

The influence of forest fragmentation and landscape pattern on American martens

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Summary

1. We investigated the effects of forest fragmentation on American martens (*Martes americana* Rhoads) by evaluating differences in marten capture rates (excluding recaptures) in 18 study sites with different levels of fragmentation resulting from timber harvest clearcuts and natural openings. We focused on low levels of fragmentation, where forest connectivity was maintained and non-forest cover ranged from 2% to 42%.

2. Martens appeared to respond negatively to low levels of habitat fragmentation, based on the significant decrease in capture rates within the series of increasingly fragmented landscapes. Martens were nearly absent from landscapes having > 25% non-forest cover, even though forest connectivity was still present.

3. Marten capture rates were negatively correlated with increasing proximity of open areas and increasing extent of high-contrast edges. Forested landscapes appeared unsuitable for martens when the average nearest-neighbour distance between open (non-forested) patches was < 100 m. In these landscapes, the proximity of open areas created strips of forest edge and eliminated nearly all forest interior.

4. Small mammal densities were significantly higher in clearcuts than in forests, but marten captures were not correlated with prey abundance or biomass associated with clearcuts.

5. Conservation efforts for the marten must consider not only the structural aspects of mature forests, but the landscape pattern in which the forest occurs. We recommend that the combination of timber harvests and natural openings comprise < 25% of landscapes ≥ 9 km² in size.

6. The spatial pattern of open areas is important as well, because small, dispersed openings result in less forest interior habitat than one large opening at the same percentage of fragmentation. Progressive cutting from a single patch would retain the largest amount of interior forest habitat.

Key-words: edge density, habitat fragmentation, *Martes americana*, proximity index, timber harvests.

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Introduction

The modification of forested landscapes through land management practices has fostered a growing interest in the effects of habitat fragmentation on wildlife.

Habitat fragmentation, originally defined as the formation of isolated fragments from a formerly continuous habitat (Wilcox 1980; Harris 1984), has taken on a broader meaning in recent times, reflecting an awareness that fragmentation can affect organisms long before the original habitat is reduced to remnant patches. In the fullest sense, fragmentation is disruption in continuity in any temporal or functional

domain (Lord & Norton 1990). Habitat fragmentation occurs along a continuum, from landscapes dominated by the original cover type to landscapes where the original type is reduced to remnant patches.

The majority of habitat fragmentation studies have focused on extreme examples of fragmentation, after the original cover type has ceased to function as the dominant landscape element. By focusing on remnant habitat patches, these studies have examined the effect that patch area and isolation have on population size, extinction and recolonization rates, and dispersal rates of individual species, as well as on species diversity (Diamond 1975; Whitcomb *et al.* 1981; Harris 1984; Rosenberg & Raphael 1986; Verboom & van Apeldoorn 1990). More recently, investigations have turned to less extreme cases of fragmentation, and have focused on the cohesiveness or contagion of the original habitat type when it is the dominant landscape element (Franklin & Forman 1987; O'Neill *et al.* 1988; Ripple, Bradshaw & Spies 1991; Spies, Ripple & Bradshaw 1994; Wallin, Swanson & Marks 1994). These studies investigate potential restrictions on the movement of organisms, the spread of fire or disease, or the flow of nutrients at the landscape scale (Turner 1987; Turner *et al.* 1989; Bartell & Brenkert 1991; Turner & Dale 1991; Wiens *et al.* 1993; Ims 1995). The area of the original habitat generally is not measured when it is the dominant landscape element, because it forms one continuous patch and may extend beyond the defined landscape boundary. The area and distance between disturbance patches are nevertheless of interest because they serve as barriers to movement and affect the spatial configuration of the original habitat.

Our study focused on low fragmentation of forested landscapes, where the extent of forest has been altered by timber harvests but still comprises the dominant landscape element. We investigated the effects of habitat fragmentation on the American marten *Martes americana* Rhoads, a carnivorous mammal typically associated with mature forest systems. American martens appear sensitive to habitat fragmentation, because populations generally are low in areas fragmented by the clearcut method of timber harvest (Soutiere 1979; Snyder & Bissonette 1987; Thompson & Harestad 1994). However, marten responses to gradual increases in fragmentation are not well known. Most studies of timber harvest effects have been in areas where levels of fragmentation were not differentiated and where fragmentation was quite high, between 41% and 60% clearcut (Soutiere 1979; Steventon & Major 1982; Snyder & Bissonette 1987; Katnik, Harrison & Hodgman 1994; Thompson 1994; Potvin & Breton 1997). In our investigation, we were primarily interested in the response of martens to a gradual increase in fragmentation when forest connectivity was maintained, and therefore focused our study on a series of forested landscapes where non-forest cover ranged from 2% to 42%.

Brainerd (1990) proposed a model of marten response to fragmentation when non-forest cover occupied 55% of a hypothetical landscape. He predicted that habitat quality would increase if cut sizes were fine-grained, permitting marten movements across the clearcuts while taking advantage of increased prey in open areas. Habitat quality was predicted to decrease with medium- and coarse-grained cut sizes because they would restrict marten movements. A similar model was later developed by Thompson & Harestad (1994) that echoed Brainerd's (1990) predictions. Examining the full range of potential fragmentation, they predicted two possible changes in marten carrying capacity with increasing removal of timber. Under the clearcut method of harvest, equivalent to Brainerd's (1990) medium-grained or coarse-grained cut sizes, they predicted a linear negative decline. With selective cutting and patch cuts <3 ha, they predicted an increase in carrying capacity at low cutting levels, followed by a precipitous decline at approximately 20–30% of forest cover removal, due to increased predation of martens in openings, high edge density, and loss of forest interior. Thus, their model differed from Brainerd's (1990) only in predicting a decline at an earlier stage of fragmentation.

Although martens avoid clearcuts and other large openings, especially in the winter (Soutiere 1979; Clark & Campbell 1979; Steventon & Major 1982; Hargis & McCullough 1984), low levels of fragmentation may have little effect on martens as long as forest connectivity is maintained. In fact, a positive response to low fragmentation may be expected, because in some locales martens forage in brushy clearcuts during summer (Steventon & Major 1982; Katnik 1992) and hunt along forest–meadow edges (Simon 1980; Spencer, Barrett & Zielinski 1983). Having a small proportion of the landscape in open areas may be favourable to martens because of the increase in abundance and diversity of small mammals associated with clearcuts, and because marten diets are not restricted to forest-associated prey (Weckwerth & Hawley 1962; Koehler & Hornocker 1977; Buskirk & MacDonald 1984). The initial positive response would be followed eventually by a negative response as forested habitat became limiting.

To test these predictions, we compared marten capture rates across a series of increasingly fragmented landscapes. Our main objective was to determine whether marten abundance changed with incremental increases in habitat fragmentation caused by the combined effects of natural openings and timber clearcuts. If a correlation was found between capture rates and fragmentation, our secondary objective was to look for specific levels of fragmentation that suggested shifts in habitat quality in either a positive or negative direction. Preliminary results from this study were reported in Hargis & Bissonette (1997). This paper reports further analyses on the effects of landscape pattern on martens as measured by several landscape metrics.

Methods

SELECTION OF STUDY SITES

We selected 18 sites in the Uinta Mountains of northern Utah where martens were known to occur. Each site was a square area covering 9 km², a size chosen to ensure that several martens potentially could be present at any given time, yet sufficiently small to allow a thorough survey of marten numbers. Open areas occupied 2–42% of each site (Fig. 1). Natural

openings in the form of meadows and boulder fields covered 2–12% of the landscapes, while timber harvests accounted for 0–42% of each site (Table 1).

