

POPULATION ECOLOGY OF MARTEN (*MARTES AMERICANA*) IN THE BOREAL FORESTS OF NORTHERN ONTARIO

Final report for NSERC, Forest Ecosystem Research Cooperative Inc,
Canadian Forest Service, and Ontario Ministry of Natural Resources

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OBJECTIVES

The American marten (*Martes americana*) is a forest carnivore species presumed to rely on patches of mature, conifer-dominated forest for its continuing persistence across a broad, heterogeneous landscape. It has been accordingly designated as an indicator species, whose ecological requirements must be met before any forest harvesting project in Ontario can be approved, as stipulated by Forest Management Guidelines set by the Ontario Ministry of Natural Resources. Recent scientific literature, however, reports anecdotal and experimental evidence that martens may be able to sustain themselves in regenerating forests with sufficient suitable structure. For the past 6 years, we have been engaged in a collaborative research programme to evaluate the sustainability of martens in regenerating forest landscapes. Goals of the programme are to compare the following ecological characteristics in mature, uncut forests with those in younger forests that are regenerating from prior forest harvesting:

- forest structure
- population dynamics of small mammal prey
- marten hunting success and body condition
- marten dispersal patterns
- marten home range use
- population dynamics of marten
- sources of mortality in martens
- marten population viability

This document summarizes our research findings at study sites near Ear Falls (2001-2005) and Kapuskasing (2003-2007). In the interests of promoting readability we have omitted description of methods and statistical details. All differences between treatments discussed below are statistically significant ($P < 0.05$) or consistent with most plausible models identified using information theoretic approaches. A full presentation of methods, statistical analyses and supporting models is under preparation as a published scientific monograph, tentatively scheduled for completion by December 2008.

RESEARCH ACHEIVEMENTS

Forest structure

The first step in our landscape analysis was to conduct detailed forest mensuration, needed to categorize complex forest landscapes of varying stand age, recent burn history, stand composition, and ecological productivity due to variation in underlying geomorphology. We have partitioned the Ear Falls

and Kapuskasing study sites into 13 predominant forest types (FRI categories) using ARCVIEW GIS. A wide variety of vegetation characteristics were measured in each stand type, including species composition and biomass of the canopy and shrub layer, snag abundance, canopy closure, stem density, ground cover, woody debris, and small mammal abundance (Thompson et al. 2007). One key difference between logged and unlogged forests is the abundance of coarse woody debris on the forest floor. Our data from Ear Falls show a substantial difference between landscapes in the abundance of coarse woody debris (Fig. 1), which can have important impact on foraging success and prey abundance for martens (Thompson et al. 2007; Andreuskiw et al. 2008).

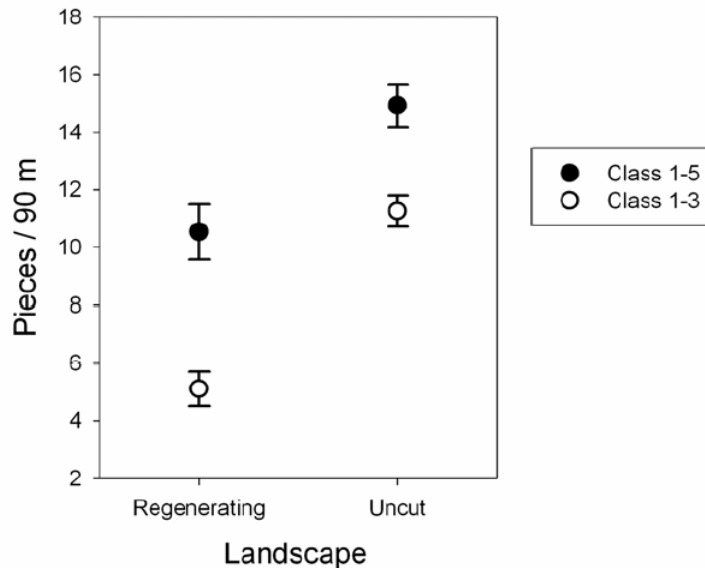


Fig. 1. Comparison of coarse woody debris in regenerating vs. mature uncut forests in Ear Falls.

We divided the logged landscape at Kapuskasing into two distinct habitat types, owing to past harvest and post-harvest treatment: horse-logged and cut mechanically. We did this because age and regeneration patterns differ markedly in the two types. Horse-logged are blocks that were logged in the 1930's and 1940's using horses to haul wood to a river. In this treatment, trees smaller than about 10-15 cm and conifer shrubs were left, dominated by black spruce and balsam fir. These stands are now conifer-dominated with moss ground cover and significant coarse woody debris with trees averaging about 12-15 m. Mechanically logged sites are about 30-45 years since cutting, are dominated by deciduous and mixed forests averaging about 8-12 m in height, have substantial coarse woody debris but with ground cover dominated by litter and herbaceous plants. Much of the mechanically logged areas were treated with post-harvest silviculture, including planting (spruce spp.), tending (aerial herbicide), and in some cases were scarified prior to planting.

Forest mensuration data from a large range of stand types and ages allowed us to compare values for variables important as marten habitat from these sites to information from the published literature, and to the information collected at Ear Falls. We are also able to take advantage of an updated (2004) forest resource inventory (FRI) within our GIS database for this study area, provided by Tembec Inc. Preliminary modelling of the data indicate that values for marten habitat variables, such as coarse woody debris, canopy cover, tree density, snag density, etc. are all within the range of values shown in previous work to be useful for marten, for all our forest types: machine-logged, horse-logged, and unlogged (natural fire origin). An ordination among the forest sites (Fig. 2) suggests that discriminating between horse-logged and uncut sites, based on variables important to marten is not possible, indicating that horse-logged sites should maintain marten populations. Lower values for variables, such as woody debris were reflected in separation of mechanically logged sites.

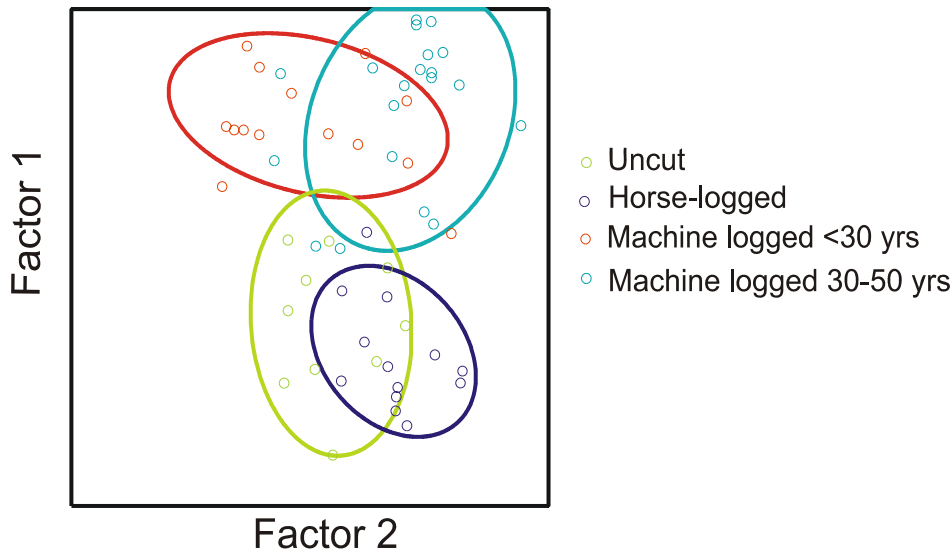


Fig. 2. Discriminant function ordination of forest stands at Kapuskasing.

