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# RELATIONS AMONG FISHERS, SNOW, AND MARTENS IN CALIFORNIA: RESULTS FROM SMALL-SCALE SPATIAL COMPARISONS

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**Abstract:** A recent publication hypothesized that deep snowfall can limit fisher (*Martes pennanti*) populations, and high fisher populations limit marten populations (*M. americana*). These hypotheses were evaluated by comparing the historic (1919-1924) and current (1989-1994) distributions of both *Martes* species in California to current snowfall distributions and forest types presumed to be habitats for each species. Data on historic distributions of fishers and martens came from the locations of trapped animals reported by Grinnell et al. (1937), whereas current distributions came from detection surveys (sets of track-plates, cameras, and both) conducted primarily by personnel of the US Department of Agriculture (USDA) Forest Service. Information on forest types came from a computerized database created by the USDA Forest Service from satellite imagery. In both time periods, areas occupied predominantly by martens were closely associated with forested areas with the deepest snow (>23 cm per winter month), areas occupied predominantly by fishers were forested areas with low monthly snowfall (<13 cm), and overlap zones with both species were in forested areas of intermediate monthly snowfalls (≥ 13 to 23 cm). In contrast, there was poor spatial correspondence in both time periods between the occurrences of fishers and martens and the small-scale distributions of forest types. Although we continue to recognize the importance of forest structure and prey populations on the distribution of both species of *Martes,* these findings suggest that climatic and interspecific factors deserve more attention as factors potentially affecting fishers and martens.

## Introduction

Based on a review of North American literature and an evaluation of the distributions of fishers (*Martes pennanti*) and martens (*M. americana*) harvested in Maine, Krohn et al. (1995) proposed that (1) fisher populations can be limited by deep snow, and (2) high fisher populations limit marten populations. These 2 hypotheses were evaluated by assessing variation across 3 regions of Maine (i.e., predominately martens in the north, a central area of overlap, predominately fishers in the south) in the age ratios of fishers and martens taken by fur trappers from 1980 to 1984. The mean number of immatures per adult fisher decreased from south to north as snowfall amounts and frequencies increased, which is consistent with the hypothesis that deep snows limit fishers (i.e., deep snow is stressful and lowers reproductive success). Age ratios of martens increased beyond their biological potential with increased densities of harvested fishers (and numbers of martens harvested decreased drastically), suggesting that most martens within predominantly fisher habitat are dispersing juveniles. Thus, patterns in marten age ratios were consistent with the hypothesis that high populations of fishers limit martens. However, Krohn et al. (1995) recognized that association does not prove causation, nor were they sure that harvested animals represented population distributions.

The purpose of this study was to assess the above *2* hypotheses with data on the distribution of fishers and martens in California. Unlike Krohn et al.'s (1995) evaluation that relied on harvested animals, California has been closed to fur-trapping for fishers since 1945-46 (Lewis and Zielinski 1996) and since 1953-1954 for martens (Kucera et a1 1995). Thus, this analysis was based, in part, on non-fatal surveys specifically established to detect fishers and martens. Although fishers, and presumably martens, are caught in traps set for other carnivores (Lewis and Zielinski 1996), the lack of legal fur-trapping for *Martes* in California means that natural environmental conditions, not direct mortality from humans, probably drive the current statewide distributions of both species. In addition to assessing current distributions, we examined the historic distributions of fishers and martens in California by plotting the harvest records reported by Grinnell et al. (1937). The historic and current datasets encompassed enough environmental variation to make meaningful comparisons of factors hypothesized to affect fisher and marten distributions over large areas (i.e., small-scale).

## Data Sources and Study Predictions

### Historic Distribution

Harvest data for fishers and martens between 1919 and 1924 were taken from Grinnell et al. (1937). Specifically, we used a copy machine to enlarge figures 67 (marten harvest) and 75 (fisher harvest) from Grinnell et al. (1937) and entered the 153 points (fishers = 75; martens = 78, excluding the Humboldt subspecies) representing harvested animals into ARC/INFO (Environmental Systems Research Institute, Redlands, California; use of commercial names does not imply endorsement by the US Government). Fisher points were assumed to be individual animals whereas the points of harvested martens were coded as ≤5 martens or >5 martens as indicated by Grinnell et al. (1937).

