

SIMULATION MODELING OF AMERICAN MARTEN (*MARTES AMERICANA*) POPULATIONS: VULNERABILITY TO EXTINCTION

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ABSTRACT.—American marten (*Martes americana*) are medium-sized mammalian carnivores inhabiting forest communities across northern North America. Martens are susceptible to local extinction from habitat alterations, trapping, and other factors. We (RCL) developed a population model called VORTEX to estimate extinction probabilities for marten populations as a management tool. The model permits managers to simulate various levels of timber harvesting, commercial trapping, and other factors to estimate their effects on marten populations. This paper describes this model and illustrates its benefits by using marten data from the Greater Yellowstone Ecosystem of northwestern Wyoming. Results are preliminary. Populations of 50 and 100 martens were simulated. The most optimistic scenario with populations of 100 individuals, no trapping, no logging, and no migrants showed a probability (66%) of surviving 100 years. Extinction probabilities were sensitive to immigration and emigration rates. Numerous scenarios were simulated and showed a range of results. Results of population viability analysis can be translated into area requirements if densities are known or can be estimated. In turn, various habitat patches and interconnecting corridors can be examined for their ability to support viable marten populations. Population modeling is invaluable to "adaptive management" of martens as well as other species.

Key words: adaptive management, American marten, demographic stochasticity, environmental variation, genetic variation, extinction, Greater Yellowstone Ecosystem, Population Viability Analysis, simulation modeling, wildlife conservation, *Martes americana*.

American marten populations are susceptible to local extinction from habitat alterations, trapping, and other factors. For this reason and because martens are sometimes considered an "indicator species" under the National Forest Management Act of 1976 by the U.S. Forest Service, it is important to have a means of estimating extinction probabilities for marten populations as a management tool. We developed such a means, a computer simulation model called VORTEX, that allows managers to carry out a population vulnerability assessment (Lacy 1993). This simulation permits managers to vary levels of timber harvesting, commercial trapping, and other factors and estimate their effects on marten populations. Population management targets can be explored with this procedure and, in the field, marten populations maintained that ensure their persistence in the face of foreseeable extinction pressures (e.g., habitat fragmentation). This paper describes this model and illustrates its utility in marten conservation and management.

The results presented in this paper are preliminary. They draw largely on marten popula-

tion data and environmental conditions in the Greater Yellowstone Ecosystem of northwestern Wyoming (Clark et al. 1989 [Demographic characteristics], Clark et al. 1989 [American marten]). The model can be rerun with better data from this area or data from other regions to estimate population vulnerability to local extinction under various conditions. This model has been used on a variety of rare and endangered species worldwide and has directly aided their conservation and management (e.g., Lacy et al. 1989, Seal and Lacy 1989, Lacy and Clark 1990, Maguire et al. 1990, Seal and Lacy 1990, Lindenmayer et al. 1991, Lindenmayer et al. in press). We are confident it can aid American marten conservation and management too.

EXTINCTION PROCESS

To understand how VORTEX works, one must first understand the extinction process (see Shaffer 1981, Gilpin and Soulé 1986, Clark et al. 1990 [Management]). As populations become fragmented and reduced in size, random fluctuations in population size can

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become more important determinants of persistence than whether mean population growth is positive. Four classes of factors affect marten population survival: demographic, environmental, catastrophic, and genetic variation. Fluctuations in population size can result from any or all of these four kinds of stochastic (random) effects.

Demographic variation results from the probabilistic nature of birth and death processes: Even if the probability of an animal reproducing or dying is always constant, we expect that the actual proportion reproducing or dying within any time interval will vary according to a binomial distribution with mean equal to the probability of the event (p) and variance given by $V = p * (1 - p) / N$. Demographic variation is thus intrinsic to the population and occurs because birth and death events are determined by random processes.

Environmental variation (EV) is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis or other time scales. Thus, EV impacts all individuals in the population simultaneously, changing the probabilities (means of the above binomial distributions) of birth and death. The sources of EV are thus extrinsic to the population itself, due to weather, predator and prey populations, parasite loads, etc.

At the extreme of environmental variation are events that could be termed catastrophes. Epidemic diseases, severe storms, forest fires, or floods might kill a substantial portion of individuals in a population or disrupt a breeding season. Such events can impact a population more severely than could be predicted from the normal range of environmental variation in reproductive and mortality rates. Moreover, such catastrophes are often the proximate cause of the final extinction of local populations. Catastrophes are individually rare and unpredictable, but most populations observed over a number of decades are likely to suffer one or more events that would commonly be termed catastrophes.

The transmission of genes is also a random process, and genetic variability is lost from small populations due to drift and inbreeding. Inbreeding can cause decline in fecundity and survival, exacerbating demographic problems and leading populations more rapidly toward

extinction (Wright 1977, Ralls and Ballou 1983, Ralls et al. 1988).