Using the Ear Falls data, we tested the accuracy of forest resource inventory (FRI) mapping by measuring tree species composition and density on 129 forest stands (Thompson et al. 2007). For each stand we did a chi-square analysis to determine significant differences between interpreted and ground data and then tallied differences to achieve percent error by stand type. We also combined stands and ground results within larger areas of 1, 2 and 5 km radii to determine whether or not errors were compensatory over large areas. We then used the corrected information in the contemporary Ontario forest modeling process to compare long-term, large-scale results of errors to modeled results from the original FRI. For this model we compared available harvest volumes for important species and habitat availability for six wildlife indicator species. We observed that 83 of 129 stands were incorrectly classified by species composition. Approximately 30% were misclassified by broad forest categories of conifer, mixed or deciduous. Common boreal species, including jack pine, black spruce and trembling aspen were incorrectly classified in about half the cases. Rates of misclassification among species between ecosystems were inconsistent. Errors were not compensatory across larger areas when stands were combined. Modeled results indicated that resulting errors in available harvest volumes were compensatory in the jack pine-black spruce dominated forests, but in the black spruce-mixedwoods ecosystems, between 10 and 20% less softwood fiber was available than was predicted from the original FRI. This result would have financial implications for forest companies. Errors in tree species classification altered preferred habitat availability for some wildlife species but not sufficiently to suggest lack of forest sustainability. The implications for researchers seeking specific stand types is that they should expect a 30-60% error rate, depending on classification, and select additional stands to ground-truth accordingly.

Small mammal populations

Small mammals have been sampled in representative forest stands over 1500 trap nights per year at Ear Falls. Red-backed voles were an order of magnitude more abundant than any other species. Because voles are a major component of marten diets, spatial and temporal variation in vole abundance is an obvious candidate for evaluating putative differences in fitness across habitats. Our data show significant variation at the stand level, due to a positive association between vole abundance and deciduous composition (Figs. 3-4). This suggests that conifer stands, which are often preferred marten habitat, do not necessarily supply higher abundance of prey in this region of Ontario, unlike the Manitouwadge area in central Ontario. While there has been substantial seasonal and annual variation in abundance, overall the means are virtually identical across both landscapes (31.1 individuals caught per 100 trap nights in the unlogged vs. 31.4 in the logged treatment).

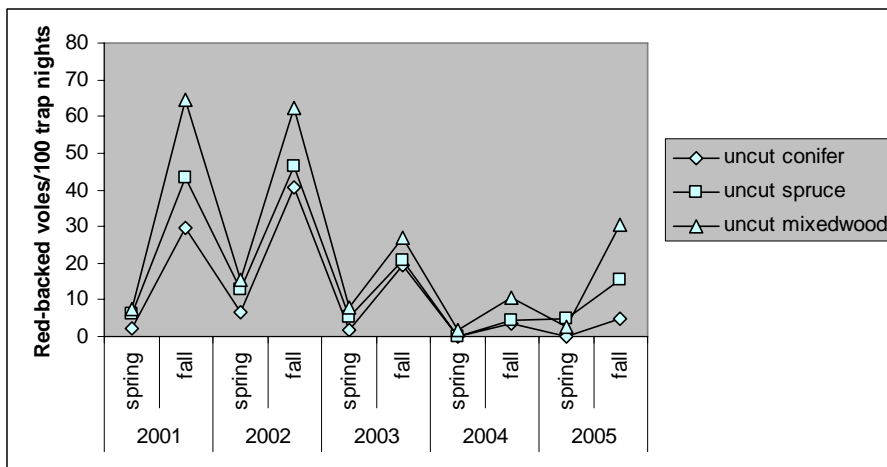


Fig. 3. Red-backed vole abundance during spring and fall trapping periods in 2001-2005 in various stand types in the unlogged landscape in Ear Falls.

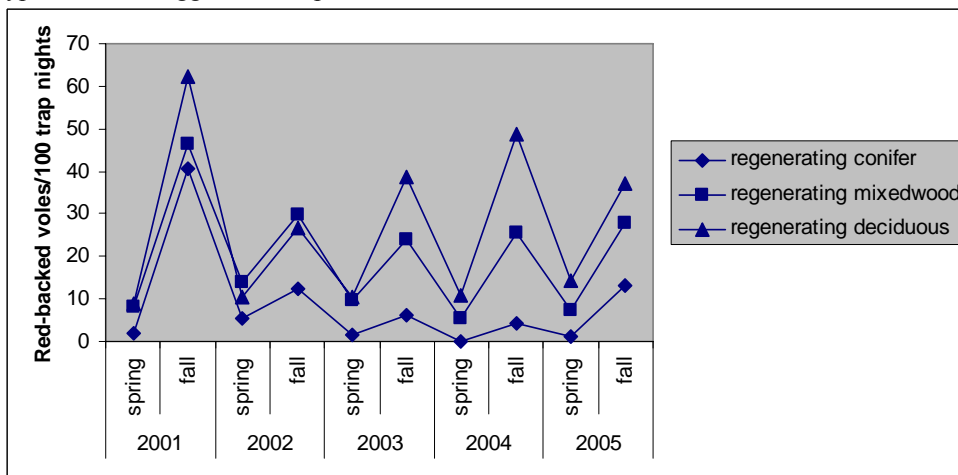


Fig. 4. Red-backed vole abundance during spring and fall trapping periods in 2001-2005 in various stand types in the logged landscape in Ear Falls.

The exponential rate of population change by red-backed vole populations at Ear Falls was well predicted by a habitat-specific Gompertz model ($R^2 = 0.39$) that ranked as the most parsimonious among a set of 9 alternative models (Akaike weight = 0.86). This suggests that year to year variation in vole populations is density-dependent, with higher population size and faster growth rates in habitats with more deciduous cover (Fig. 5).

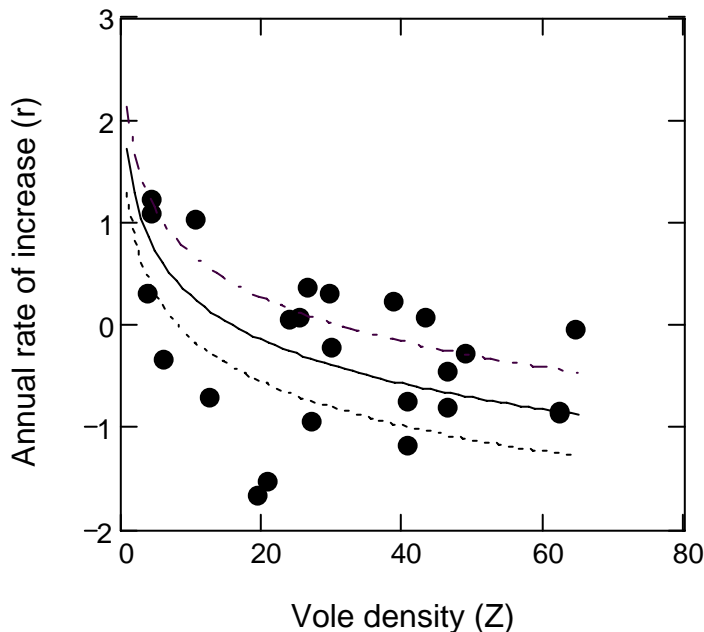


Fig. 5. Exponential growth rate of red-backed voles in deciduous (dashed line), mixed (solid line), and coniferous (dotted line) forest stands.

Small mammal data from Kapuskasing (Figs. 6-8) provided an informative contrast to the patterns observed at Ear Falls. Numbers of the two major species, red-backed voles and deer mice, were extremely low at the beginning of our field study. Red-backed voles began to recover in 2005 and 2006. Deer mice although higher in 2006, did not show a pronounced increase in abundance until fall 2007, when numbers tripled or greater in most sites, except horse-logged sites where numbers did not recover. We observed wide variation in abundance among stands within treatments in 2006, but this was reduced in 2007. In 2007, numbers of red-backed voles were lower than in 2006 while deer mouse numbers rose markedly. Two interesting patterns were observed for red-backed voles in Kapuskasing. First, population recovery of red-backed voles started 1 year earlier (2005) in horse-logged forests than in all other sites but was not so pronounced in 2007. Second, there was exceptionally high over-winter survival of animals during the winter of 2005-06 in all sites, which probably reflected exceptionally mild over-winter conditions. Although over-winter survival is understood to be variable in red-backed voles, the latter result is previously unknown in boreal forests. Overall, densities of red-backed voles at Kapuskasing were much lower than at Ear falls. The lowest number of voles at Ear falls was >4 times greater than the low at Kapuskasing in unmanaged forests. Further, numbers of red-backed voles were on average >3 times higher in mature uncut forests than in mechanically logged forests, unlike at Ear Falls where the means were equivalent during the study. The mean density of red-backed voles in Kapuskasing (6.6 in mature uncut forests and 2.0 in regenerating forests) was substantially lower than in Ear Falls (31.1 in mature uncut forests and 31.4 in regenerating forests). There was no consistent difference in small mammal abundance between coniferous and mixed stands in Kapuskasing.

