95	30	42	10	9	9	701
1982	319	143	89	58	8	33	7	4	666
1983	416	157	51	46	35	5	27	6	749
1984	292	162	90	26	26	26	3	19	650
1985	557	183	95	54	20	19	22	3	972
1986	201	281	119	44	43	9	17	13	741
1987	298	85	113	64	33	34	2	15	661
1988	266	137	52	60	52	29	18	2	635
1989	406	96	66	36	29	42	20	13	719
1990	564	201	44	47	20	14	34	15	954
1991	231	338	108	31	36	16	10	29	813

sis, leaving five years of completed cohorts for which unbiased estimates of harvesting mortality could be obtained.

Preponderance in the harvest sample (young vs old or male vs female) could arise in two different ways: some animals could be more vulnerable to trapping than others, or preponderance in the harvested sample could simply reflect high frequency in the live population. One way to discriminate between these possibilities is by comparing the risk of mortality due to harvesting for different population components from completed cohorts. Mortality risk due to harvesting was statistically indistinguishable in males and females (t = -0.397, P = 0.693), but mortality risk due to harvesting declined with age ($y = 0.369 - 0.0377x$; $r^2 = 0.08$, $F_{1,58} = 5.033$, $P = 0.029$). The preponderance of males in the harvest sample could therefore simply reflect their relative abundance in the live population (average male population = 646 and average female population = 332). A more likely explanation, however, is that natural mortality differed between the sexes, which would bias the overall magnitude of our reconstructed population estimates, but need not greatly bias the inferred population changes over time. Harvest vulnerability tended to decline with age in both sexes (Fig. 1).

The population abundance of martens varied 3-fold

Table 2. Age composition of harvested female martens in the Bracebridge District during 1972-1991.

	Females harvested per age class (years)								
Year	0	1	2	3	4	5	6	7	Total
1972	3	2	0	0	1	0	0	0	6
1973	69	21	24	0	2	2	0	0	118
1974	49	6	8	12	2	0	2	2	82
1975	25	18	16	2	5	5	2	0	82
1976	38	11	3	1	3	0	1	3	66
1977	65	9	7	2	2	4	0	0	89
1978	85	26	14	2	2	2	0	3	133
1979	75	27	33	4	0	0	0	0	142
1980	59	28	14	9	2	2	0	0	115
1981	88	29	20	4	0	2	0	4	149
1982	92	45	14	6	2	0	0	0	158
1983	82	26	21	6	7	2	6	2	151
1984	49	22	5	4	0	0	0	0	80
1985	111	10	20	10	12	7	2	0	172
1986	60	66	23	11	9	13	9	0	198
1987	64	8	31	3	5	3	0	0	116
1988	72	23	7	5	2	4	0	2	116
1989	82	17	12	0	0	0	0	0	114
1990	85	21	11	2	5	4	5	0	133
1991	46	43	14	5	3	1	3	1	119

Table 4. Age composition of the female marten population prior to harvest in the Bracebridge District during 1972-1991.

	Estimated living females per age class (years)								
Year	0	1	2	3	4	5	6	7	Total
1972	54	65	12	24	9	9	3	8	187
1973	105	44	55	10	21	7	7	3	263
1974	90	32	20	27	9	16	4	7	216
1975	53	36	22	10	13	6	14	2	170
1976	107	25	15	6	7	7	1	10	184
1977	165	60	12	11	4	4	6	0	267
1978	173	86	44	4	8	2	0	5	328
1979	182	77	53	26	2	5	0	0	353
1980	159	93	44	17	19	2	5	0	343
1981	303	87	57	26	7	15	0	4	502
1982	164	188	51	32	19	6	11	0	471
1983	165	63	124	32	23	15	6	10	438
1984	129	73	32	90	23	13	12	0	378
1985	257	69	44	23	75	20	11	10	516
1986	91	127	52	21	11	55	11	8	390
1987	125	27	53	24	9	3	37	2	292
1988	141	53	17	20	19	4	0	32	294
1989	149	60	26	9	12	15	0	0	304
1990	239	58	37	13	8	11	13	0	405
1991	103	134	32	23	10	2	6	7	339