The combination of these random forces—demographic stochasticity, environmental variation, catastrophes, and genetic drift—destabilize small populations and mutually exacerbate the effects of each level of stochasticity. For example, the random loss of genetic variation that occurs as populations become small due to low fecundity and high mortality in turn causes further decreased fecundity, greater mortality, and susceptibility to environmental variation and catastrophes. The feedback among the various forces destabilizing small populations has been termed the “extinction vortex” (Gilpin and Soulé 1986).

POPULATION VIABILITY ANALYSIS

Population viability analysis (PVA) is a relatively recent procedure for estimating the viability of small populations of organisms (Shaffer 1981). Clark et al. (1990 [Population viability]:1) defined PVA as a “procedure that allows wildlife managers to simulate, using computer models, extinction processes that act on small populations, and therefore to assess their long term viability.” In both real and simulated populations, a number of interacting demographic, environmental, catastrophic, and genetic processes determine the vulnerability of a population to extinction. Life table analyses yield average long-term projections of population growth (or decline) but do not reveal the fluctuations in population size that would result from stochastic processes. Computer models can simulate the four interacting types of extinction processes, and the effects of both deterministic and stochastic forces can be explored. By using this procedure, one can also simulate the outcome of alternative management options, such as maintaining habitat or increasing it, reducing mortality, supplementing the population, or other management options. As a result, PVA gives managers a powerful tool to aid in determining the vulnerability of populations and in setting management targets. PVA is especially useful for managing rare and endangered species (Clark et al. 1989 [Designing and managing], Clark et al. 1990 [Management], Clark et al. 1990 [Population viability]).

PVA also provides quantitative predictions of population growth, demographic fluctua-

tions, and decay of genetic variation, based on explicitly stated assumptions. Thus, PVA can provide both an explicit model of population dynamics and the testable predictions that are necessary to bring the projection and management of wildlife populations into the realm of falsifiable science. The outcome of management based on PVA can provide a test of the adequacy of our understanding of the population dynamics, by comparison of quantified predictions to population performance, while achieving the goals of the management plan. PVA has also been coupled with other analytical approaches, such as risk assessment and decision analysis, to better manage species populations (Maguire 1986, Maguire et al. 1990).

VORTEX: COMPUTER PROGRAM FOR MODELING POPULATION DYNAMICS

The complex interactions among demographic and genetic factors as they can impact populations of American martens were examined by computer simulation modeling, using the program VORTEX. VORTEX is a powerful, but user-friendly, program for modeling vertebrate population behavior by way of Monte Carlo simulation of demographic and genetic events in the history of the population (Lacy 1993). Some of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James Grier of North Dakota State University (Grier 1980a, 1980b, Grier and Barclay 1988).

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, whether each adult female produces litters of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Fecundity is assumed to be independent of age (after an animal reaches reproductive age). Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. The mating system can be specified to be either monogamous or polygynous. In either case, the user can specify that only a subset of

the adult male population is in the breeding pool (the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females of each pre-reproductive age class, and a specified number of males and females of breeding age. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus, and the user specifies the severity of inbreeding depression (expressed in the model as an increase in juvenile mortality in inbred animals). The computer program simulates and tracks the fate of each population and then outputs summary statistics on the probability of population extinction over specified time intervals, the mean time to extinction of those simulated populations that went extinct, the mean size of populations not yet extinct, and the levels of genetic variation remaining in any extant populations.

A population carrying capacity is imposed by a probabilistic truncation of each age class if the population size after breeding exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically by selecting at the beginning of each year the population age-specific birth rates, age-specific death rates, and carrying capacity from distributions with means and standard deviations specified by the user. EV in birth and death rates is simulated by sampling binomial distributions, with the standard deviations specifying the annual fluctuations in probabilities of reproduction and mortality. EV in reproduction and EV in mortality can be specified to be acting independently or jointly (correlated in so far as is possible for discrete binomial distributions).

Unfortunately, rarely do we have sufficient field data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. (The population would have to be monitored for long enough to separate, statistically, sampling error, demographic variation in the number of breeders and deaths, and annual variation in the probabilities of these events.) Lacking any data on annual variation, a user can try various values, or set

EV = 0 to model the fate of the population in the absence of any environmental variation.

VORTEX can model catastrophes, the extreme of environmental variation, as events that occur with some specified probability and reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e., a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor specified by the user. Similarly, the probability of surviving each age class is multiplied by a severity factor specified by the user.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. These numbers of immigrants and removals are modeled as constants, not dependent on population size. VORTEX outputs the observed rate of population growth separately for the years of supplementation/harvest and for the years without such management, and allows for reporting of extinction probabilities and population sizes at whatever time interval is desired (e.g., summary statistics can be output at 5-year intervals in a 100-year simulation).