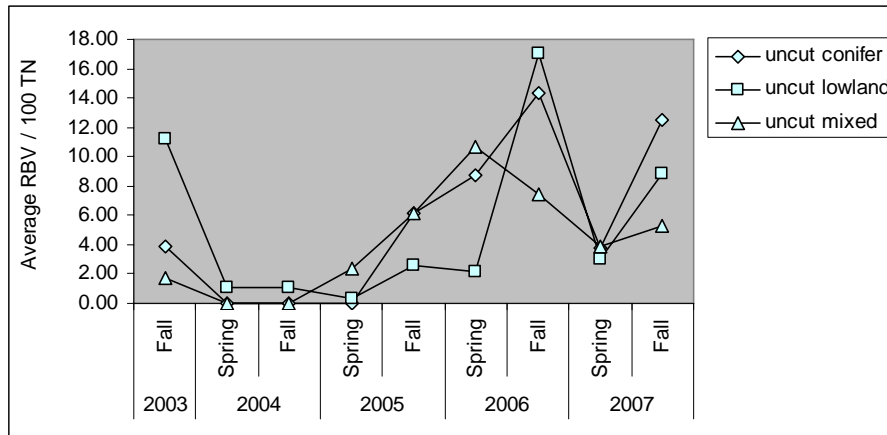


Fig. 6. Captures of red-backed voles in Kapuskasing mature, unlogged forests (2003-2007).

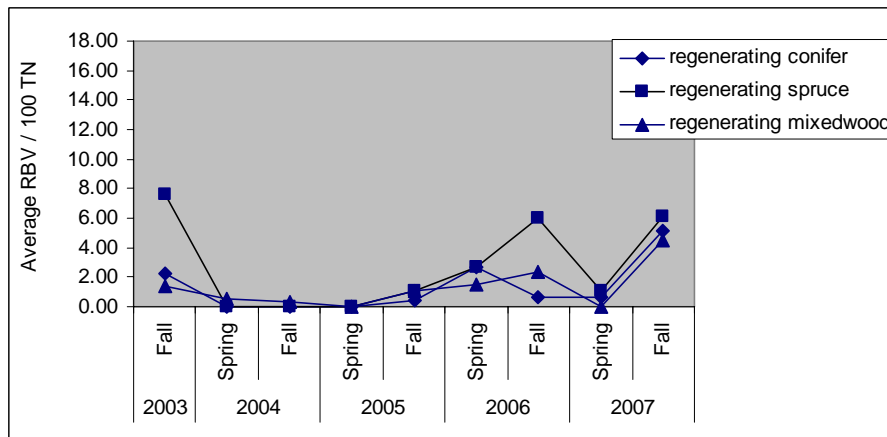


Fig. 7. Captures of red-backed voles in Kapuskasing mechanically-logged forests (2003-2007).

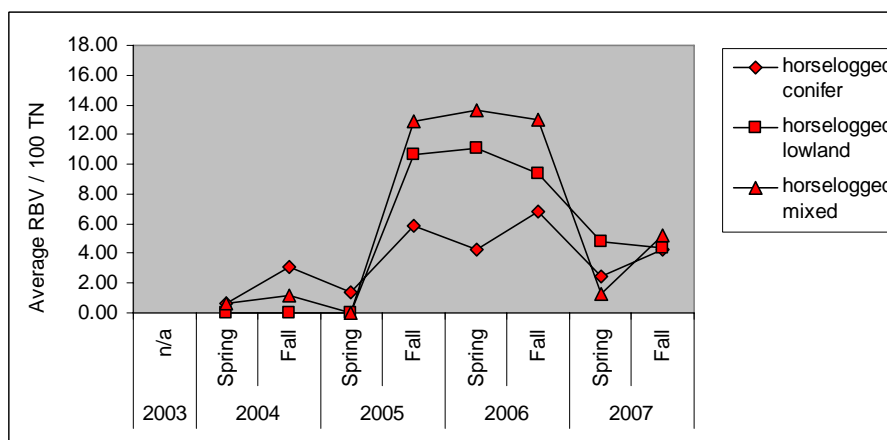


Fig. 8. Captures of red-backed voles in Kapuskasing horse-logged forests (2003-2007).

Marten hunting efficiency and body condition

The probability of prey encounter, attack, capture, and kill are often hypothesized to depend on habitat structure, but field evidence in terrestrial systems is rare. We tested whether predation efficiency by the American marten and fear of predation by their primary prey, the red-backed vole, differed between 20-50 year-old regenerating forest stands and older uncut stands (Andruskiw et al. 2008). Snow tracking of 34 martens, covering >100 km of movement trajectories, indicated that both attack frequency and total hunting success were 50-100% higher in the mature uncut forest than in the regenerating forest landscape (Fig. 9). Our results showed that the frequency of prey encounter, prey attack, and prey kill were higher in old uncut forests, despite the fact that small mammal density was similar to that in younger logged forests. These differences in predation efficiency were linked to higher abundance of coarse woody debris, which seems to offer sensory cues to martens, thereby increasing the odds of hunting success. Red-backed voles in regenerating forest stands exhibited increased wariness compared to voles living in old uncut forest, suggestive of a behavioural response to habitat-mediated variation in predation risk. These results suggest that one of the benefits of mature stands to martens is increased access to prey (Andruskiw et al. 2008), even when prey density does not differ between forest stands.

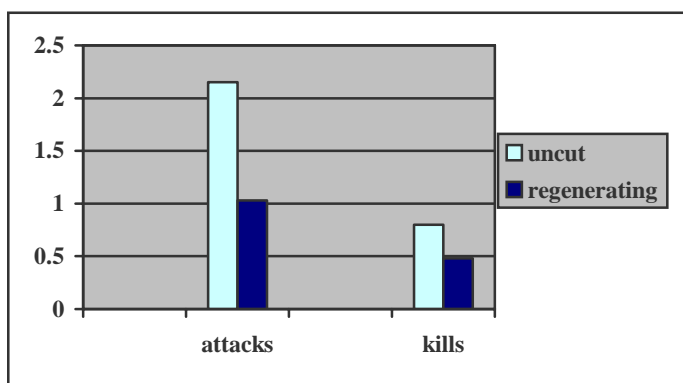


Fig. 9. Number of attacks and successful kills per km of searching by martens in mature uncut versus younger regenerating landscapes.

We assessed body condition from live-trapped animals by examining residuals of length-weight allometric regressions. Martens captured in mature uncut forests tended to be in slightly better body condition than did animals from younger regenerating forests (Fig. 10), probably as a consequence of improved hunting success. For example, juveniles of average length in uncut forests were 25g heavier than their counterparts in regenerating forests.

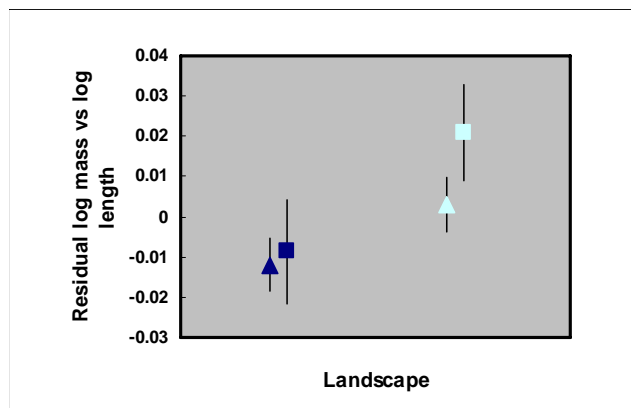


Fig. 10. Body condition of martens in mature uncut (light shading) versus young regenerating (dark shaded) landscapes. Juveniles shown by triangles, adults by squares.

Dispersal

Differences in habitat quality between mature uncut forests and younger regenerating forests could result in different movement strategies among dispersing juvenile marten. We used four metrics to assess differences in movement patterns by 143 juveniles at Ear Falls: dispersal distances, movement rates, turn angles and temporal patterns in net displacement (Johnson 2008). Some aspects of juvenile movement differed between the landscapes. Juveniles from the regenerating landscape travelled more slowly than juveniles from the uncut landscape. Reduced hunting efficiency may increase the energetic costs of dispersal in regenerating forests, forcing juveniles to stop and feed while in transit. The distributions of turn angles and temporal patterns in net displacement were similar in both landscapes. The distribution of turn angles among dispersers was non-uniform with juveniles showing a bias for reversing direction. Patterns of net displacement indicated that juveniles moved back towards their location of capture after about 30 days before moving on. These results suggest that juvenile dispersal is not completely random.