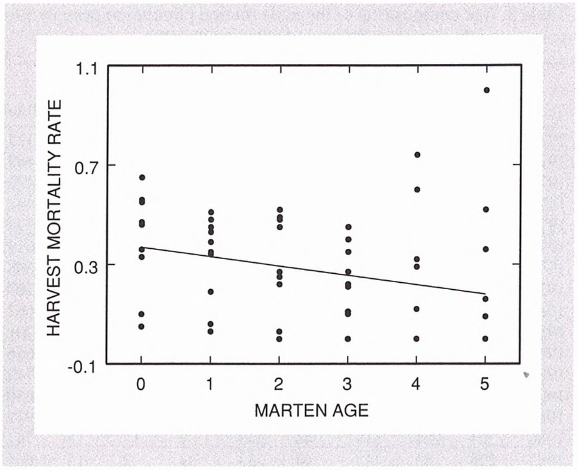

Figure 1. Risk of marten mortality due to trapping in relation to age, based on completed cohorts (1972-1977). Data for males and females were lumped because there was no statistically significant difference between sexes.

during the 1972-1991 study period (Fig. 2). This was reflected by even wider variation in trapping quotas and subsequent harvests. Harvests equaled or surpassed the allocated quotas in only four of 20 years, with harvest averaging 70% of the quota. This indicates that harvests were not constrained solely by management objectives, so we considered a range of factors that could conceivably influence success by trappers.

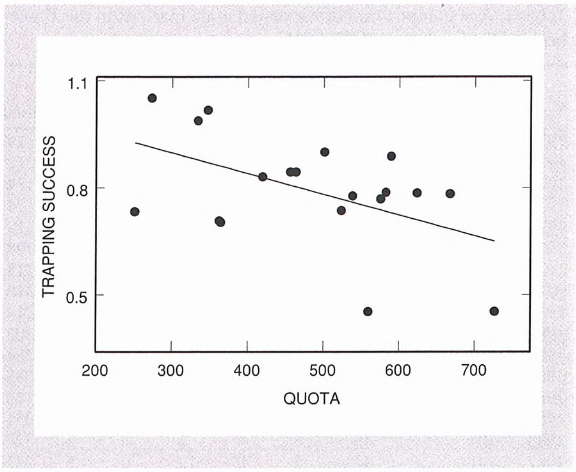

Figure 3. Trapping success in a given year in relation to the harvest quota set by management authorities.

Trapping success (% of the quota caught by trappers) was significantly related to the harvest quota ($y = 1.05 - 0.0005x$; $r^2 = 0.312$, $F_{1,18} = 8.161$, $P = 0.010$), such that low quotas tended to yield nearly 100% success, whereas high quotas led to 60-70% success (Fig. 3). By the same token, trapping success was marginally related to the proportion of young-of-the-year in the harvest ($y = 0.42 + 0.69x$; $r^2 = 0.185$, $F_{1,18} = 4.071$, $P = 0.059$). The latter pattern supports the point of view that success is related to availability of naive, young animals that are more vulnerable to trapping than are older animals, and that disperse widely across the forest landscape in search of a suitable territory.

Annual changes in quotas were significantly related to trapping success the preceding year (Fig. 4; $y = -364 + 484x$; $r^2 = 0.310$, $F_{1,17} = 7.63$, $P = 0.013$). Hence, years of high trapping success tended to lead to augmented quotas, whereas the opposite occurred in years following low trapping success. There was an even stronger relationship between changes in quotas and the proportion of young in the previous year's harvest (Fig. 5; $y = -538 + 1000x$; $r^2 = 0.415$, $F_{1,17} = 12.05$, $P = 0.003$).