VORTEX can track multiple sub-populations, with user-specified migration among the units. The migration rates are entered for each pair of sub-populations as the proportion of animals in a sub-population that migrates to another sub-population (equivalently, the probability that an animal in one migrates to the other) each year. Because of migration (and, possibly, supplementation), there is the potential for population recolonization after local extinction. VORTEX tracks the time to first extinction, the time to recolonization, and the time to re-extinction.

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because VORTEX is a detailed model of population dynamics, it is not practical to examine all possible factors and all interactions that may affect a population. It is therefore incumbent upon each user to specify those parameters that can be estimated reasonably, to leave out of the model those that are believed not to have a substantial impact on the population of inter-

est, and to explore a range of possible values for parameters that are potentially important but very imprecisely known.

VORTEX is compiled for use on microcomputers running the MS-DOS (Microsoft Corp.) operating system. VORTEX and a manual describing its use are available from the office of the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124. Descriptions of the program structure and underlying assumptions are given in Lacy (1993). Detailed descriptions of the algorithms used in VORTEX, as well as the source code (in the C programming language), are given in Lindenmayer et al. (1991).

POPULATION BIOLOGY PARAMETERS FOR MARTENS

We modeled a variety of scenarios of marten population behavior (Fig. 1). For these preliminary analyses, age of reproduction, mean birth and age-specific death rates, degree of polygyny, and sex ratio were obtained from published studies. Age of first reproduction (time at which females give birth to their first litters) was set at 2 years for females, following the report by Strickland et al. (1982) that 80% of yearling females (approximate age 16 months) usually become pregnant, giving birth about 8 months later. Although males sexually mature as yearlings also, we assumed that males usually do not breed successfully until a year later (their first offspring born when sires are about 3 years of age).

Litter sizes were assumed to be typically 3 (60% of adult females), but occasionally smaller (25% of adult females producing litters of 2, 10% producing litters of 1, and 5% not breeding in an average year). The mean litter size produced by the distribution used is 2.53 (mean fecundity of adult females = 2.40, considering also the 5% that fail to breed). The sex ratio at birth was assumed to be 1:1 (Clark et al. 1987).

Breeding males have been reported to have home ranges large enough to encompass the territories of three females (Clark et al. 1989 [American marten]), and we therefore assumed that the average successfully breeding male mates with three females. Given the differential mortality assumed to act on the