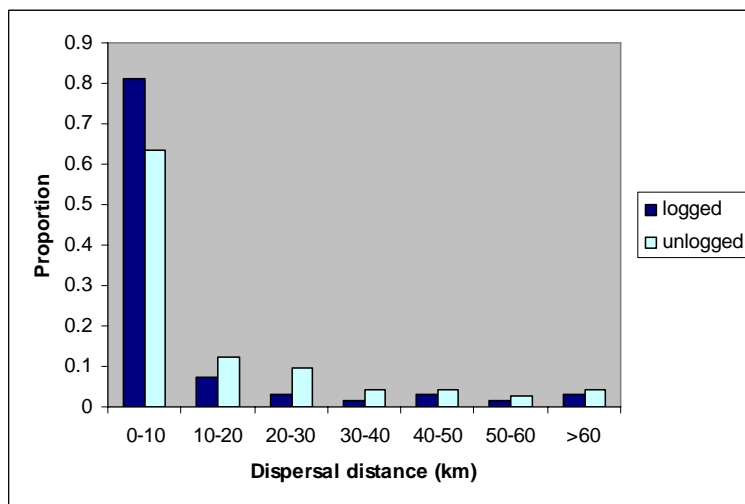


Fig. 11. Dispersal distance of juveniles in mature uncut forests versus younger regenerating forests.

We compared patterns of dispersal in the territorial American marten (*Martes Americana*) between a younger, regenerating forested landscape and an uncut landscape dominated by mature forest stands to test whether differences in the probability of survival influenced how far juveniles dispersed (Johnson 2008). Juveniles travelled shorter distances in the regenerating landscape compared to the mature uncut landscape (Fig. 11). Restricting our analysis to juveniles that survived to adulthood yielded similar results, suggesting that the short dispersal distances in the regenerating landscape was not a consequence of dispersers dying prematurely in transit. Long distance dispersers were less likely to survive than juveniles that dispersed a short distance in both landscapes. Mortality risk at a given distance was twice as high in regenerating forests as in mature uncut forests (Fig. 12). Although commercial harvesting contributed to the increased mortality at long distances, the effect of commercial harvesting appeared to be similar between landscapes, suggesting some other factor was responsible for the observed landscape-specific difference in juvenile mortality. Landscape differences in hunting success and body condition shown earlier suggest that juveniles from the regenerating landscape may have been less able to deal with the energetic demands of dispersal compared to juveniles from older forests.

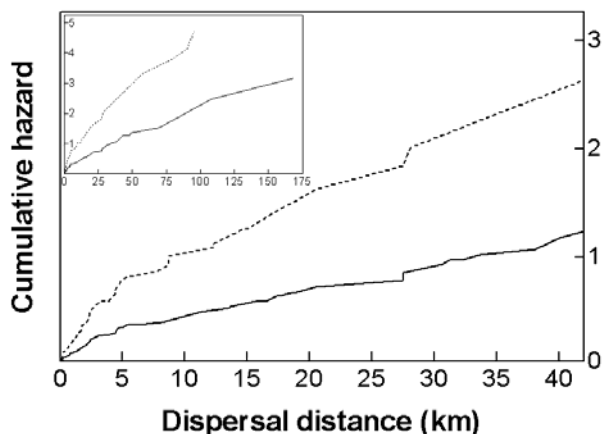


Fig. 12. Cumulative mortality hazard in relation to distance for dispersing juveniles in regenerating forests (dashed line) versus those in mature, uncut forests (solid line) at Ear Falls, Ontario.

Habitat use by marten

We tested whether patterns of settlement among juvenile marten were consistent with the predictions of Ideal Despotism Distribution (IDD) theory (Johnson 2008). Convention suggests that IDD should result in habitat segregation, with adult despotism forcing smaller, subordinate juveniles to settle in lower quality habitats than adults. As predicted, juvenile body condition was lower than that of adult marten after adjusting for differences between the sexes. However, both adults and juveniles preferentially settled in old forests, avoiding younger, regenerating forests (Fig. 13). The similarities in habitat use were not a consequence of extensive territory overlap. Territories overlapped on average by 8%. Territory size was well predicted by body mass, with no apparent difference in the relationship between juveniles and adults, based on a non-parametric kernel estimator (Fig. 14). Both adults and juveniles had similar proportions of older forest stands within territories. These results suggest that juveniles can compete successfully for suitable territories against older individuals. Size can be an important determinant of territory size in martens and may be the most useful metric of social dominance.

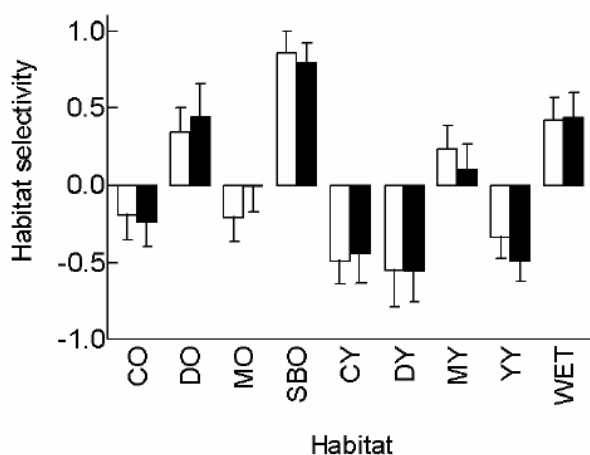


Fig. 13 Habitat selectivity by adult (open bars) versus juvenile (shaded bars) martens in Ear Falls (C = coniferous, D = deciduous, M = mixed, SB = black spruce, O = old, Y = young, and wet = marsh or fen).

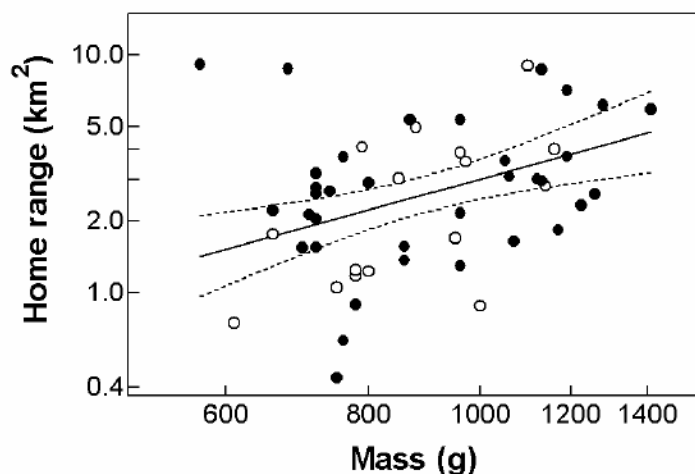


Fig. 14. Home range size in relation to body mass in juvenile (open symbols) and adult (filled symbols) martens in mature uncut forests of Ear Falls.

Successful management requires an understanding of the scale at which species use resources in their environment. Previous research shows considerable variability in resource preferences of American martens across North America, but this variability may be an artefact of the data resolution used in analyzing resource selection. To test the effects of resolution, we evaluated resource selection by martens at two resolutions at the Kapuskasing study site (McKague 2007). Coarse-resolution models were developed using radio-telemetry and forest resource inventory data using a geographic information system (GIS) at the level of forest stands, whereas fine-resolution models were developed using microhabitat data collected while snow-tracking martens. Resource selection models were compared using Akaike's Information Criterion and model performance was evaluated by the ability of the models to correctly classify resource use events by martens. None of the predictor variables reliably explained resource use by martens at the coarse resolution. Fine-resolution models, however, suggested that martens selected resource use locations with abundant supplies of coarse woody debris and a high proportion of eastern-white cedar. On average, fine-resolution models performed 10 times better than coarse-resolution models at classifying resource selection by martens. Our study illustrates how fine-resolution data can increase the predictability of resource use locations by martens, and suggests that incorporating fine-resolution data into spatial frameworks (such as GIS) may increase our ability to successfully manage boreal forests for martens.