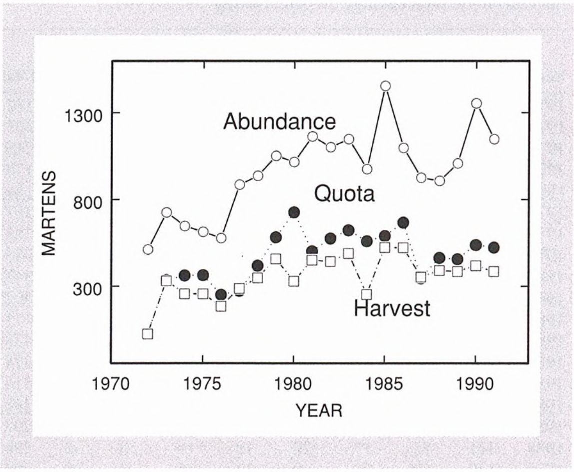

Figure 2. Estimated population size, harvest quota and harvest of martens from the Bracebridge District, Ontario, during 1972-1991.

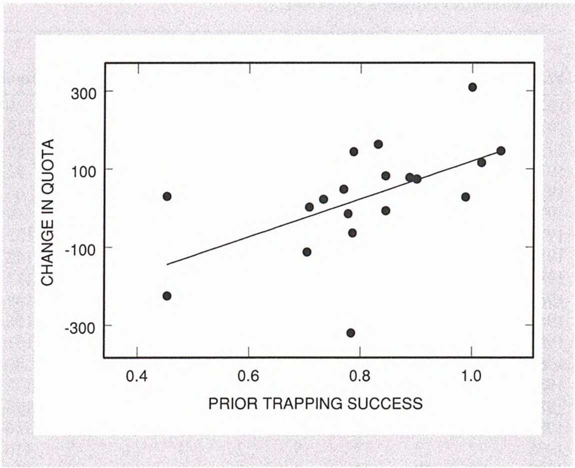

Figure 4. Annual changes in the quota of harvested martens in relation to trapping success the preceding year.

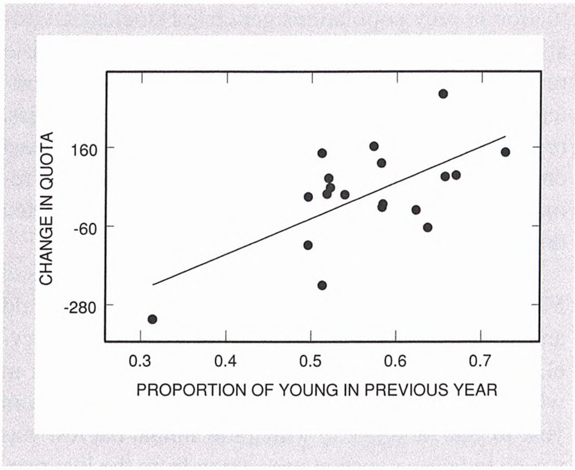

Figure 5. Annual changes in the quota of harvested martens in relation to the proportion of young in the preceding year's catch.

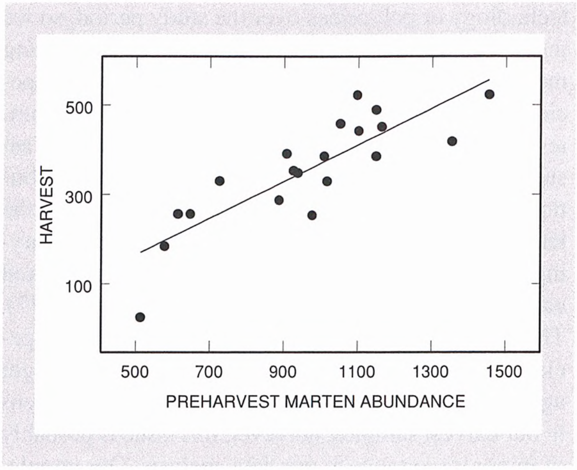

Figure 7. Annual marten harvest in relation to pre-harvest marten abundance in the Bracebridge District, Ontario, during 1972-1991.