Marten Population Vulnerability

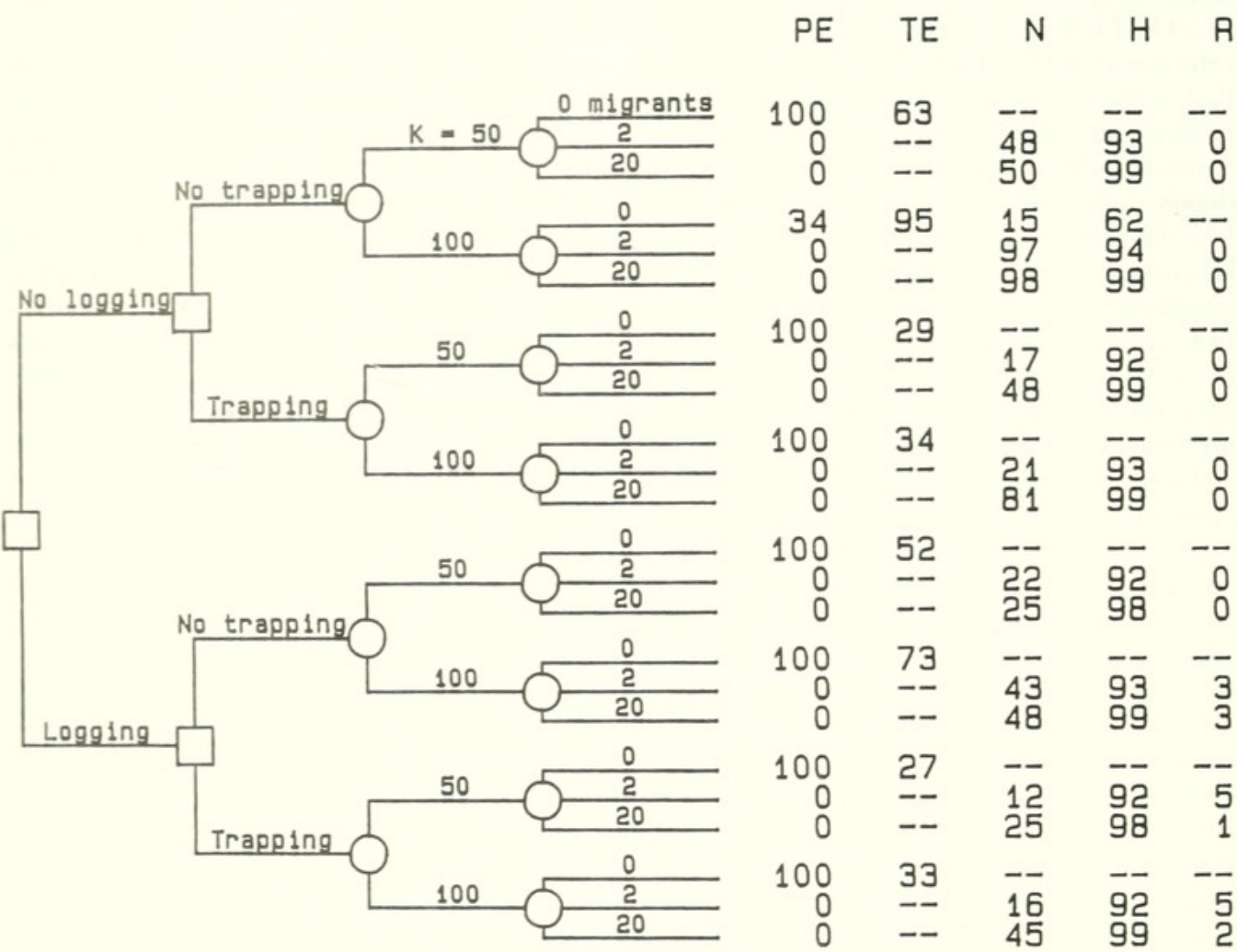


Fig. 1. Scenarios tested for population vulnerability, and results obtained from 1000 simulations of 100 years for each scenario. Nodes with boxes indicate management decisions; nodes with circles indicate random variables determined by population and habitat structure. See text for descriptions of scenarios. PE = probability of extinction; TE = mean time to extinction; N = mean number of martens in nonextinct populations after 100 years; H = mean percent of initial heterozygosity remaining in extant populations at 100 years; R = number of populations undergoing temporary extinction and recolonization during the 100-year simulation.

sexes (see below), and the delayed breeding by males, the expected ratio of adult (>2 years of age) males to adult (>1 year of age) females is 1:1.76 (obtained from life table analysis). Some adult males (37%) were assumed to be excluded from the breeding population, so that, with Poisson distribution of reproductive success, the mean successfully breeding male would sire 3.0 litters. (The calculations to determine the necessary proportion of adult males in the breeding pool to yield the desired degree of polygamy, given the age-sex structure of the population and a Poisson distribution of reproductive success, are done automatically by the VORTEX program.)

We assumed 50% first-year mortality (as reported by Strickland et al. 1982), 25% sec-

ond-year mortality of males, and 10% annual mortality of males older than 2 years and females older than 1 year. We further assumed that martens senesce after their tenth year. Given the mortality schedule, very few (about 0.25%) animals would live beyond 10 years of age, and the assumption of senescence in the model has very little impact on the results obtained.

Lacking any information on the impact of inbreeding on survival of martens, we modeled the effect of inbreeding depression by assuming that inbreeding would depress survival to the extent (3.14 lethal equivalents) reported by Ralls et al. (1988) as the median of 40 mammalian populations. This level of inbreeding depression reduces the survival of the progeny of full-sib matings by about 32%.

The populations studied by Ralls et al. were all captive (in zoos or research labs), provided with unlimited food, and protected from exposure to disease, predation, and inclement weather. The impact of inbreeding on wild populations may be greater if inbreeding reduces an animal's ability to cope with stresses.

Environmental variation in the above demographic parameters was modeled by assuming that the probability of breeding by adult females varies across years according to a binomial distribution with mean 95% (as described above) and standard deviation of 5%. Environmental variation in mortality rates was modeled for each age-sex class by setting the binomial standard deviation at one-fourth the mean (i.e., 50% \pm 12.5% first year mortality, 25% \pm 6.25% second-year mortality of males, and 10% \pm 2.5% annual mortality of adults).

Two types of catastrophes were modeled, each with a probability of occurrence of 1% each year of the simulation. The first type of catastrophe (e.g., disease) was assumed to kill, on average, 30% of the population but to have no effect on reproduction of the survivors. A second type of catastrophe (e.g., fire) was assumed also to kill 30% of the animals but then to reduce reproduction by 10% during that year.

Population size and migration between populations are likely to vary widely among populations, and we tested several possible values (populations of 50 or 100, with exchange of 0, 2, or 20 martens per year) to determine the sensitivity of a population to these parameters. The simulated populations were started at the stable age distribution calculated from the mortality schedule.

Finally, some aspects of the population dynamics are under direct control of resource managers. We examined the impact of trapping (modeled as a harvest of 20% annually) and logging (modeled as a loss of 1% of habitat per year over 50 years) on population viability to help define acceptable levels of human disturbance.