We also evaluated patterns of resource selection by red-backed voles within marten territories, on the assumption that marten micro-habitat preferences are shaped in part by access to prey. Our results suggested that red-backed voles preferred moist sites (based on the importance of soil moisture in this model) with a relatively high habitat complexity and low lichen content, although substantial variation in resource selection was observed among different marten territories and even within single territory (Pulfer 2007). There has been much discussion in the habitat selection literature regarding the most appropriate scale for measuring a given species interaction with its environment. Our results suggest that both micro and macro scales influence habitat selection by red-backed voles. The favoured variables in the most plausible model contribute to either cover (fern, fine woody debris, horizontal density), and/or food (lichen, fine woody debris, and fern) for red-backed voles.

Genetic structure in marten populations

Species with extensive dispersal ability are expected to be genetically homogeneous. Dispersal distance in martens is strongly leptokurtic, which could result in detectable genetic structure within local populations of marten. We tested this hypothesis based on microsatellite DNA gathered from fur-trapped animals in both the mature uncut and regenerating forest landscapes in Ear Falls (Broquet et al. 2006a). Genetic structure using pair-wise genetic distances between individuals showed a significant pattern of isolation by distance, most apparent in the marten population in the landscape with mature uncut forests. This is consistent with expectations from our telemetry study of juveniles, showing a fat-tailed, leptokurtic distribution of dispersal distances in both populations, with a small proportion (<10%) of individuals dispersing very long distances (up to 82 km), whereas most individuals ($\approx 90\%$) were more philopatric (dispersal distance ≤ 5 km). Concordant estimates of the mean squared parent-offspring axial distance (σ^2) inferred both from the genetic pattern of isolation by distance and from radio-telemetry showed that most juveniles make little contribution to gene flow. This suggests that leptokurtic dispersal contributes to detectable local genetic structure in martens.

Empirical studies of landscape connectivity, as defined by the interaction between the structure of a landscape and the movement of individuals, are often limited by the difficulty of directly measuring animal movement. "Indirect" approaches of dispersal involving genetic analyses provide a complementary tool to the "direct" methods. We investigated the effect of ecological barriers on marten dispersal (Broquet et al. 2006b), using a genetic model of isolation by distance, based either on straight-line distance between individuals (termed Euclidean distance) or the minimum travel distance around ecological barriers such as water bodies or recently logged patches (termed ecological distance). Isolation by distance was more evident in the mature, uncut landscape whereas no such pattern was found in the regenerating forest landscape. Effective ecological distances computed using least-cost modeling was better correlated to genetic distance in both landscapes than was simple Euclidean distance, demonstrating that landscape features have a detectable influence on genetic structure, presumably due to limitations on marten dispersal. The extreme simplifying assumptions of these genetic models limit their utility, however, in quantifying the effect of landscape structure on dispersal via connectivity.

Marten population dynamics

Over the course of some 9,368 trap nights over 5 years (2001-2005) we captured 194 marten individuals in the unlogged landscape versus 155 martens in the logged landscape at Ear Falls. Marten density has been assessed by the number of captures of individuals per 100 trap nights. Our results suggest that marten densities have been comparable, but slightly higher, in the unlogged than the logged landscapes (Fig. 15).

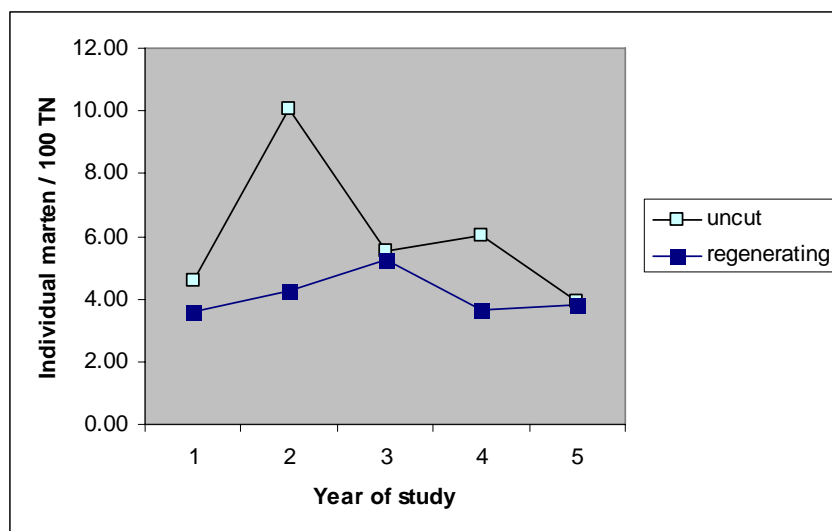


Fig.15. Marten caught per 100 trap nights in mature uncut vs. regenerating forests in Ear Falls.

Marten numbers at Kapuskasing were on average about half as abundant as at Ear Falls (Fig. 12), and the maximum number captured was 30% lower than the maximum at Ear Falls. We captured 115 marten during the years 2003-2007 (Fig. 16). Throughout the study, numbers of marten in mechanically-harvested stands, at 30-50 years of age have been consistently lower than in unmanaged stands or in one of the areas that had been horse-logged (55-65 years of age). Marten abundance in all treatments were initially high, declined during the middle of the study, then recovered sharply in the last 2-3 years, reminiscent of changes in red-backed voles discussed earlier.

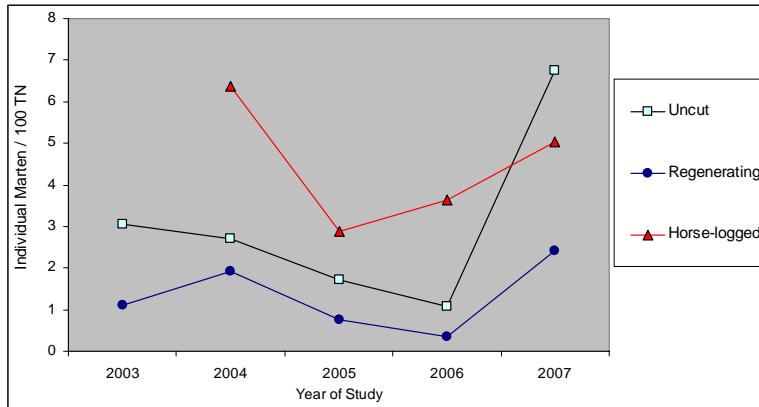


Fig. 16. Marten caught per 100 trap nights in mature uncut vs. regenerating forests in Kapuskasing.

We merged our times series data from both Ear Falls and Kapuskasing to evaluate 20 plausible models to predict rates of marten population growth. A multi-factor model with terms for marten density, prey density, and forest harvest treatment was clearly favoured (Akaike weight = 0.74), explaining 78% of the observed variation in growth rates. The most parsimonious model indicated that population growth by martens was non-linearly density-dependent (Fig. 17), probably due to the effect of competition for territories in both sexes. Growth rates at any given marten density were consistently lower in regenerating forests than in mature uncut forests, based on AIC values of treatment-specific vs homogeneous models.

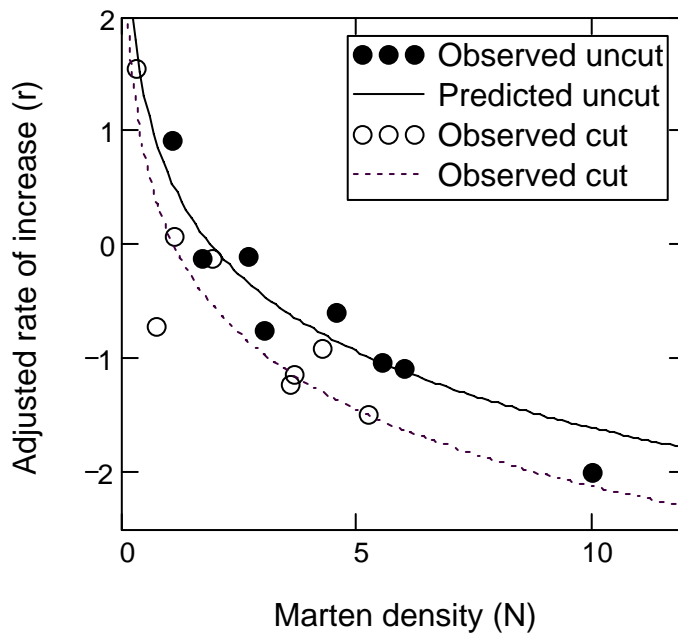


Fig. 17. Rate of marten increase in relation to martens caught per 100 trap nights, adjusted for vole density.