## Current Distribution

The distribution of fishers and martens for the period 1989-1994 was determined from the results of field surveys conducted throughout these species' historic ranges in northern and central California (Zielinski et al., this volume). Most of the surveys were conducted by USDA Forest Service personnel, or contractors, on National Forest lands using enclosed track plates or line-triggered cameras (Zielinski 1991). However, the sample also included a significant number of surveys on state and private forested land. Each of the 217 surveys consisted of multiple stations (mean ± SD = 18.3 ± 13.2) distributed at about 1-km intervals along forest roads and checked every 12.6 ± 3.9 days. Almost all surveys were conducted during the snow-free season (May through October). Most surveys were initiated by biologists interested in determining whether either marten or fisher occurred in an area scheduled for timber harvest (Zielinski et al., this volume). Thus, these surveys do not represent a formal sampling design.

Successful surveys (*n* = 85) were defined as those surveys where 1 or more *Martes* were detected; unsuccessful surveys (*n* = 132) were those where no fishers or martens were detected. Adjacent surveys may be dependent in the sense that an individual animal could have visited more than 1. Because martens have smaller territories (Katnik 1992) and dispersal distances (Phillips 1994) than fishers (Arthur et al. 1989, 1993), dependent surveys could be more of a problem with fishers than martens. To allow readers to judge the independence of individual surveys, the scaled diameters of dots representing all surveys in this paper are =15 km in diameter. This compares to a mean maximum dispersal distance for juvenile fishers of 16.4 ± 4.5 km (Arthur et al. 1993).

We excluded the Humboldt marten (*M. a. humboldtensis*) from our spatial analyses because only sparse historic data exist (Grinnell et al. 1937), and the subspecies is now extremely rare or extinct (Kucera et al. 1995). However, we included this subspecies in our discussion of factors potentially affecting the distributions of *Martes* in California.

## Snowfall Data

Monthly mean snowfall data for California were obtained from the National Climatic Data Center, National Oceanic and Atmospheric Administration (NOAA), in Asheville, North Carolina. Data for 1915-16 through 1925-26 were available from too few stations (*n* = 17) to allow us to plot the distribution of snowfall for this period. Therefore, we had to compare the historic distributions of *Martes* to current snowfall patterns. Current snowfall data covered the winter of 1982-83 through 1991-92. This period was presumed to be long enough to have affected current *Martes* populations, should such relations exist, and recent enough to coincide with the years most surveys were run. Spatial distribution of snowfalls was characterized for each weather station using the amount of snowfall per month from December through March. Weather stations with fewer than 8 years of data over the 10 years of interest were excluded from our analyses. Out of a total of 463 weather stations statewide, 390 had usable data. Contours of mean monthly snowfalls calculated from the 390 stations were made using the software package SURFER Version 4 (Golden Software, Golden, Colorado). SURFER will interpolate a grid of ≤255 cells, so the north-south dimension of California was interpolated using 255 cells (each = 4.1 km/side) with 200 cells spanning east-west. An inverse distance weighting was used to calculate grid values. The snowfall grid was imported into ARC/INFO and printed.

To compare the locations and sizes of snowfall regions to the distributions of fishers and martens, we calculated means and standard deviations of mean monthly snowfalls (cm), 1982-1991, corresponding to the locations of *Martes* in both the historic and current datasets. Statistics were calculated for sites with only fishers (8.1 ± 12.7; *n* = 121), both species (17.8 ± 18.7; *n* = 11), and only martens (27.6 ± 23.1; *n* = 106). The midpoints between fishers and both species (13 cm), and between both species and martens only (23 cm), defined snowfall regions that were then overlaid onto the *Martes* distribution data. If the fisher/snow and fisher/marten hypotheses function as proposed (Krohn et al., 1995), then the small-scale distributions of both species should coincide with the snowfall zones defined by these mid-points (i.e., <13 cm: mostly fishers; 13-23 cm: overlap of 2 species; >23 cm: mostly martens).

## Forest Types

We also looked at the current and historic distributions of the 2 *Martes* species in relation to forest types, as defined and mapped in 1979 by the California Vegetation Map (CALVEG) (Matyas and Parker 1980). The CALVEG forest types were mapped at 1:250,000 scale by visual inspection of color infra-red satellite imagery with results being verified from current soil-vegetation maps and by field checking approximately 8052 km (Matyas and Parker 1980). Mapped forest types were assigned as used by fishers or martens based on personal experience (WJZ) and a review of studies done in California (Table 1). We compared the species' distributions, as measured by successful surveys, to the distributions of habitats used by fishers, martens, and both species. Because of a

Table 1. Fisher and marten habitats based on forest-type associations observed and reported[a]. Forest types as defined by the California Vegetation Map (Matyas and Parker 1980).

| Fisher[b] | Marten[c] |
|---|---|
| Douglas fir-tanoak-madrone | Lodgepole pine |
| Douglas fir-pine-madrone | Mixed conifer-fir[d] |
| Jeffrey pine | Mountain hemlock |
| Tanoak-madrone | Redwood-Douglas fir[d] |
| Madrone-black oak | Red fir |
| Mixed conifer-fir[d] | White fir[d] |
| Mixed conifer-pine | |
| Oregon white oak | |
| Ponderosa pine | |
| Redwood-Douglas fir[d] | |
| White fir[d] | |

[a] Includes observations made by W. J. Zielinski on fishers in northwestern California and the southern Sierra Nevada Mountains, and on martens in the southern and northern Sierra Nevadas.