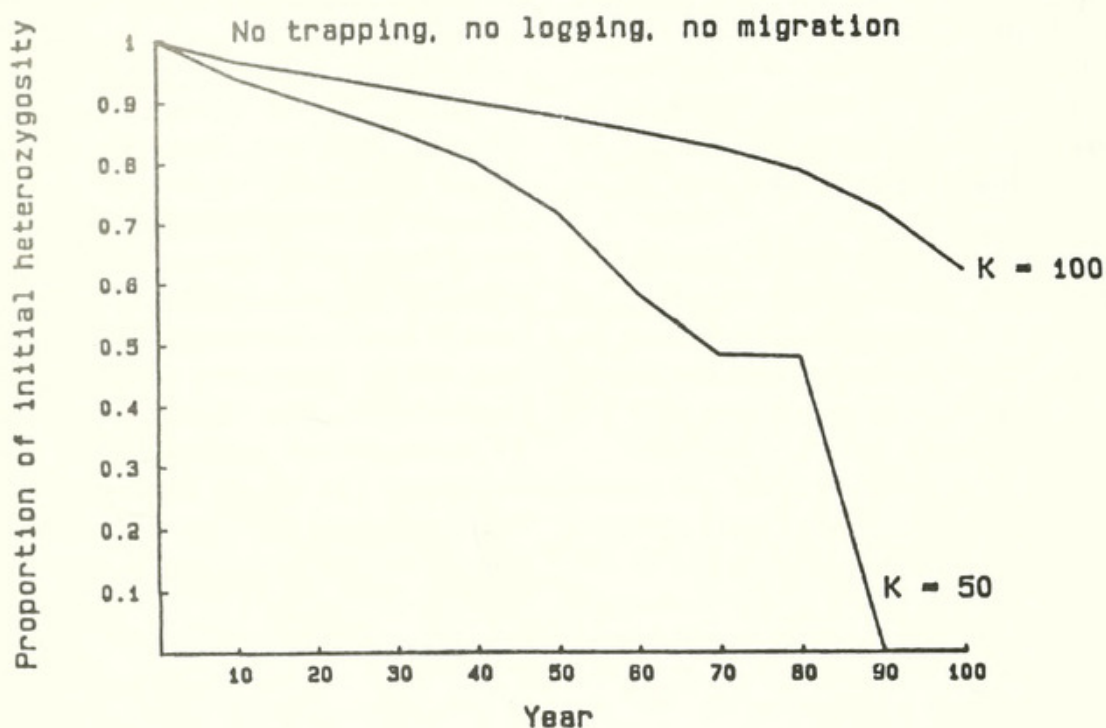
SIMULATION RESULTS

The marten population scenarios listed above were simulated, and results were expressed in terms of probability of extinction

(PE), mean time to extinction (TE), number of animals (N) remaining at the end of the simulation (in those simulated populations not extinct), mean percent of initial heterozygosity remaining (H), and number of recolonizations (R) out of 1000 simulations (Fig. 1). Each population was simulated for 100 years and was repeated 1000 times for each set of parameters. These results are not sufficient to specify precisely the vulnerability of marten populations to local extinction. Without detailed data on a specific population of interest, such conclusions cannot be obtained with the VORTEX simulation program or by any other technique. The results do, however, illustrate how computer simulation can be used to examine the vulnerability of marten populations under various possible scenarios. The scenarios examined might represent the range of plausible values of population parameters that are poorly known, or various possible management options, or (as illustrated below) both.

Life table analysis using the Leslie matrix approach (Leslie 1945), carried out by the VORTEX program in addition to stochastic modeling, yields a mean expected population growth rate of 29.2% with the basic birth and death parameters specified above, and 3.4% mean population growth under the scenarios with survival reduced by 20% due to trapping. Although mean population growth was initially positive in each scenario modeled (and growth observed in simulated populations closely matched the expected population growth calculated from the life table), genetic and demographic fluctuations resulted in high probability of population extinction in all cases in which the population was isolated from other populations. In the absence of exchange of migrants, only the most optimistic scenario (no trapping, no logging, carrying capacity of 100) had a probability (66%) of surviving 100 years (Fig. 1, line 4). Without immigration and emigration, the genetic variability was rapidly eroded in populations of 50 or 100 martens (Fig. 2a), resulting in steady reduction in viability (inbreeding depression) and eventually population crash to extinction (Fig. 2b). The exchange of just a pair of migrants per year was sufficient to prevent damaging losses of genetic variation (Figs. 3a,b). Exchange of 10 pairs per year (i.e., a population open to regular interchange) prevented