Growth rates by marten populations in both Ear Falls and Kapuskasing were also non-linearly dependent on variation in prey density across years (Fig. 18). Similar numerical responses to changing prey availability have been demonstrated in other marten populations in Ontario (Thompson and Colgan [1987] *J. Wildl. Manage.* 51:824-835; Fryxell et al. [1999] *Ecology* 80:1311-1321), suggesting that fluctuation in prey abundance is an important source of environmentally-driven variation in marten abundance. At any given level of prey abundance, population growth rates were lower in regenerating forests than in more mature uncut forests, probably due to differences in coarse woody debris, hunting efficiency, and therefore body condition, as we discussed earlier (Andruskiw et al. 2008).

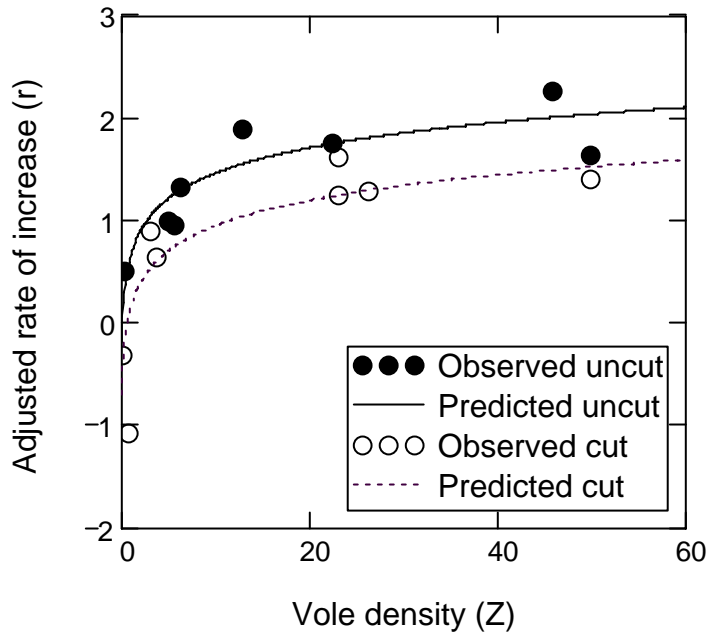


Fig. 18. Rate of increase by marten in relation to population density of red-backed voles (animals caught per 100 trap nights) at the landscape scale (averaged over each habitat type, with equal weight), adjusted for marten density.

Sources of mortality in martens

We placed radios on roughly equal numbers of adults and juveniles at Ear Falls, with roughly equal representation between the sexes. Both landscapes had similar sample sizes of radio-collared individuals (uncut: 228 marten years; regenerating: 205 marten years). Crude rates of natural and trapping mortality were similar in the two landscapes (Fig. 19). The data clearly demonstrate that a large part of the mortality stemmed from commercial trapping of animals that ventured away from the areas in which they were originally marked, clearly emphasizing the importance of coordinating forest habitat management and fur-bearer harvesting policies at a regional landscape level. Fur trapping plays a more important role in adult and juvenile mortality of males, perhaps because they move more than females and are thus more likely to be fur trapped.



Fig. 19. Mortality of American martens in regenerating versus mature uncut forests at Ear Falls.

The majority of Kapuskasing marten dying in regenerating forests were killed by commercial trapping (>30% in logged areas, Fig. 20). The unmanaged area at Kapuskasing was isolated, resulting in much lower marten mortality in the mature uncut forest (<7% than we saw at ear Falls (>12%). Natural mortality (mostly sickness) resulted in about 10-15% deaths among our captured sample of marten.

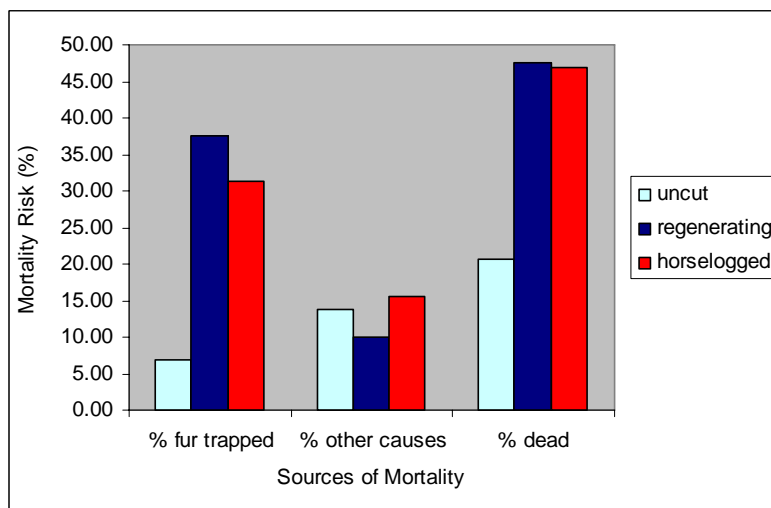


Fig. 20. Mortality of American martens in regenerating versus mature uncut forests at Kapuskasing.

Population viability analysis

Population viability analysis (PVA) was conducted using two alternative approaches, one based on a non-spatial modelling framework and the other based on spatially-explicit, individually-based models. Each set of models had a similar underlying biological basis and identical parameters for modeling the demography of martens and red-backed voles. The rate of change of marten populations was predicted by the following formula, based on the best-fit parameters:

$$N_{t+1} = N_t \cdot \exp[a - b \cdot \ln(N_t) + c \cdot \ln(Z_t) + d \cdot F + \varepsilon_t] - \eta \cdot \hat{N}_t \quad \text{eq. 1}$$

where the intercept $a = 0.118$, the coefficient for the density-dependent relationship $b = 0.973$, marten density in autumn is N , the coefficient for the prey-dependent relationship $c = 0.359$, prey density in autumn is Z , the coefficient for the effect of forest age $d = 0.513$, and residual stochastic variation (of both environmental and demographic origin) ε is normally distributed with mean = 0 and standard deviation = 0.375. Forest age F is a dummy variable set at 0 for regenerating forests 40 years post-harvesting and 1 for forests 90 years post-harvesting. We modelled fur trapping as an additive source of mortality, with harvest rate ($h = 0.15 + \eta$) proportionate to marten population density. We assume that managers cannot know current marten productivity (and therefore sustainable harvest) precisely, but rather project recruitment on the basis of fall marten density and average prey density. Note that our demographic models were parameterized at a fur harvest level of ca. 15%, so η represents harvest beyond 15%.

The rate of change of red-backed vole populations was predicted by the following formula:

$$Z_{t+1} = Z_t \cdot \exp[e - f \cdot \ln(Z_t) + g \cdot H + \gamma_t] \quad \text{eq. 2}$$

where the intercept $e = 0.888$ for Ear Falls, the coefficient for the density-dependent relationship $f = 0.619$ for Ear Falls, the coefficient for the habitat-dependent relationship $g = 0.413$ for Ear Falls, and residual variation (of both environmental and demographic origin) γ is normally distributed with mean = 0 and standard deviation = 0.591 for Ear Falls. Habitat type H is a dummy variable set at 0 for coniferous-dominated stands, 1 for mixed stands, and 2 for deciduous-dominated stands, so vole growth rates are highest in those stands that are most heavily dominated by deciduous tree species.

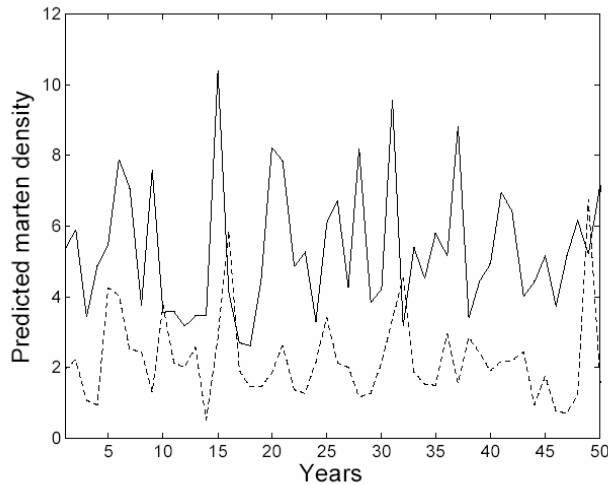


Fig. 21. Typical population trajectories for martens in mature deciduous forests (solid line) versus regenerating coniferous forests (dotted line) in the absence of fur trapping.