The picture that emerges is one in which years with strong offspring recruitment tended to lead to high trapping success and a subsequent increase in quotas. This is not surprising, because resource managers in the Bracebridge District were committed to a policy of closely monitoring changes in juvenile recruitment to assess the sustainability of trap-line quotas (Strickland 1994).

Because population managers did not have information on population abundance, however, they had no way of assessing whether population growth rates were actually responsive to changes in the proportion of young in the harvest. Our reconstructed population estimates indicate that there was a strong positive relationship, as presumed by local resource managers, between the exponential rate of increase and the proportion of young in the harvest (Fig. 6; $y = -0.305 + 1.471x$; $r^2 = 0.77$, $F_{1,17} = 58.1$, $P < 0.001$). Hence, scaling of quotas to changes in the proportional harvest of young was an efficient means of responding quickly to changes in population growth potential. As a result of this policy, trappers harvested a constant 34% of the marten live population (Fig. 7; $y = 37.34 + 0.34x$; $r^2 = 0.67$, $F_{1,17} = 34.6$, $P = 0.016$).

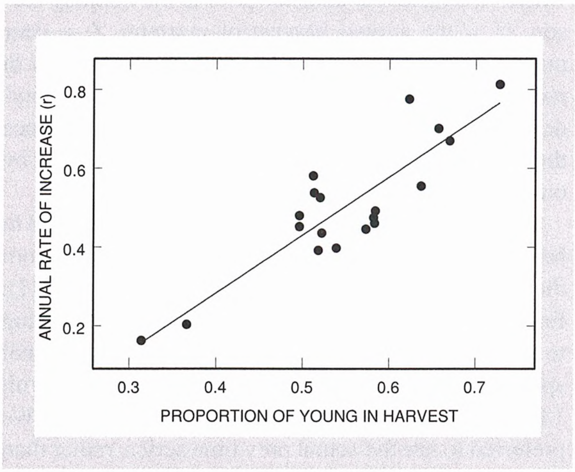

Figure 6. Annual rate of increase by marten in relation to the proportion of young found in the harvest sample.

Discussion

Application of cohort analysis to catch-at-age data for martens provided a useful source of information for evaluating ecological interactions as well as harvest dynamics in southern Ontario. To our knowledge, there have been no previous publications on the use of catch-at-age techniques for estimating temporal changes in fur-bearer abundance. The short life-span of small fur-bearers, ease of handling carcasses, precise methods for ageing animals, and governmental requirement for precise enumeration of fur-bearer harvests provide ideal conditions for applying catch-at-age methodologies. Such information could be enormously useful in evaluating site-specific as well time-specific variation in fur-bearer abundance and costs much less than direct field methods for population censusing.

Like any population estimator, however, there are a number of key assumptions that must be considered. Cohort analysis assumes that trapping methods 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 this assumption is defensible. Harvesting methods tend to change fairly slowly for fur-bearer species, perhaps because trapping is an ancillary economic activity for many individuals. The method also assumes that there is no sample error in the age distribution sampled in the terminal year. Sample error in the terminal year affects prior population estimates to varying degree, with most recent years greatly affected and earlier years little affected (Pope 1972, Ulltang 1977). This potential bias is most serious for long-lived species or for species in which harvesters avoid younger age groups. Given the preponderance of young martens in our harvest samples, however, this issue is probably of minor importance to our data analysis. Our population estimator is also affected by variation in natural mortality rate, particularly if it is large relative to the harvest mortality rate. Hence, sex-specific differences in natural mortality could lead to the skewed sex ratios estimated for the live population. Finally, our method of cohort analysis assumes that trapping effort has remained relatively constant over time. This is probably not true, because quotas were variable, but without further information it is impossible to evaluate the magnitude of potential bias. We regard the latter two issues as priorities for future research.