a



b

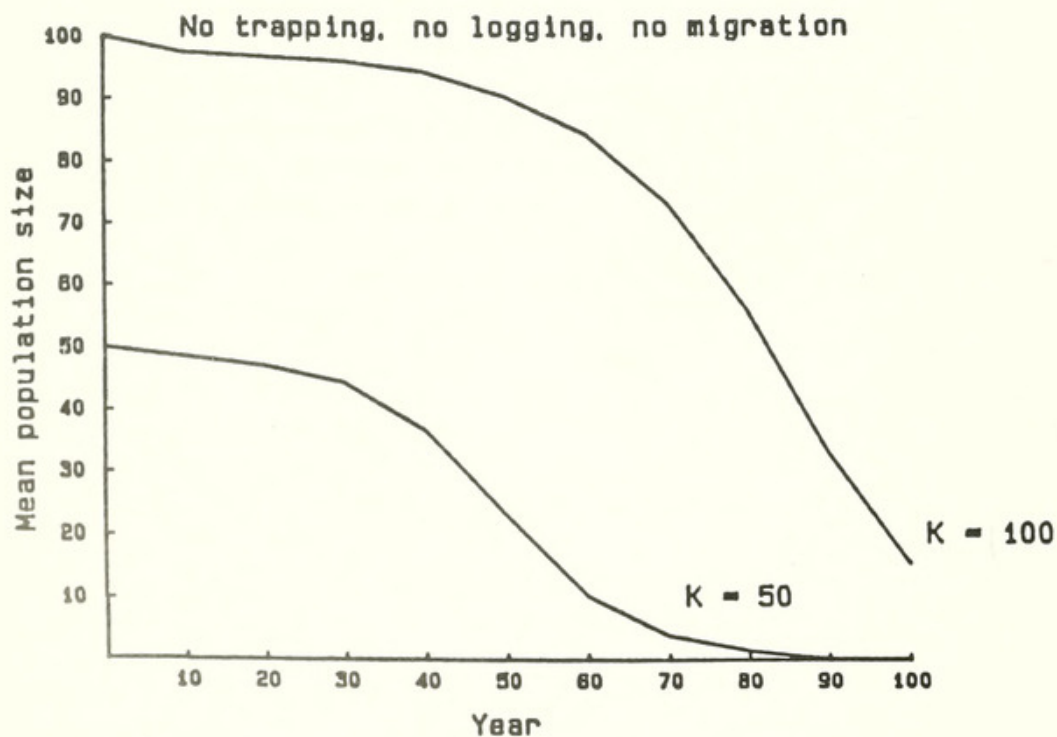


Fig. 2. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with no trapping, no logging of habitat, and no immigration or emigration, in habitats with carrying capacity (K) of 50 or 100.