[b] Schempf and White (1977), Buck (1982), and Self and Kerns (1992).

[c] Schempf and White (1977), Simon (1980), Zielinski (1981), Spencer et al. (1983), Hargis and McCullough (1984), Martin (1987), and Self and Kerns (1992).

[d] Forest types used by both species.

lack of historic forest type data, distributions of fishers and martens for 1919-1924 had to be compared to current distributions of forest types. Because major vegetation types were mapped at a small scale, and types are strongly associated with landforms such as deserts and mountains (Matyas and Parker 1980), we believe CALVEG to be a reasonable small-scale representation of forest types.

## Study Predictions and Statistical Analyses

If snow limits fisher populations in California, then fishers should mostly occur in those forested portions of the state where snowfall is low to moderate (<13 cm per winter month; see Snowfall Data, above, for rationale). If fishers occur in areas of deep snowfall, these areas would be expected to be largely covered with closed-canopy, coniferous forests that alter the structure of snow accumulating on the ground. Areas where both species occur should be in transitions between deep and low snowfalls (13-23 cm), or between open and closed-canopy forests where snow amounts are high and similar. If high fisher populations limit martens, then high marten populations will coincide with areas without fishers or with low densities of fishers, specifically in an area or areas of deep snow (>23 cm).

The mean monthly amounts of snowfall at sites with fishers and martens were compared with *t*-tests. Specifically, we tested for equality of group means between species, in both the historic and current data, without assuming equal variances (Zar 1984). Chi-square tests were used to compare, in both datasets, the distribution of each species by snowfall categories presumed to represent 3 degrees of suitability (as defined above in Snowfall Data). Similarly, chi-square tests were also used to evaluate the distribution of both *Martes* species relative to forest types (as defined in Table 1) presumed to be suitable *versus* unsuitable habitats.

## Results

### *Martes* Distributions

The historic distribution of martens consisted of a large, central core corresponding to the locations of the Sierra Nevada Mountains (Fig. 1B). In the north, there was a small zone of overlap; in the south, the Marten Core graded into an elongated zone with both species (Fig. 1B). Note that if *M. a. humboldtensis* were included (Fig. lA), the western edge of Group A (Fisher North: Fig. 1B) would have included martens. Areas where fishers predominated were located at the northwest and southwest ends of the 2 overlap areas (Fig. 1B).

Because successful and unsuccessful surveys were roughly distributed the same (Fig. 2A), we deleted unsuccessful surveys from the determination of the current distributions. In ignoring unsuccessful surveys, we assumed that they represent either no fishers or martens, or a *Martes* population similar in composition to adjacent successful surveys. We believe that successful surveys are an unbiased small-scale representation of the current distributions of fishers and martens in California, excepting the east side of the southern Sierras that was poorly sampled (Fig. 2B) and possibly the western side of the central Sierras that had few successful surveys (Fig. 2A). Again, current survey data show a large area occupied by martens along the Sierra Nevadas that grades both north and south into overlap zones, and then into 2 areas occupied mostly by fishers (Fig. 2B). In terms of the composition of the surveys that made up the 5 spatial groups, Fisher North consisted of 29 surveys, 28 with only fishers and 1 with both species; Overlap North included 4 surveys, 3 with both species and 1 with martens only; the Marten Core had 23 marten-only surveys; Overlap South had 12 surveys, 6 with both species, 3 with fishers only, and 3 with martens only; and Fisher South consisted of 17 surveys: 15 with only fishers, 1 with martens only, and 1 with both species.