Our earlier work has shown that population fluctuations in three small mammal species, *Peromyscus maniculatus, Tamiasciurus hudsonicus* and *Glaucomys sabrinus*, are correlated positively with changes in marten abundance in the Bracebridge District (Fryxell, Falls, Falls, Brooks, Dix & Strickland 1999). Fluctuations in *Peromyscus* populations in Ontario have been hypothesized to arise from tree seed production occurring during the preceding year, the magnitude of which is positively linked with summer temperatures the preceding year (J.B. Falls & E.A. Falls, unpubl. data). Hence, the carrying capacity of martens is at least partially dependent on stochastic weather conditions experienced earlier. Similar linkages between weather or seed fall and rodent abundance have been recorded in several other temperate (King 1983, Pucek, Jedrzejewska, Jedrzejewska & Pucek 1993, Elkinton, Healey, Buonaccorsi, Boettner, Hazzard, Smith & Liebhold 1996, Wolff 1996, McShea 2000) and tropical systems (Leirs, Stenseth, Nichols, Hines, Verhagen & Verheyen 1997, Lima, Keymer & Jaksic 1999). Prey-induced fluctuations in mustelid populations have also been recorded in several other studies (Tapper 1979, King 1983, Thompson & Colgan 1987, Hanski, Turchin, Korpimäki & Henttonen 1993, Hanski & Korpimäki 1995).

From a harvesting point of view, year-to-year fluctuation in prey populations generated stochastic variation in patterns of population recruitment by Ontario martens (Fryxell et al. 1999). By responding to short-term changes in age distribution and trapping success, regional managers were able to scale harvests to past changes in recruitment in such a manner that they removed a constant proportion (34%) from the marten population.

To evaluate the effectiveness of this policy, we used Monte Carlo simulation to predict the long-term yield and extinction risk associated with a given harvest level. We used two alternate harvesting policies, one in which the annual harvest (H_t) was held constant from year to year, and one in which the annual harvest was varied to take a constant proportion from the live population. The latter policy seems most consistent with the recent management of this population, whereas the former policy has been used in many other jurisdictions. In a sister publication, we will deal with other policies, such as harvesting above a stated threshold, which might be even better alternatives (Lande, Engen & Sæther 1994, Lande, Sæther & Engen 1997).

Population dynamics were based on our previous time series analyses of the Bracebridge marten population (Fryxell et al. 1999, J. Fryxell, unpubl. data). Stochastic terms precluded perfect prediction of population growth, as would occur in real-world applications. In each simulation, we set initial marten abundance at the highest population equilibrium that balances harvest and net recruitment. We then projected population dynamics of martens forward over time according to the following non-linear stochastic model:

$$N_t = (N_{t-1} - H_{t-1})\exp[0.57 + 0.0016Z_t - 0.0005(N_{t-1} - H_{t-1}) + \epsilon_t],$$

where N_t = marten abundance prior to the trapping season, H_t = the annual harvest of martens, Z_t = deer mouse abundance, and ϵ_t = unexplained variability in recruitment. This equation specifies that both density-dependent and density-independent processes influence the per capita rate of change by martens, as shown by our earlier work (Fryxell et al. 1999).

Stochastic variability in recruitment was assumed to be normally distributed, using the residual variance from the fitted Ricker logistic model (approximately 0.011). Each simulation was run for 46 years, corresponding to the length of our time series data for small mammal species (Fryxell, Falls, Falls & Brooks 1998), with 1,000 replicates for each parameter combination. We preferred to use the actual prey time series, rather than sample prey abundance from a general probability distribution, because small mammal fluctuations can

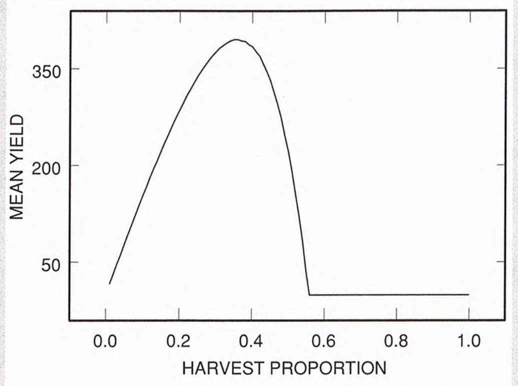

Figure 8. Arithmetic mean yield of martens during Monte Carlo simulations in relation to harvest proportion.