All sites were located in mature forests containing Engelmann spruce *Picea engelmannii* Parry ex Engelm., lodgepole pine *Pinus contorta* Dougl. ex Loudon and scattered subalpine fir *Abies lasiocarpa* [Hook.] Nutt., with canopy cover > 30%, large diameter trees, and abundant coarse woody debris (Table 2). Elevations ranged from 2700 to 3200 m. Similarity in vegetative conditions was important to minimize variation among sites from factors other than fragmentation.

We limited our study to the clearcut method of timber harvest, because marten responses to selective cutting may differ (Thompson & Harestad 1994). We chose sites where clearcutting had occurred at least 5 years before to maximize the possibility of a stable marten response relative to this disturbance. However, one site contained cut blocks < 2 years old, and two sites contained clearcuts that had been harvested the previous year, but these totalled < 2% of each landscape.

In most cleared openings, average tree heights were < 2 m because of planting failures and slow growth at high elevations. Dominant vegetation was grasses and forbs, providing a distinct contrast with adjacent forests. Harvested areas lacked coarse woody debris because logging slash was normally piled and burned.

Our investigation involved four parts: estimation of marten use within each site, quantification of landscape fragmentation, estimation of potential prey abundance and characterization of forest structure. The first two aspects were associated directly with the question of forest fragmentation effects on the American marten. The latter two assessed whether factors other than fragmentation contributed to differences in marten use among sites.

ESTIMATION OF MARTEN USE

We used summer capture rates of individual martens, excluding recaptures, as a means of comparing marten use at each site. Twenty-five live traps were placed in a systematic grid covering each entire site (750 m spacing) and were monitored for 6 consecutive nights. This design potentially yielded 150 trap nights per site, but actual trapping effort varied among sites due to trap disturbance, damage and other field conditions. Each site was sampled at least once during four trapping periods between 1991 and 1993. We surveyed nine sites twice in separate years to examine potential differences in capture rates between years, and one site was surveyed in all three summers. To examine potential differences in capture rates from early to late summer, we resurveyed four sites twice during the same summer. Captured martens were sedated with ketamine, weighed and ear-tagged. We recorded the weight, gender, and overall body condition of each

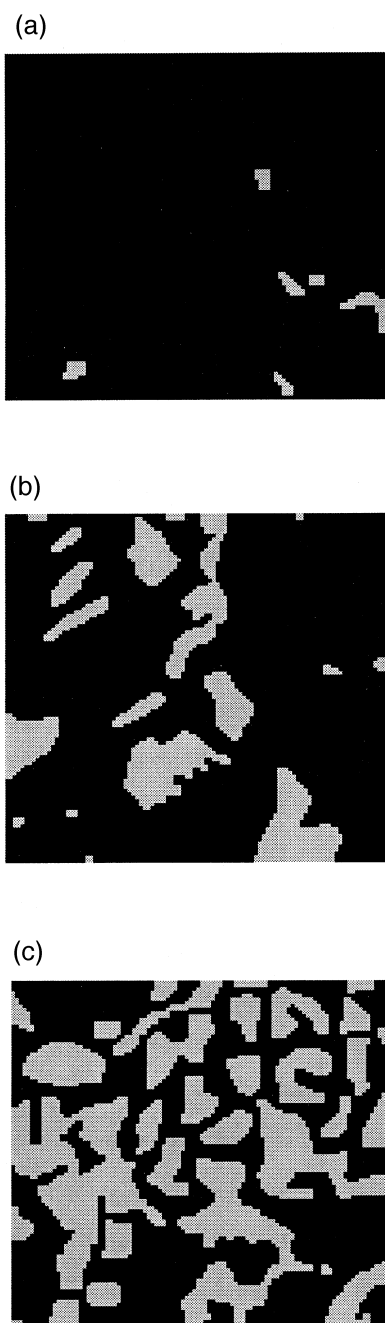


Fig. 1. Representative sites from the Uinta Mountains of northern Utah used in the study of forest fragmentation effects on the American marten: (a) Beaver Meadow (b) Hayden Pass and (c) East Park. Black represents forest and grey represents open areas.

Table 1. Landscape characteristics of 18, 9-km² landscapes in the Uinta Mountains of Utah

Site	% of site in openings*	% of site in clearcuts	Edge density	Mean proximity index	Nearest neighbour distance	Mass fractal dimension
Beaver†	1.7	0.0	5.0	3.7	523	1.99
Anderson	4.6	3.4	11.1	10.8	181	1.98
Highline	5.8	2.9	13.2	0.8	370	1.99
Spirit	7.6	0.0	14.3	2.3	252	1.98
Sims	8.3	5.0	19.3	9.9	102	1.97
Marsh East	9.1	8.9	17.6	36.6	224	1.97
Bull	9.9	0.0	17.6	23.4	337	1.96
Manila	14.2	9.9	24.6	21.6	150	1.96
Sheep	14.3	11.2	24.7	97.8	118	1.97
Cliff	15.6	3.3	28.3	39.0	132	1.96
Chepeta	16.7	12.1	34.0	43.7	83	1.94
Hayden†	16.8	10.5	26.8	10.6	216	1.93
Dahlgreen	19.5	18.4	39.4	25.2	95	1.92
Deer	21.6	15.2	39.4	28.3	123	1.89
Marsh West	25.3	19.6	35.2	106.7	84	1.91
Long Park	36.1	31.2	52.5	149.4	99	1.86
Gold	39.1	8.8	50.3	305.5	75	1.84
East Park†	41.9	41.9	64.2	169.8	62	1.78

* Natural openings and clearcuts combined to form two-attribute landscapes.

† Illustrated in Fig. 1.

Table 2. Forest structure characteristics of lodgepole pine–spruce forests in 18 sites in the Uinta Mountains of Utah. Variables above the dashed line were similar among sites (Fig. 2)

Structural attribute	Mean	Standard deviation
Basal area (m ² ha ⁻¹)	37	5
Overstorey basal area (m ² ha ⁻¹)	29	5
Canopy cover (%)	45	8
Stand density index	839	141
Stand d.b.h. _q (cm)	22	3
Diameter of sound logs (cm)	18	2
Diameter of rotten logs (cm)	21	3
Metric tons ha ⁻¹ of sound logs	15.3	8.6
Metric tons ha ⁻¹ of rotten logs	18.2	10.9

Overstorey d.b.h. _q (cm)	27	6
Overstorey lodgepole pine d.b.h. _q (cm)	19	5
Overstorey spruce d.b.h. _q (cm)	15	11
% of live overstorey in lodgepole pine	61	25
% of live overstorey in spruce	25	18
Live crown ratio of overstorey trees	51	13
% of total stems in snags	29	15
% of overstorey stems in snags	34	19
% of basal area in snags	35	18
% of overstorey basal area in snags	36	20

martens, and noted the appearance of lactation in females.

Because high capture rates do not necessarily imply high quality habitat (van Horne 1983; Pulliam 1988), we used reproductive status, weight, body condition and recapture in subsequent years to assess whether

high capture rates were generally associated with other indicators of good health and reproduction. This information was qualitative because sample sizes were insufficient for statistical analyses.

Martens were not harvested commercially during our study. A 5-year moratorium on commercial trap-

ping of martens in the Uinta Mountains was initiated in 1990, one trapping season prior to the onset of our study. Additionally, no trapping had occurred in the 2 years prior to the moratorium (Utah Division of Wildlife Resources, unpublished data), and prior to that there had been sporadic harvesting by only two trappers, most of which occurred outside our study sites.