In the absence of fur trapping, the models predict that marten populations in mature uncut landscapes should have carrying capacities of 5.31 different martens/100 trap nights in deciduous forests, 4.15 in mixed forests, and 3.25 in coniferous forests. Marten densities are predicted to be lower in regenerating forests, with carrying capacities of 3.14 in deciduous forests, 2.45 in mixed forests, and 1.92

in coniferous forests. In each case, stochastic variation in growth rates of both predator and prey are expected to interact, producing highly variable dynamics over time (Fig. 21). Note that variation in marten density capacity due to successional stage (regenerating versus mature uncut) is of similar magnitude as that stemming from differences in prey abundance in deciduous versus coniferous stands.

Population viability analysis requires a time frame and point of reference with respect to threat, termed the quasi-extinction threshold, as well as substantial replication. The quasi-extinction threshold is a population level at which wildlife managers recognize serious threat and therefore of extreme conservation concern. We arbitrarily set our quasi-extinction threshold at 10% of marten carrying capacity in a pristine ecosystem with mature forest cover of mixed composition. Simulations were replicated 10,000 times for each assessment of risk, with a fresh set of stochastic deviates for each replicate.

Our results suggest that at fur trapping levels ($h = 15\%$) seen during the course of our field studies at Ear Falls, the risk of extinction is miniscule in either a regenerating or mature uncut forest (Fig. 22a,b). At higher levels of fur trapping, however, extinction risk rises sharply, particularly in the case of regenerating forests (Fig. 22a). This is due to differences in marten productivity we have already documented, probably stemming from reduced hunting efficiency by martens in younger stands with little coarse woody debris.

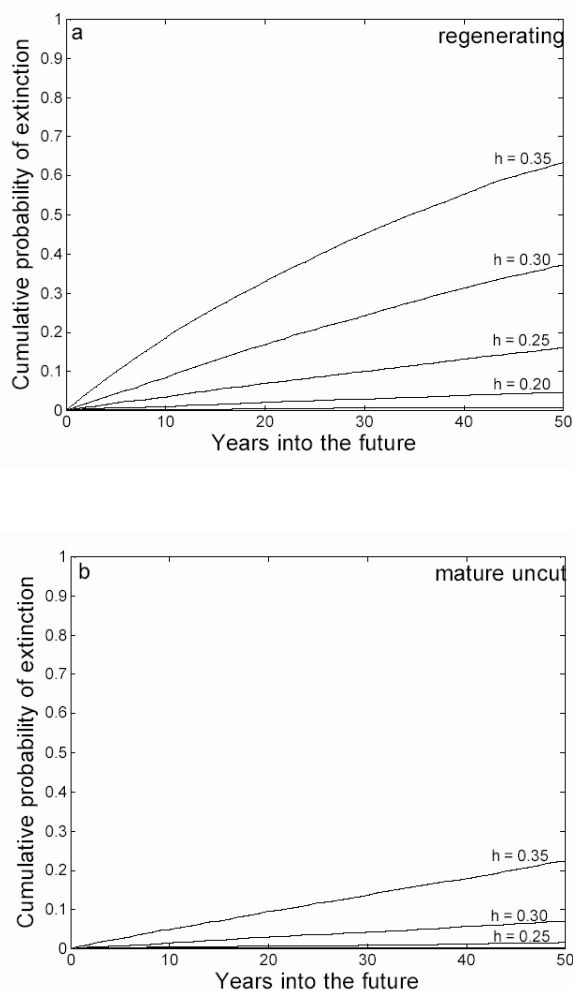


Fig. 22. Extinction risk over time for marten populations in regenerating (a) or mature uncut forests (b) of mixed composition in relation to fur trapping mortality levels (h).

One drawback to PVA based on simple population models is that they do not incorporate variation in ecological conditions over time that the focal species must face. To circumvent this problem, we ran our spatially-explicit, individually-based marten model on a landscape that changes over time due to normal processes of forest succession. We performed the simulations on a 50 km x 50 km Cartesian grid (with 2500 pixels each measuring 1 km x 1 km) centered on the regenerating landscape south-east of Ear Falls (Fig. 23).

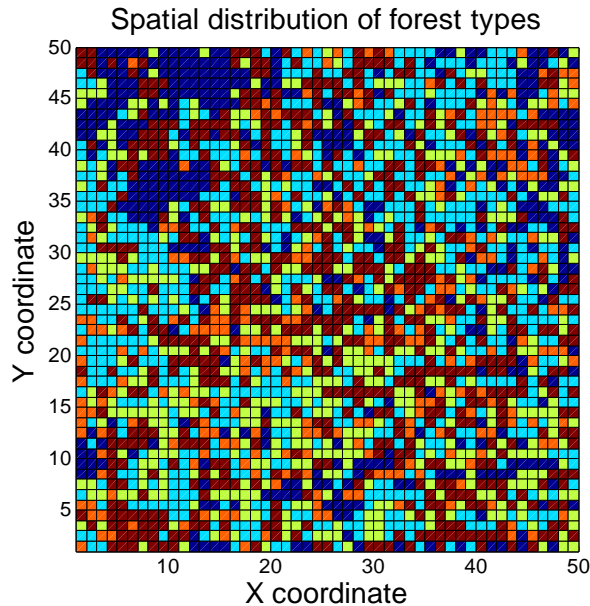


Fig. 23. Initial grid used for the spatially-explicit Ear Falls simulations (red: deciduous stands, orange: mixed stands, light blue: black spruce stands, green: conifer stands, dark blue: water).

This landscape, derived from average stand composition from FRI maps, was run through the B-folds forest succession model to generate yearly snapshots of changing stand composition at the landscape scale. Succession is an intrinsically stochastic process, of course, so stand composition changes with each run, adding an additional element of change that can either help or hinder the sustainability of martens. The B-folds simulations predicted that spruce and mixed stands would generally decrease in frequency, whereas conifer and deciduous stands would increase in frequency (Fig. 24).

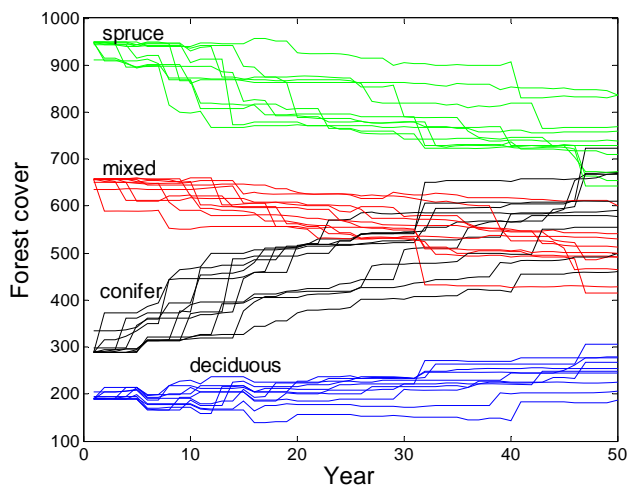


Fig. 24. Changing stand composition for 10 replicate runs on the Ear Falls landscape.