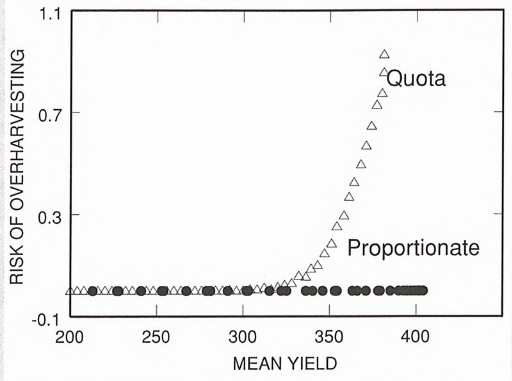

Figure 9. Risk of marten overharvesting (i.e. local extinction) in relation to mean yield for a constant harvesting proportion policy versus a constant quota policy.

have complex time dynamics that defy simplistic statistical representation (Hanski et al. 1993, Pucek et al. 1993, Hanski & Korpimäki 1995, Elkinton et al. 1996, Stenseth, Bjørnstad & Saitoh 1996, Wolff 1996, Leirs et al. 1997, Turchin & Hanski 1997, Stenseth, Falck, Chan, Bjørnstad, Odonoghue, Tong, Boonstra, Boutin, Krebs & Yoccoz 1998).

Results of the Monte Carlo procedure showed that the expected yield should be maximized at a harvest proportion of 36% (Fig. 8), very close to the observed average of 34% recorded during 1971-1990. Considering that regional managers had no direct estimates of population size, they did a remarkably good job of managing marten harvests, nearly maximizing the biological potential. It would be very useful to know why managers in Bracebridge did so well. This could stem from the close cooperation between trappers and regional managers, because a high proportion of trappers participated voluntarily in the age determination program. More important, in our view, were the strong links between population growth rate of martens, marten abundance, and the proportion of young animals in the harvest. Without this information, local managers would have been hard pressed to change harvest levels at appropriate times.

At proportionate harvests below 55%, the risk of overharvesting should be negligible (see Fig. 8), so the observed harvesting policy was ecologically safe, as well as being economically sound. By comparison, similar long-term yields obtained from a constant quota policy imply much greater risk of overharvesting, leading to local extinction (Fig. 9). While it seems unlikely that local extinction would be long-lived, given the pronounced dispersal capability of the species, such overharvesting is clearly undesirable for both social and biological reasons. Hence, constant proportion harvesting should be useful in reducing the risk of overharvesting in mustelid carnivores, as it is in many fisheries (Clark 1976, May, Beddington, Horwood & Shepherd 1978, Ludwig, Hilborn & Walters 1993, Rosenberg, Fogerty, Sissenwine, Beddington & Shepherd 1993, Hilborn, Walters & Ludwig 1995, Ludwig 1998). In recent years, however, some regional biologists have ceased usage of age-specific data that were previously used to monitor population changes, largely due to constraints on manpower and funding. This may lead to less responsive harvesting policies that could have negative ecological consequences, particularly if managers try to maintain quotas near the long-term yields obtained in the past.

Usage of weather data and monitoring data on small mammal abundance could further improve the management response to changing environmental conditions. Such an ecologically-based system of management should be relatively simple to implement as well as cost-effective. The long-term advantage of such a management policy, particularly in reducing the risk of overharvesting, can be considerable (J. Fryxell, unpubl. data).

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