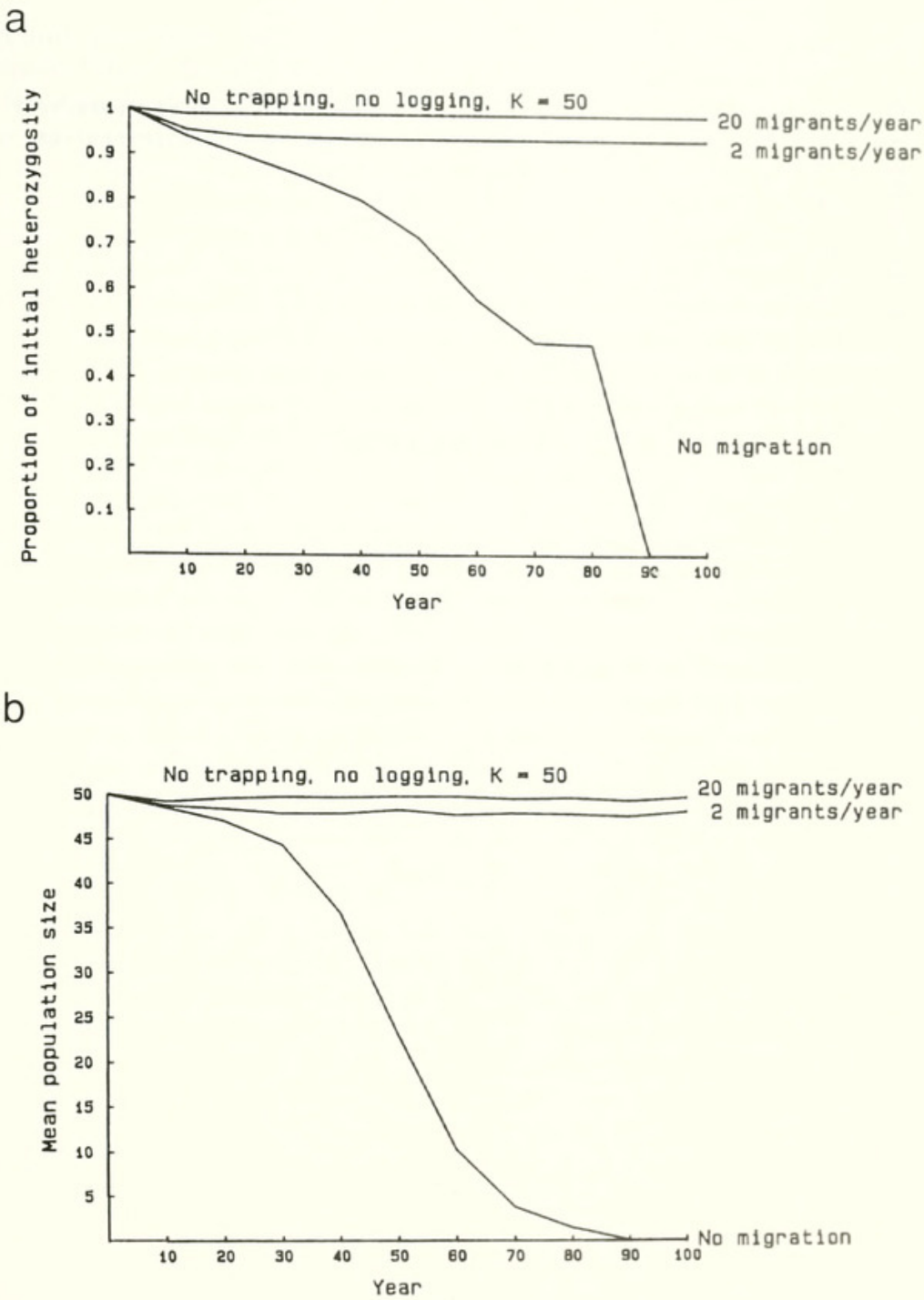


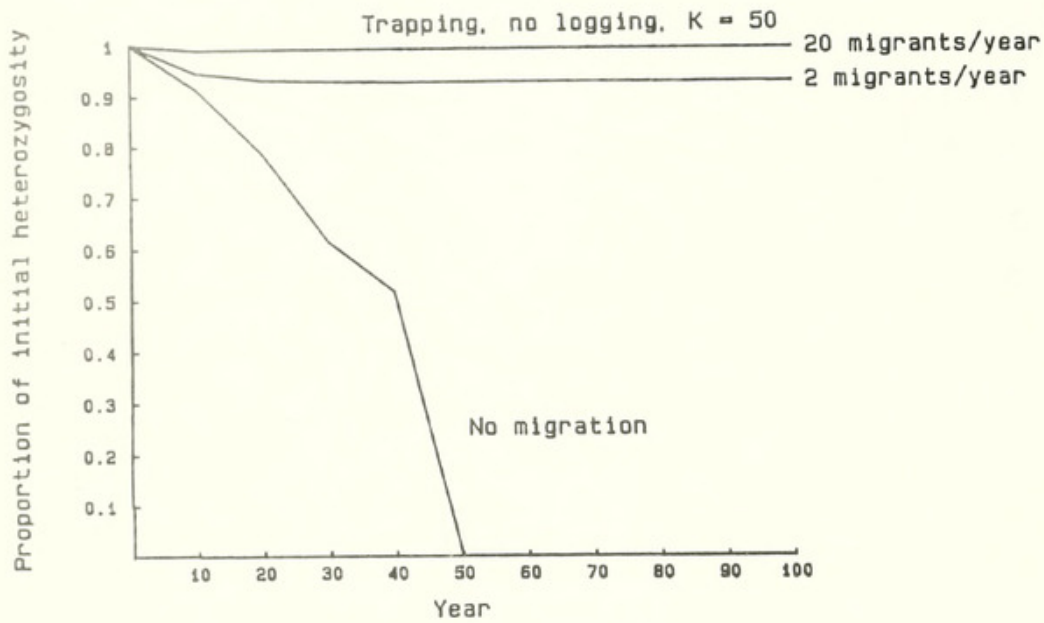
Fig. 3. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with no trapping, no logging of habitat, carrying capacity of 50, and 0, 2, or 20 migrants exchanged per year.

virtually any loss of genetic variation. In a few of the 1000 simulated populations in each scenario incorporating migration, the modeled populations went temporarily extinct due to random fluctuations in reproduction and mortality, but they were successfully recolonized by immigrants (Fig. 1, last column).

Trapping, removing 20% of each age class annually, accelerated the loss of genetic variation and consequent extinction in closed pop-

ulations but was sustainable in populations that received continued input of genetic variation via immigration (Figs. 4a,b). Logging, a reduction in 50% of the habitat (and therefore a reduction of 50% in the habitat carrying capacity) over 50 of the 100 years of the simulation, similarly accelerated inbreeding and extinction when there was no migration, but was also sustainable if genetic variation was continually restored via exchange with other