ANALYSIS OF FRAGMENTATION

We obtained raster images of our study sites by extracting the relevant areas from an existing vegetation map of the Uinta Mountains. The vegetation map was derived from LANDSAT TM data (30-m resolution) and had been classified into 35 vegetation types with corrections for slope, aspect and elevation (Homer *et al.* 1997). Our extracted images contained 12 of the 35 vegetation types, and we aggregated these into two classes: forests and open areas (clearcuts and natural openings combined). We reduced mapping error by comparing the classified images to aerial photos, and corrected all misclassified pixels to match the shapes of vegetation polygons on the photos.

We further simplified the maps to remove fragmentation 'noise' that occurred at a finer grain than perceived by martens. Assuming that martens readily cross 30-m openings (Koehler & Hornocker 1977; Hargis & McCullough 1984), patches < 30 m were removed by blending all single pixel openings with the surrounding forest polygon. Likewise, isolated forest pixels were reclassified to match the clearcut or natural opening in which they occurred.

We quantified habitat fragmentation using five measures: the percentage of landscape in openings, edge density (m ha^{-1}), mean proximity index, mean nearest-neighbour distance between open areas (m), and mass fractal dimension. The first five measures were calculated with a spatial pattern analysis program, FRAGSTATS (McGarigal & Marks 1995). Mass fractal dimension was calculated using software developed by B. Milne and T. Keitt at the University of New Mexico.

We calculated the percentage of landscape in openings as the combined percentages of clearcuts and natural openings within each study site. Edge density was the sum of all edge pixels divided by total landscape area, expressed as metres of edge per hectare.

Mean proximity index quantified the mean isolation of each open patch from all other openings within a specified search radius, taking into account the size of all other openings as well as the distance between them. The mean proximity index was derived from individual proximity indices for each patch in the landscape, when each patch is viewed as a 'focal patch'. The proximity index for each patch was calculated as the sum, for all patches within the search radius of the focal patch, of patch area (m^2) divided by nearest edge-to-edge distance squared (m^2) (McGa-

rigal & Marks 1995, modified from Gustafson & Parker 1992). High values of the mean proximity index indicated closer proximity between open patches. We used the full extent of each study site (3000 m) as the search radius for each patch.

We calculated mean nearest-neighbour distance between openings as the average edge-to-edge distance between each non-forested patch in the landscape and its nearest neighbour. This measure differed from the proximity index by ignoring patch size and by defining interpatch distance only with the nearest open patch. Mean nearest-neighbour distance yields an absolute value that only can be used to compare landscapes with the same extent and resolution (Gustafson & Parker 1992), but our sites met these criteria.

Mass fractal dimension was used to describe the fractal nature of the forest matrix. We chose this fractal measure over a perimeter-area fractal because it characterized the shape of the forest matrix caused by placement of open patches, rather than measuring the irregularity of individual patch perimeters. Mass fractal dimension represents the scaling relationship between the average number of forested pixels contained within a subsample of a landscape and the length of the box defining the subsample. Computationally, it is the slope derived from the log of the average number of pixels associated with a series of increasing box sizes regressed on the log of the box lengths (Voss 1988; Milne 1991). We calculated mass fractal dimension by counting the mean number of forested pixels in subsamples of the landscape contained within square boxes with edge lengths of 3, 9, 15, 21 and 27 pixels. Theoretical limits of this measure are between 0 and 2. A value of 2 is achieved when the forest completely fills the 2-dimensional landscape, and is reduced to some dimension < 2 as non-forest patches are added.

ESTIMATION OF PREY DENSITY

We estimated small mammal populations on 12 of the sites during a 7-week snap-trap survey between 22 July and 8 September 1992. Each site was surveyed with 12 trap lines consisting of 16 stations spaced 20 m apart, with each station consisting of 2 Victor mouse traps and 1 Victor rat trap, except for the last station which had one mouse and one rat trap. Lines were placed in forested areas, clearcuts and meadows in approximate proportion to the availability of each of the three habitat types, and were run for 2 nights (1200 trap nights per site). Actual trap nights were calculated by subtracting all traps that malfunctioned or were sprung each night. We estimated the relative abundance of each species as captures per 100 trap nights, and calculated total biomass of mammals per line from measured weights. Data were summarized by site and by habitat types within each site.

ANALYSIS OF FOREST STRUCTURE

Various aspects of forest structure appear important to martens, particularly a fairly closed canopy and

abundant coarse woody debris (reviewed by Buskirk & Powell 1994). To determine whether marten capture rates might be influenced by forest structure, we measured structural attributes of forested habitat within each site. Using a modified plotless cruise at 25 points, mean values were derived for 19 structural variables for each site. Points were located at random compass directions and random distances 1–30 m from each marten trap. For marten traps located in openings or at the edge of openings, points were randomly selected within the nearest forest. We used a basal area prism to establish the number of trees included within the point sample, and recorded height, diameter at breast height (d.b.h.), species, crown class, live crown ratio and snag decay class of each tree included. Live crown ratio was a visual estimate of the percentage of total tree height in live branches. We identified two crown classes: understory and overstorey, and seven snag decay classes based on Thomas (1979). Live trees with dead tops (snag class 2) were classified as snags rather than live trees.

We calculated the stand density index (Reineke 1933) as the relationship between quadratic mean diameter (d.b.h._q) and trees per ha (t.p.h.) using the formula $SDI = t.p.h. (d.b.h._q/25)^{1.6}$ (Daniel & Sterba 1980). We estimated the amount of conifer reproduction by tallying all trees < 7 cm d.b.h. within four 2-m radius plots located five paces from each sampling point in the cardinal directions. Canopy cover was measured with a densiometer at the centre of these four plots.

We determined abundance of coarse woody debris by establishing two 15-m transect lines that extended from the plotless cruise sampling point in random directions (Brown 1974). We recorded the diameter of all woody material > 10 cm intersecting the lines and classified woody debris as being either sound or rotten. We calculated biomass density (kg ha⁻¹) for sound and rotten decay classes, using formulae developed by Brown (1974).

STATISTICAL ANALYSES

At the end of the 3-year survey period, we had surveyed each of the sites 1–3 times out of four possible sampling periods. Because repeated trapping efforts within each site were not independent, we used a bootstrap technique (Efron & Tibshirani 1993) to select randomly one trapping effort from each site, including the number of individual martens caught and total trap nights for that trapping effort. We repeated this procedure to generate 35 unique combinations of trapping efforts, each containing one trapping effort per site ($n = 18$ for all 35 data sets). This procedure enabled us to mix capture results from all years and from early or late summer seasons in a variety of combinations.

We used Poisson regression analysis (Frome, Kutner & Beauchamp 1973) to test for differences in

marten capture rates among sites due to fragmentation, prey availability and forest structure. The analysis was run on all 35 data sets, and from this an average *P*-value and 95% confidence interval (CI) was calculated. We chose the Poisson model because marten captures were counts that occurred at a low rate, and the data most closely fit the Poisson distribution. Our data were overdispersed, leading us to use a quasi-likelihood method for estimating model parameters, and a χ^2 statistic was used to test for significance of these parameters (McCullagh & Nelder 1989).