Within this dynamic landscape, the lives of individual martens were played out, with probabilities of birth and death derived directly from our study populations. We first translated our metric for marten (catch per 100 trap nights) into a realistic level of absolute abundance. Under optimal conditions (old deciduous stands), the estimated equilibrium density of martens in the best parts of our study area was 5.31 martens per 100 trap nights. Under ideal conditions, we presume that martens could completely occupy the non-water habitat in our 2500 km² model landscape. Given a territory size of 3-4 km, this implies a population of 550 individual martens on this landscape at their ecological carrying capacity. We then used the coefficient $\theta = 5.31/550$ to rescale densities so we could predict fitness of each individual. Following a common convention in ecology, we defined Malthusian fitness of individuals as follows:

$$W_t = a - b \cdot \ln(\theta \cdot N_t) + c \cdot \ln(Z_t) + d \cdot F + \varepsilon_t \quad \text{eq. 3.}$$

When marten abundance across the landscape and prey availability within an individual's territory were such that fitness $W = 0$, then we presumed that no offspring were produced and the adult faced a probability of mortality due to fur trapping $= \eta$. When $W > 0$, then the probability of producing an offspring was W , with a random number generator used to decide which adults successfully bred. Both offspring and adult faced a probability of mortality $= \eta$, also applied to specific individuals using a random number generator. When $W < 0$, then no offspring were produced, and mortality risk for each adult $= \exp(W) + \eta$. This procedure implies that birth and death are chance processes, whose expected values mirror that in the population model (eq. 1), but with additional variation due to demographic stochasticity, particularly when the population is small. We assumed that landscapes fully mature within 100 years following disturbance. The regenerating landscapes were assumed to be 50 years of age, so $F = t/50$, with t measured in years. Dispersal of surviving offspring was modeled using the observed distance-dependent probabilities (Fig. 11). Territories were 3 km² in size, with adults redistributing every year until they were centered on high quality habitat without overlap with another adult. Stand types within each territory dictated prey densities (Z) and habitat quality (F) for that individual.

Results of these Monte Carlo simulations show that the additional variability due to demographic stochasticity and changing landscape conditions generate higher risks of quasi-extinction, defined once again as 10% of the density in a mature, pristine landscape (Fig. 25). Notice that average density increases over time, as the forest stands mature across the landscape. As a result of these changing densities, quasi-extinction events are more frequent in young regenerating landscapes compared to those that have had time to mature.

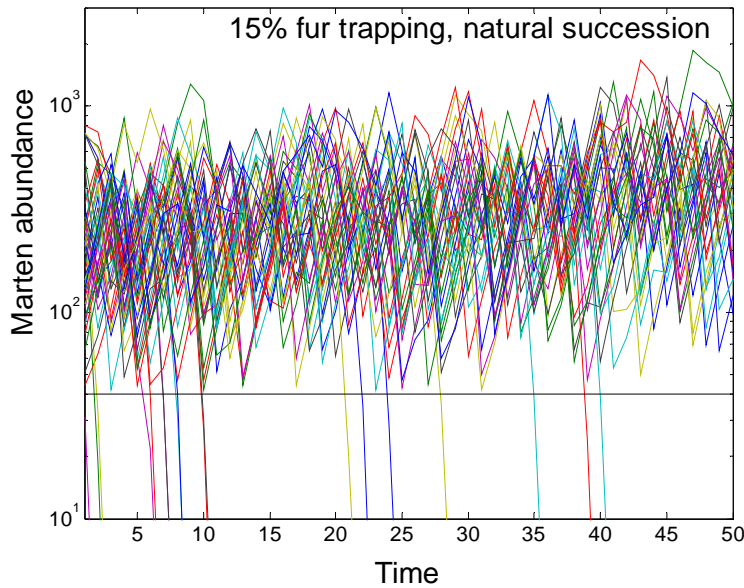


Fig. 25. Time dynamics of 100 simulations in a regenerating forest landscape that is mature by year 50.

Because of the increased variability due to demographic stochasticity, quasi-extinction risk in commonly increases in individually-based models, as it does in our models. Results of these Monte Carlo simulations suggest that fur trapping levels typical of those recorded during our study pose relatively minor risk of serious decline. Higher trapping rates are another matter, with fur trapping rates $> 25\%$ leading nearly always to population collapse (Fig. 26). One way to improve the odds of marten viability is to leave core areas of mature stands in a matrix of regenerating stands following logging. We simulated this in our model by holding core areas in a mature stand composition that would normally require 50 years of successional dynamics. Matrix areas outside these square cores were subject to commercial forest harvest and presumed to undergo a normal pattern of succession. Maintaining 40% of the overall landscape as mature cores was sufficient in our model to reduce risk of quasi-extinction to less than 10%, even at elevated levels of fur trapping (Fig. 26a). Marten viability is improved even more by an integrated resource management policy that maintains cores in a mature successional stage as well as making these cores no-trapping reserves (Fig. 26b).

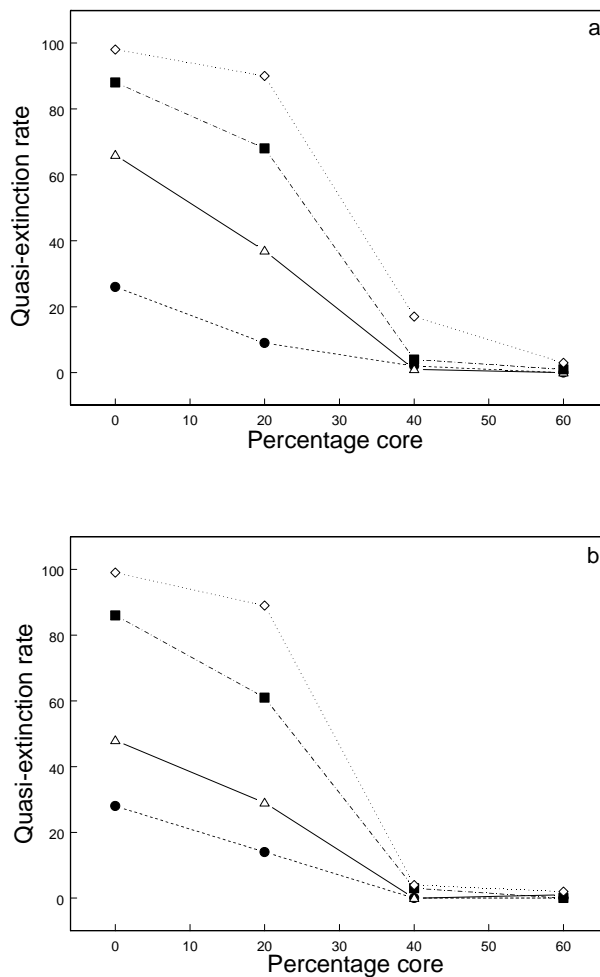


Fig. 26. Extinction risk for various combinations of mature core size and fur-trapping levels (a: core areas are also trapped, b: core areas are no-trapping reserves).

CONCLUSIONS AND RECOMMENDATIONS

Our results point to several key conclusions vis-à-vis forestry guidelines for the boreal zone of Ontario.

- There is strong evidence that marten populations are capable of sustaining themselves in regenerating forests of 30-60 years age, albeit at lower densities at higher risk of decline due to chance events than those in mature forests. In other words, we reject the source-sink hypothesis that forms the logical basis for current marten habitat guidelines.
- A key consideration for marten viability is the level of fur-trapping mortality. At low levels of fur trapping mortality (<15% per year), there is a high probability that both mature and regenerating forests can sustain martens. At moderate levels of fur-trapping pressure (ca. 15-25% per year), regenerating forests may not be able to sustain martens whereas mature forests can. At high levels of fur trapping pressure (>25%), martens cannot be sustained anywhere in Ontario. We see an urgent need to link furbearer management policy with land-use policy. Both need to be better integrated to maintain desirable levels of population viability of key indicator species, such as marten.
- Observed differences in marten population dynamics between regenerating and mature forests are mirrored by significant differences in the abundance of coarse woody debris, hunting efficiency, marten body condition, juvenile survival during dispersal, dispersal distance, and genetic structure. We therefore accept the fitness variation hypothesis.
- Core areas of undisturbed mature habitat in a matrix of regenerating stands may be a powerful means of improving the viability of species like marten that occur at higher densities in more mature forests. We suggest that a target of 30-40% mature forest across forest management units should be sufficient to reduce risk of population collapse < 10%.
- Size of mature forest cores is probably not of critical importance, but should still encompass 5-10 individual marten territories (15-30 km²), to ensure adequate opportunities for successful breeding and high dispersal success by offspring.
- No-harvest reserves, particularly if these are in core areas with mature forests that are particularly productive for martens, may be a valuable tool in managing fur-bearer species like martens that face demographic challenges from both landscape modification and hunting.
- Comparison of machine-logged to horse-logged stands suggests that forestry activities that maintain complex habitat structure, such as plentiful supplies of coarse woody debris may be a useful means of mediating some of undesirable ecological consequences of forest harvesting.

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