a



b

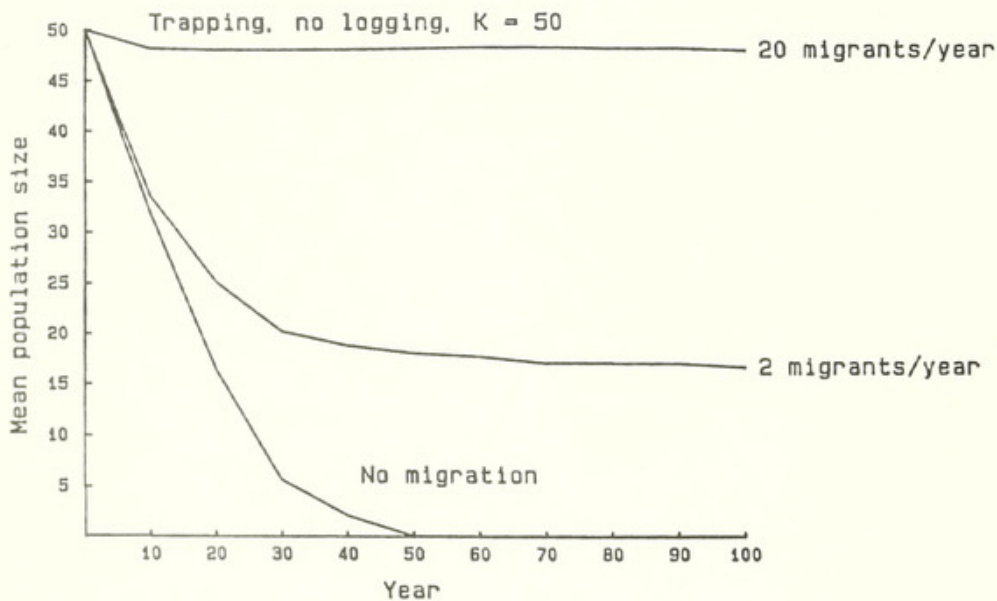


Fig. 4. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with survival of each age-sex class reduced 20% by trapping, no logging of habitat, carrying capacity of 50, and 0, 2, or 20 migrants exchanged per year.

populations (Fig. 1, lower half). When immigration was low into trapped and/or logged populations, the effects of inbreeding depressed the mean population sizes below the carrying capacities modeled but did not lead to steady erosion of population viability (see Figs. 4a,b, and compare lines of Fig. 1 with 2 migrants to adjacent lines with 20 migrants).

DISCUSSION

Population modeling is essential to "adaptive management" of martens and other species. Adaptive management uses actual management practices as an experiment to learn from, and modify as needed (Holling 1978). PVA not only permits trends in marten populations under current management to be

identified and quantified, but also permits determination of those factors that exert influence on the trends. Modeling population behavior is an important advantage in the conservation and management of populations. There are few, if any, other techniques currently available to synthesize the cumulative impacts of a complex of factors on a population (Lindenmayer et al. 1991). This is important because many recent studies have shown that the dynamics of populations change in relation to their size and context. As a result, PVA is useful in addressing key marten management questions. For example, (1) What is the relationship between population size and population stability? (2) At what population size do random events become important and which of these factors are most critical? (3) What population target will ensure marten population persistence in the management unit? Thus, PVA can be used to model these and other questions and the likely consequences of various management options.

The outcomes of management actions, which must be monitored to permit adaptive management, provide a test of the adequacy of the model and data used to guide the management and provide refined data for improving the accuracy of PVA that will be used to guide future management. As better data and better models become available, PVA modeling should be repeated and reexamined. Used in these ways, PVA can be a key tool in adaptive management and a powerful method for improving and testing our understanding of population biology.

It is important to recognize that, like any model of the natural world, the results of PVA are only as accurate as the data that are fed into the model. Moreover, while PVA allows exploration of the interacting effects of many population processes, any PVA model is still a simplified picture of the real world. Factors that are not modeled or not critically examined might be influencing population dynamics in unknown ways (Lindenmayer et al. in press). Critical management plans should therefore incorporate margins of error appropriate to the uncertainty about the completeness of the models used, the accuracy of the data, and the potential cost of failed management.

PVA is useful in identifying declining marten population trends at an early stage,

the essence of adaptive management, thus allowing populations to be managed appropriately before they become highly vulnerable to extinction. PVA can help identify population processes that are likely to endanger a population in the future if corrective management actions (e.g., development of corridors to allow genetic and demographic exchange) are not taken. Management of a species is relatively inexpensive and organizationally simple when multiple healthy populations still exist compared to when the species becomes endangered (Clark et al. 1989 [Designing and managing]).

Results of the marten PVA can be translated into area requirements needed by local populations. For illustration, assume that a manager wants to maintain a marten population, and because of circumstances beyond his control, with no possibility of immigration. The preliminary PVA results in Figures 1 and 2 indicate that well over 100 individuals are needed. If a male and three female marten occupy about 3 km², 100 martens would require 75 km². PVA results, combined with field studies of home ranges, can be used to determine habitat area needed for wild marten populations. Various combinations of habitat patches and interconnecting corridors can be examined, in part, through PVAs to explore extinction probabilities and management options. Additionally, management options can be further explored by coupling PVA with decision analysis (Maguire et al. 1990). PVA combined with decision analysis, using reliable field data on marten populations, offers the best adaptive management approach currently for this fascinating forest carnivore.

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