We tested five fragmentation models, one for each measure described in the section on fragmentation, and evaluated the relative strength of each model based on a comparison of *R*²-values. We did not generate a model containing all fragmentation variables because initial data exploration revealed high correlation among measures. We were interested, however, in determining whether any of the measures were more strongly correlated with marten numbers than others.

Prior to conducting the regression analysis, we evaluated 18 measures of forest structure and seven variables from the small mammal survey to determine whether there were sufficient differences among the sites, in either forest structure or prey abundance, to warrant inclusion in the analysis of fragmentation. Due to the large number of these variables relative to the sample size of landscapes, we used data exploration techniques to eliminate variables that either did not appear to differ among sites, or that differed but were not correlated with marten captures. We examined box plots for each variable for differences among sites, and where differences were observed we used correlation coefficients between each variable and marten captures to determine whether the variable should be added to the fragmentation models.

Results

INFLUENCES OF FOREST STRUCTURE AND PREY AVAILABILITY

Nine forest structure variables showed close similarity among sites, and 10 variables differed, based on exploratory analysis using box plots (Table 2). Canopy cover and several measures of coarse woody debris were among the variables that were similar among sites (Table 2 and Fig. 2). None of the forest structure measures was strongly correlated with marten captures, and only the measures of snag abundance had correlation coefficients > |0.20| (Table 3). Based on a forward stepwise regression of the 10 variables that differed among sites and marten captures, only percentage of total stems in snags (henceforth called snag abundance) explained sufficient variation in marten captures to be included in subsequent models of fragmentation, and all other forest structure variables were dropped from further analysis.

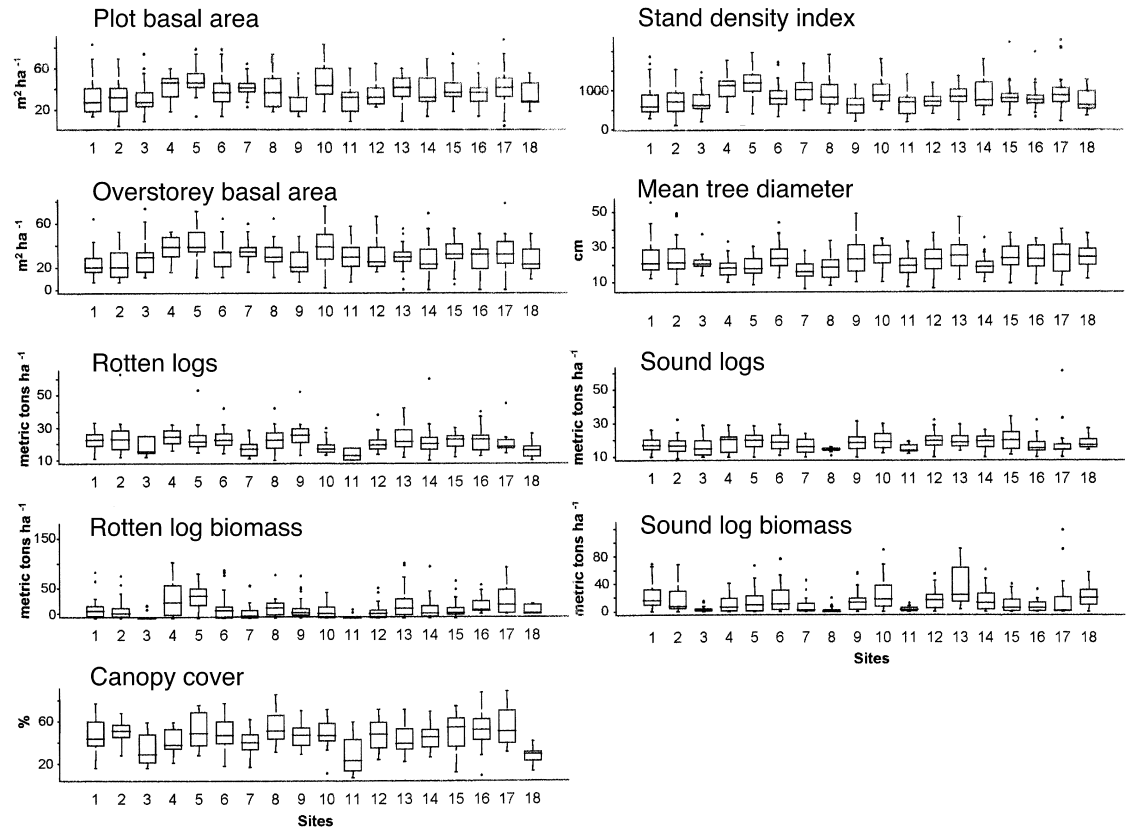


Fig. 2. Box plots for forest structure variables having similarity among sites, with sites arranged from highest to lowest marten capture rates. The solid line in the box represents the median value, the box defines the first and third quartiles, and extreme values are shown as dots.

Table 3. Pearson correlation coefficients between marten capture rates and forest structure variables, with coefficients $>|0.20|$ highlighted in bold

Variable	r
Basal area ($\text{m}^2 \text{ha}^{-1}$)	-0.17
Stems ha^{-1}	0.01
Stand density index	-0.10
Canopy cover	0.00
Live crown ratio of overstorey trees	0.04
Stand d.b.h. _q (cm)	-0.15
Overstorey dbh _q (cm)	0.15
Overstorey lodgepole pine d.b.h. _q (cm)	0.11
Overstorey spruce d.b.h. _q (cm)	0.05
% of live overstorey in lodgepole pine	-0.02
% of live overstorey in spruce	0.04
% of total stems in snags	-0.52
% of basal area in snags	-0.44
% of overstorey stems in snags	-0.48
% of overstorey basal area in snags	-0.42
Diameter of rotten logs	-0.02
Diameter of sound logs	0.02
Metric tons ha^{-1} of sound logs	-0.04
Metric tons ha^{-1} of rotten logs	0.15

found a positive relationship between snag abundance and the percentage of site in clearcuts ($F = 6.54$, d.f. = 1,16, $P = 0.02$, $R^2 = 0.25$) and a negative correlation between snag abundance and canopy cover ($F = 10.85$, d.f. = 1,16, $P = 0.005$, $R^2 = 0.37$). Marten captures, however, were not correlated with canopy cover ($r = -0.01$), because cover was within an acceptable range for marten habitat suitability at all sites. Canopy cover ranged from 28% to 55%, and a lower limit of 30% is considered suitable (Koehler & Hornocker 1977; Spencer, Barrett & Zielinski 1983). There was no significant correlation between snag abundance and biomass density of coarse woody debris ($F = 0.15$, d.f. = 1,16, $P = 0.70$, $R^2 = 0.0$) or between snag abundance and vole densities ($F = 1.29$, d.f. = 1,16, $P = 0.27$, $R^2 = 0.02$).

The small mammal survey resulted in 1753 captures in 11 417 trap nights, excluding sprung traps. The five most commonly trapped species were the southern red-backed vole *Clethrionomys gapperi* Merriam, deer mouse *Peromyscus maniculatus* Osgood, Uinta chipmunk *Eutamias umbrinus* J. A. Allen, least chipmunk *Eutamias minimus* A. H. Howell, and the vagrant/masked shrew complex *Sorex vagrans* Merriam and *S. cinereus* Kerr. We investigated seven variables that related to prey availability: captures per 100 trap nights for each of the five common species (five variables); total biomass per trap nights of all mammals

captured per site; and total captures per 100 trap nights per site. Total biomass was the total weights of all mammals trapped per site, excluding the weights of incidental snap-trap captures of snowshoe hare *Lepus americanus* Erxleben. We found differences among sites for all prey variables, but all were weakly correlated with marten captures (Fig. 3 and Table 4). Vole captures showed the highest correlation with marten captures ($r = 0.72$) but were not a significant predictor of marten captures either when used alone (mean P of 35 bootstrap samples = 0.68, CI = 0.65, 0.71) or in

combination with one of the fragmentation measures and snag abundance (mean P of 35 bootstrap samples = 0.53, CI = 0.50, 0.56). The correlation between marten and vole captures was primarily due to one site that had both the highest number of martens and an extremely high density of voles (Fig. 4b). When this site was omitted, the correlation coefficient was 0.53.

Although prey availability was not correlated with marten captures, we found differences in prey among forests, meadows and clearcuts that were useful in interpretation of marten response to fragmentation. The

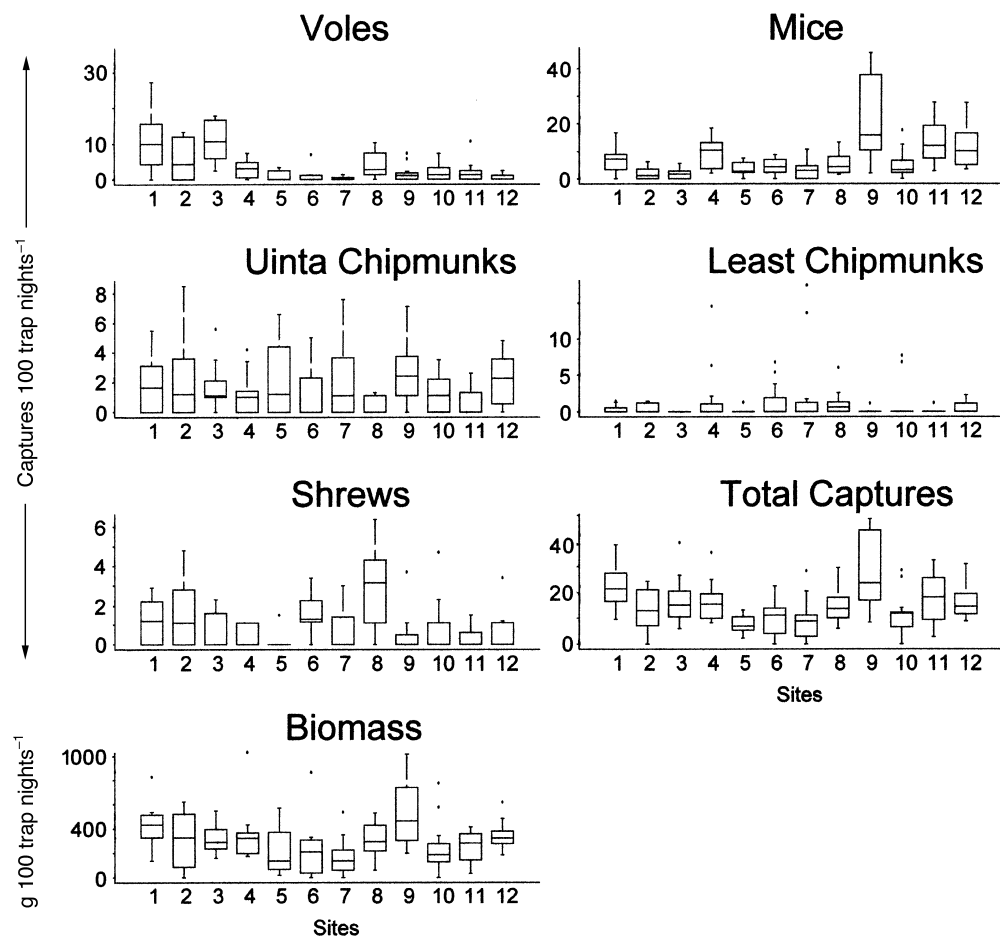


Fig. 3. Box plots for prey variables, with sites arranged from highest to lowest marten capture rates. The solid line in the box represents the median value, the box defines the first and third quartiles, and extreme values are shown as dots.

Table 4. Pearson's correlation coefficients between marten capture rates and prey variables

Variable	r
Voles 100 trap nights ⁻¹	0.72
Deer mice 100 trap nights ⁻¹	-0.37
Uinta chipmunks 100 trap nights ⁻¹	0.21
Least chipmunks 100 trap nights ⁻¹	-0.14
Shrews 100 trap nights ⁻¹	0.12
Total mammals 100 trap nights ⁻¹	0.16
Biomass 100 trap nights ⁻¹	0.29

density of small mammals was highest in clearcuts, followed by forests and meadows (χ^2 for clearcuts vs. forests = 20.12, d.f. = 1, $P = 0.001$; χ^2 for meadows vs. forests and clearcuts = 16.14, d.f. = 1, $P = 0.001$). We captured an average of 21 mammals 100 trap nights⁻¹ in clearcuts, 14 mammals 100 trap nights⁻¹ in forests, and 6 mammals 100 trap nights⁻¹ in meadows. The total biomass was highest in clearcuts, followed by forests and meadows ($F = 17.5$, d.f. = 2, $P < 0.001$).

MARTEN RESPONSE TO FRAGMENTATION

We captured 53 individual martens (34 males and 19 females; 46 adults and 7 juveniles) in 4983 trap nights,

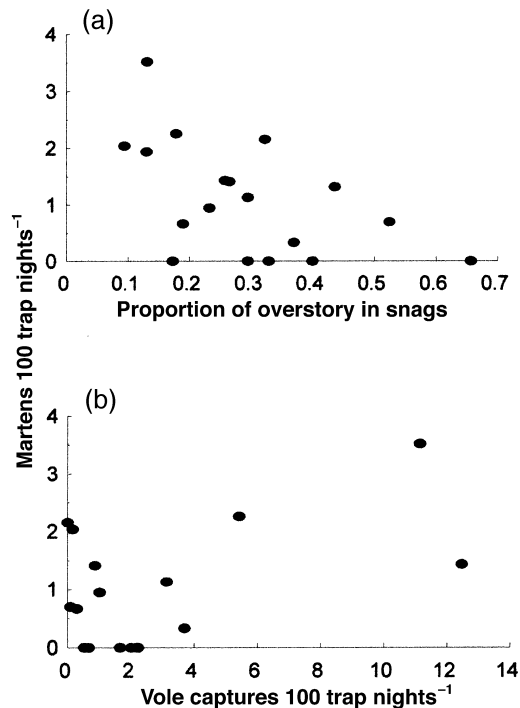


Fig. 4. Scatterplot of individual marten captures with (a) percentage of total stems in snags and (b) vole captures 100 trap nights⁻¹.

with 0–8 individual captures per site during any given trapping period. Although capture rates differed among sites (described below), we found no significant difference in capture rates among trapping periods within any given site ($\chi^2 = 2.89$, d.f. = 3, $P = 0.41$). Sites with high captures were consistently high, and sites with zero captures remained low, resulting in a nearly stable ranking of sites across all years, and confirming that differences in capture rates were due to factors other than seasonal variation or sampling error.

Marten captures were negatively correlated with loss of forest habitat, as measured by the percentage of each site in open areas, and this relationship was significant ($P = 0.03$) when snag abundance was added to the model (Table 5). Capture rates were variable in sites with low fragmentation, but only one marten was captured in 937 trap nights in the four sites having >0.25% open areas (Fig. 5a).

Martens showed significant responses to landscape pattern as well as loss of habitat (Fig. 5b–d and Table 5). Capture rates were lowest in landscapes with large, closely spaced open areas, as measured both by mean proximity index and nearest-neighbour distance. Landscapes with an average distance between open areas <100 m had no marten captures. Also, landscapes with high edge density had fewer marten captures. We did not observe a significant correlation between marten captures and mass fractal dimension, although the trend was for low to zero captures in landscapes where the forest matrix was highly convoluted (Fig. 5e and Table 5).

COMPARISON OF FRAGMENTATION MODELS

We examined correlations between percentage of each site in openings and the four measures of landscape pattern to assess the degree of additional information provided by these measures (Table 6). Correlations were generally high, with mass fractal dimension having the highest correlation with habitat loss ($r = -0.97$) and nearest-neighbour distance the lowest ($r = -0.67$). In addition, the four measures were interrelated among themselves, with edge density and mass fractal dimension having the strongest correlation ($r = -0.96$).

Partly as a consequence of these interrelationships, nearest-neighbour distance, edge density and percentage of site in openings were similar in their role as explanatory variables of marten capture rates. Used alone, each explained approximated 20% of the variation in marten capture rates and P -values were similar. When used in combination with snag abundance, percentage of site in openings and edge density became better predictors, but the relationships for nearest-neighbour distance were weakened. Mass fractal dimension provided the poorest fit of all fragmentation measures examined, both when used alone or in combination with snag abundance.

The combined effects of mean proximity index and snag abundance provided the best fit for explaining differences in marten capture rates, based on a comparison of P -values and R^2 terms from all fragmentation models examined (Table 5). The contribution of mean proximity index was greater than that of percentage of site in openings, which became an insignificant term when both measures were included in a model (mean P for each variable, respectively, based on 35 bootstrap runs = 0.37 and 0.01).

Discussion

Martens appeared to respond negatively to low levels of habitat fragmentation, based on a significant decrease in capture rates observed across a series of increasingly fragmented landscapes. Martens were rarely detected in sites with >25% open areas, even though forest connectivity was still present.

Martens were sensitive not only to loss of habitat but also to the size and proximity of open areas. As measured by the mean proximity index, marten capture rates decreased as open patches became more closely situated (Fig. 5b). When the average nearest-neighbour distance between open patches was <100 m, nearly all forest interior had been converted to narrow strips of forest that functioned only as edge habitat (Fig. 1c).

We provide several caveats to aid in interpreting these results. First, R^2 values associated with all significant relationships were low. It may be unrealistic to expect high R^2 values in a study design where landscapes are the units of replication, but nevertheless

Table 5. Statistical significance of fragmentation models explaining individual marten capture rates, with mean *P*-values (confidence intervals in parentheses) derived from chi-square tests performed on 35 bootstrap data sets per model (error d.f. = 15 in each model). Models with *P* < 0.05 are indicated with an asterisk. The second column contains both the mean univariate *P*-value and the mean multivariate *P*-value of the fragmentation measure when snag abundance is added to the model

Model parameters	<i>P</i> -value of fragmentation measure	<i>P</i> -value of snag abundance in multivariate model	<i>R</i> ²
% of site in openings	0.06 (0.05, 0.07)		0.23 (0.21, 0.25)
* % of site in openings, snag abundance	0.03 (0.02, 0.04)	0.01 (0.01, 0.01)	0.50 (0.48, 0.52)
* Proximity index	0.01 (0.01, 0.01)		0.48 (0.47, 0.49)
Proximity index, snag abundance	0.04 (0.03, 0.05)	0.07 (0.06, 0.08)	0.59 (0.58, 0.60)
* Nearest-neighbour distance	0.03 (0.03, 0.03)		0.21 (0.20, 0.22)
* Nearest-neighbour distance, snag abundance	0.05 (0.02, 0.08)	0.03 (0.01, 0.05)	0.42 (0.40, 0.44)
Edge density	0.08 (0.07, 0.09)		0.19 (0.17, 0.21)
* Edge density, snag abundance	0.05 (0.01, 0.09)	0.01 (0.00, 0.02)	0.47 (0.45, 0.49)
Mass fractal dimension	0.12 (0.10, 0.14)		0.17 (0.15, 0.19)
Mass fractal dimension, snag abundance	0.11 (0.04, 0.18)	0.02 (0.01, 0.03)	0.43 (0.39, 0.47)

the low *R*² values indicate substantial unexplained variation in marten capture rates.

Secondly, the size chosen for study areas was small relative to marten home range scale. The size of marten home ranges in the Uinta Mountains is unknown, but in the neighbouring state of Wyoming the mean summer home ranges (95% minimum convex polygon) of seven females was 669 (± 67 SE) ha and that of eight males was 1820 (± 153 SE) ha (O'Doherty, Ruggiero & Henry 1997), sizes that would suggest only 1–2 martens per landscape. Nevertheless, we expected several martens to occur in each landscape because home range boundaries were unlikely to correspond to study area boundaries, and therefore partial home ranges of several martens could be represented. Martens exhibit intrasexual territoriality (reviewed by Powell 1994) but > 1 female range typically occurs within those of males. Non-territorial juveniles sometimes share ranges with territorial adults (Archibald & Jessup 1984). Rather than view these landscapes from a home range perspective, we viewed each landscape as a window providing a snapshot of marten numbers at a given point in time.

A third caveat is that marten capture rates represent relative, not absolute, marten numbers. Sites with no marten captures may have contained martens but at densities too low to detect during the 6-night trapping period. To increase our confidence in interpreting zero values, we resampled all sites in which no martens

were caught, and in all cases no martens were captured during these second attempts. Nevertheless, we cannot conclude that no martens were present.

Also, we were unable to determine whether martens in our samples were residents or transients. This is an important consideration because high numbers of transients could indicate a population sink (Pulliam 1988). Although we do not know how many transients occurred in each site, we do know that sites with high marten captures contained residents. The two sites with the highest number of captures were the only sites where we recaptured the same individuals in subsequent years. These sites also represented two of the four sites with lactating females, denoting reproductive activity. In the site with the highest capture rate, the average weight of males was above average for all sites, and general body condition was fair to excellent. Thus, there is no evidence to suggest that sites with high captures were simply areas of dispersal.

Our final caveat regards the apparent threshold in marten occurrence when open areas were approximately 25% of the total landscape. Martens in our sites may have exhibited a stronger response to low levels of fragmentation than would be expected in geographical areas with less harsh conditions. The clearcuts in our sites provided no habitat for martens because cut areas generally were stripped of both vegetation and logging slash after timber harvest. Moreover, the top soil was considerably disturbed, often

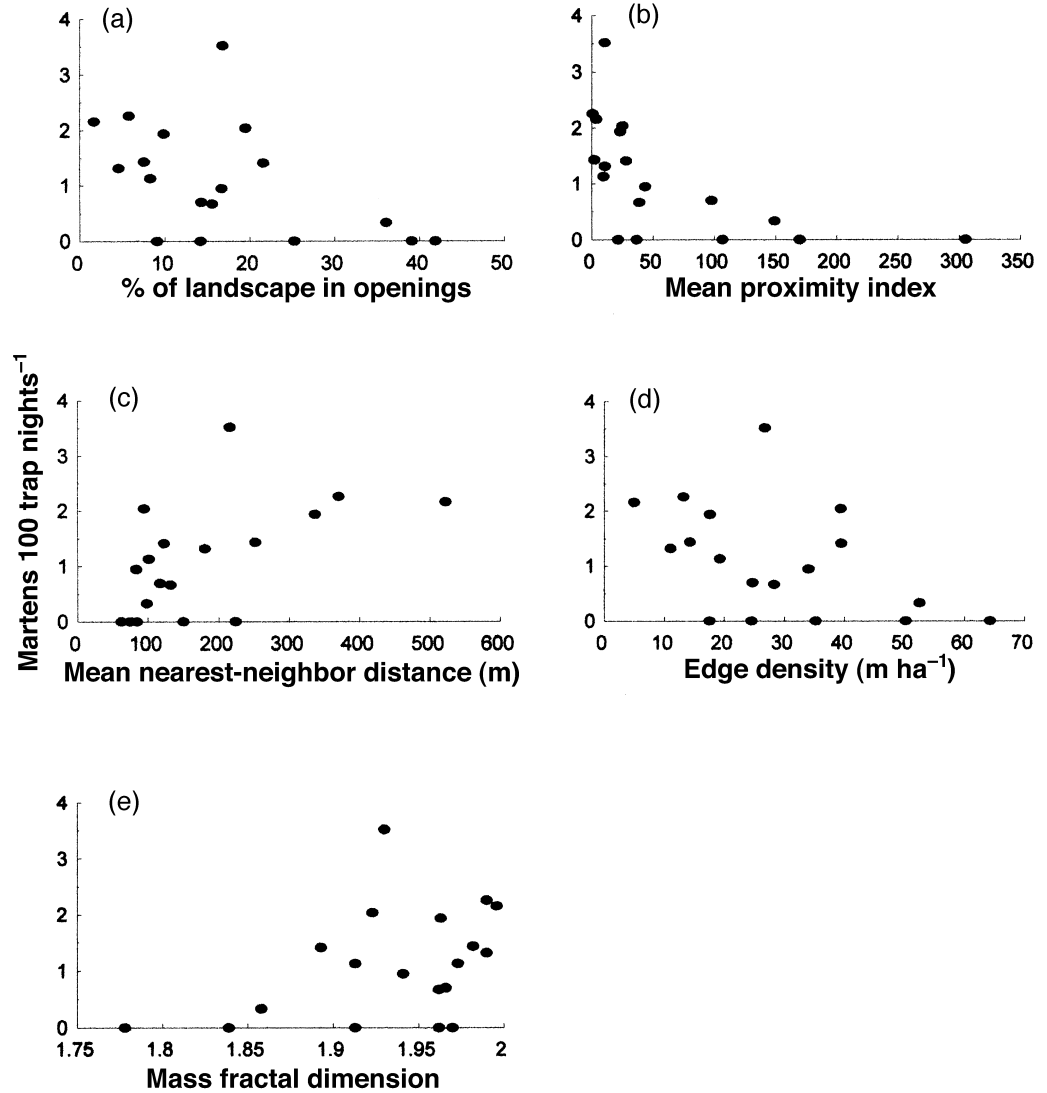


Fig. 5. Scatterplot of marten capture rates with five measures of fragmentation: (a) percentage of site in openings; (b) mean proximity index; (c) mean nearest-neighbour distance; (d) edge density; and (e) mass fractal dimension.

Table 6. Correlation matrix for landscape metrics and snag abundance, with all coefficients >|0.70| highlighted in bold

	Marten	% open	Edge density	Proximity index	Nearest neighbour distance	Mass fractal dimension	Snags
Marten	1.00	-0.50	-0.45	-0.59	0.56	0.41	-0.53
% open		1.00	0.97	0.85	-0.67	-0.97	0.28
Edge			1.00	0.74	-0.72	-0.96	0.26
Proximity index				1.00	-0.50	-0.79	0.28
Nearest-neighbour distance					1.00	0.59	-0.26
Mass fractal dimension						1.00	-0.32
Snags							1.00

retarding the establishment of conifer growth for a decade or more.

Elsewhere, martens apparently can forage in clearcuts containing structure in the form of regenerating deciduous or conifer vegetation and brush (Stevenson

& Major 1982; Katnik 1992; Potvin & Breton 1997) and may tolerate higher levels of fragmentation under these circumstances. Soutiere (1979) found marten using areas that were 60% cut in Maine, although at lower population levels than in uncut areas. We find it

noteworthy, however, that Chapin & Harrison (1998), working in the same general vicinity as Soutiere, found no adult female marten territories where >31% of the landscape was in regenerating vegetation. The median percentage of home range area in regenerating patches was 20% for 14 resident adult females and 22% for 13 resident adult males (Chapin & Harrison 1998). Also, Thompson (1994) found resident marten at only one of five sites with logged forests, and clearcuts on these sites were vegetated with shrubs and quaking aspen *Populus tremuloides*. These studies indicate that marten residency, if not marten presence, may be affected by fairly low levels of fragmentation, regardless of the vegetation present in open areas. In areas where openings are poorly vegetated for long periods, we anticipate that martens would respond to fragmentation at approximately the same level that we observed. For example, clearcut management comparable to that of the Uinta Mountains occurs in much of the lodgepole pine and spruce forests of the intermountain states of western North America, and we consider our results relevant to marten conservation in that geographical area.

Our findings may be pertinent to the conservation of the Eurasian pine marten *Martes martes* Linnaeus as well. Of 46 British mammals analysed for vulnerability to fragmentation, the pine marten was considered one of the most vulnerable due to relatively low population density, slow breeding, fairly poor dispersal capabilities and close affinity to semi-natural habitats (Bright 1993). In the former USSR, notable declines in marten abundance were apparent when mature forest was reduced to 25–35% of total area (Grakov 1972). In northern Sweden, pine marten densities were found to be two to three times higher within an old-growth forest reserve than in the surrounding landscape of commercially managed, fragmented forest (Björvall, Nilsson & Norling 1977; cited in Brainerd 1997). In southern Sweden and south-eastern Norway, pine martens consistently preferred later-successional seres of spruce-dominated forest and avoided open habitats throughout the year (Brainerd 1997).

Martens in Scotland appear to tolerate high levels of forest fragmentation, but Balharry (1993) found that the normal rodent diet is supplemented by carrion, mostly from red deer *Cervus elaphus* culling operations and, to a lesser extent, from hill sheep *Ovis aries*. Carrion accounted for 35% of the estimated weight intake of all marten foods in two study sites. Nevertheless, some minimum area of woodland seemed important for establishing breeding territories, because breeding adults had significantly more woodland in their territories than juveniles and non-breeding adults (Balharry 1993). In a comparison of two study sites in Scotland, Balharry (1993) found that male marten home ranges were three times larger in the site having only 3.5% woodland than in the site with 27% woodland.

American martens may be somewhat more sensitive

to fragmentation than pine martens, and may require a certain proportion of forest interior within their home ranges. As summarized by Buskirk & Powell (1994), martens appear to use structural components of mature forests to avoid predators (Drew 1995), to gain access to prey in winter (Hargis & McCullough 1984; Corn & Raphael 1992; Sherburne & Bissonette 1993; Sherburne & Bissonette 1994) and to gain thermal advantages, especially while resting (Buskirk *et al.* 1989; Taylor 1993; Raphael & Jones 1997). Each of these could be affected by loss of forest interior habitat. Forest patches <100 m wide may not provide sufficient escape cover from known predators such as red fox *Vulpes vulpes*, coyote *Canis latrans* and raptors (Hodgman *et al.* 1997; Thompson 1994). Availability of preferred prey may also be a factor. Mills (1995) found lower densities of California red-backed voles *Clethrionomys californicus* near edges than in forest interiors, and Nordstrom (1995) found lower densities of southern red-backed voles in narrow forest corridors compared to contiguous forest blocks during a low population year. Thermal advantages may also be lost in forests that have been reduced to narrow strips. Chen, Franklin & Spies (1995) found that microclimatic edge effects can extend >240 m into old-growth Douglas-fir forests. Therefore, a forest interspersed with closely spaced open patches may lack the thermal conditions normally associated with mature forests due to landscape pattern.

Edge habitat *per se* is not necessarily detrimental to martens. Marten use of edge may depend on the habitat composition on either side (Buskirk & Powell 1994). In California, martens showed preferential use of edge that bordered mesic meadows (Simon 1980; Spencer, Barrett & Zielinski 1983) and in Maine edge between residual conifer forests and regenerating clearcuts was used in proportion to availability (Chapin 1995; Chapin & Harrison 1998). In our study, the correlation between edge density and mean proximity index made it difficult to determine whether martens responded negatively to edge, or whether the actual response was to the loss of forest interior from closely spaced patches, and edge was simply a covariate.

In addition to loss of interior habitat, martens may avoid landscapes with abundant openings due to the increased energetic costs of circumventing the open areas. It may be energetically prohibitive to defend a territory or forage in a home range that is widely diffused and interspersed with large patches of unsuitable habitat (Thompson & Colgan 1994).

We found no evidence that martens benefit from the increase in abundance and diversity of prey associated with clearcuts. We cannot state this conclusively because we did not collect dietary information, but our trapping data did not indicate a positive response to prey in clearcuts. Although small mammal densities were higher in clearcuts than in forest habitat, marten capture rates were not correlated with biomass of prey found in clearcuts, or with the abundance of any

species associated with clearcuts. Information on red squirrel (*Tamiasciurus hudsonicus* Trouessart) or snowshoe hare abundance, which we did not obtain, would not have changed the relationship between martens and clearcut-associated prey, because both are associated with forests (Raphael 1988; Thompson & Colgan 1994). Seven of the eight incidental captures of snowshoe hares were in forests.

We found a negative correlation between marten capture rates and snag abundance, but martens showed a positive response to snags in other studies (Spencer, Barrett & Zielinski 1983; Lofroth 1993; Drew 1995), partly because of their use of large diameter snags for resting sites (Campbell 1979; Spencer, Barrett & Zielinski 1983). In our study, snags were a common habitat feature in all sites and may not have been limiting to martens, but snag abundance varied among sites due to differences in mortality from mountain pine beetle *Dendroctonus ponderosae* Hopkins. The representation of snags in the overstorey ranged from 9% in an uninfected site to 65% in a heavily infected area. Sites with high beetle mortality were frequently selected for salvage timber harvests, and therefore sites with high snag densities also had the greatest number of clearcuts. Thus, the negative correlation between martens and fragmentation is mirrored by the negative correlation between martens and snag abundance. Because snag abundance improved the fit of all fragmentation models (Table 5), however, it is more than a correlate with fragmentation, and may be influencing marten ecology in ways that our data did not reflect. The more open canopy cover associated with high snag densities may cause edge effects to extend further into forests, causing a greater loss of forest interior at any given level of fragmentation than sites with low snag abundance.

RECOMMENDATIONS FOR MANAGEMENT AND RESEARCH

Our study was designed to assess changes in marten capture rates over a range of habitat fragmentation, but we were unable to separate the effects of habitat loss from the effects of landscape pattern. All measures of landscape pattern except mass fractal dimension were significantly correlated with marten captures, but each change in the measure of pattern was associated with a change in available habitat. To isolate the effects of landscape pattern, it would be necessary to sample martens in several landscapes having the same level of habitat loss but differing in landscape pattern. Landscapes with 20–35% of the area in openings appear fruitful for further investigations, based on the notable change in capture rates we encountered at this level. We predict that within this range of fragmentation martens are sensitive to landscape pattern alone, and that landscapes lacking forest interior may not sustain reproducing populations.

The effects of patch size and spatial distribution on forest interior are illustrated using three landscape patterns at the same level of fragmentation, with each landscape having approximately 20% of the area in openings (Fig. 6). The first landscape represents one of our study sites with open areas in a dispersed pattern that has resulted in the loss of much of the forest interior (Fig. 6a). The other images are of two simulated landscapes having 20% openings in which the openings are either clustered (Fig. 6b) or aggregated

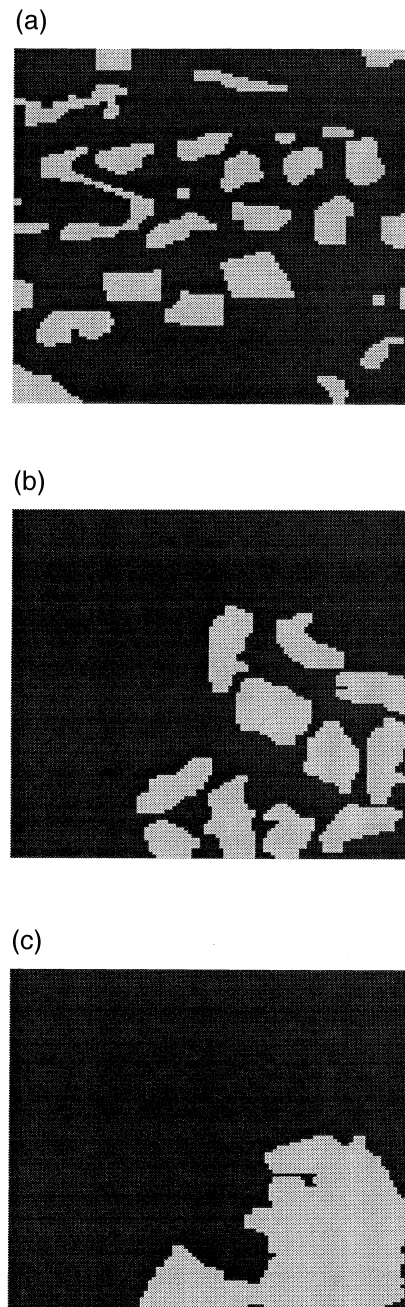


Fig. 6. Three landscape patterns with approximately 20% of the area in openings: (a) an actual landscape in Utah; (b) a simulated landscape with clustered patches; and (c) a simulated landscape with openings aggregated into a single patch to maximize forest interior. Black represents forest and grey represents open areas.

into a single patch (Fig. 6c). The simulations were created with a computer program that places patches on a landscape at any specified proportion and spacing (Hargis, Bissonette & David 1997), using digitized clearcut patch shapes from the Uinta Mountains. The comparison clearly illustrates the greater size of forest interior and fewer disruptions in continuity of habitat that occurs when unsuitable habitat is clustered or occupies a single patch.

Assuming American martens do require forest interior for reproductive habitat, management should consider the guidelines developed by Franklin & Forman (1987) for conservation of forest interior species in managed landscapes. They recommend that timber harvests be undertaken progressively outward from a single patch or in clustered cuts so that disturbance patches are consolidated and larger areas of undisturbed forest could be maintained. For martens, progressive cutting rather than clustered cuts would be preferred, because the forested buffers left between tightly clustered clearcuts have little apparent value to martens, and represent additional loss of habitat rather than useable forest. Progressive cutting from a single patch would create maximum aggregation of disturbance and retain the largest amount of interior forest habitat.

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