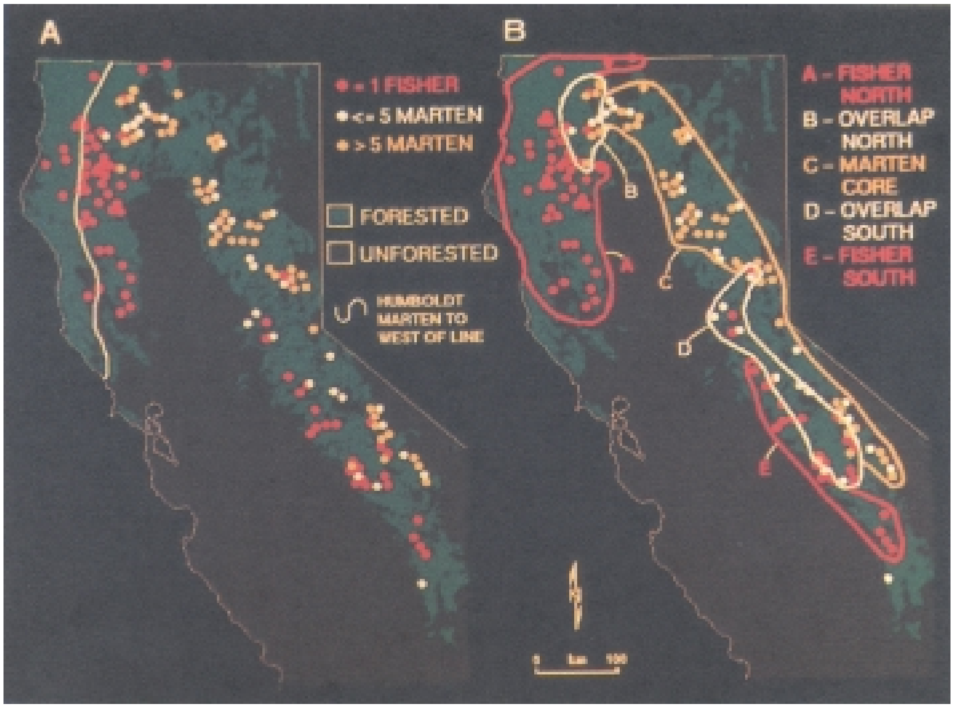

Figure 1. Distributions of forested lands, and fishers (*Martes pennanti*) and martens (*M. americana*) in California as indicated by the harvest records in Grinnell et al. (1937) for 1919-1924 (A). Spatial groupings of *Martes* (excluding the Humboldt marten, *M. a. humboldtensis,* which went extinct) are shown in B. Data on forest coverage from California Vegetation Map (Matyas and Parker 1980).

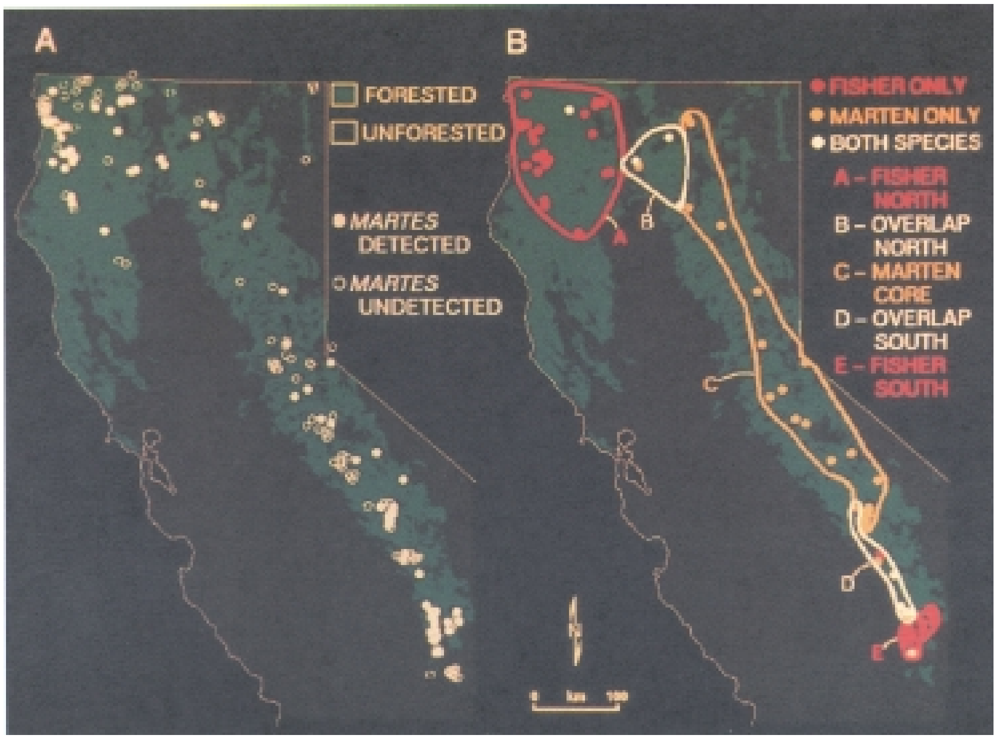

Figure 2. Distribution of forested lands and *Martes* surveys (A), and species groupings from surveys where *Martes* were detected (B) in central and northern California, 1989-1994. Data on forest coverage from California Vegetation Map (Matyas and Parker 1980).

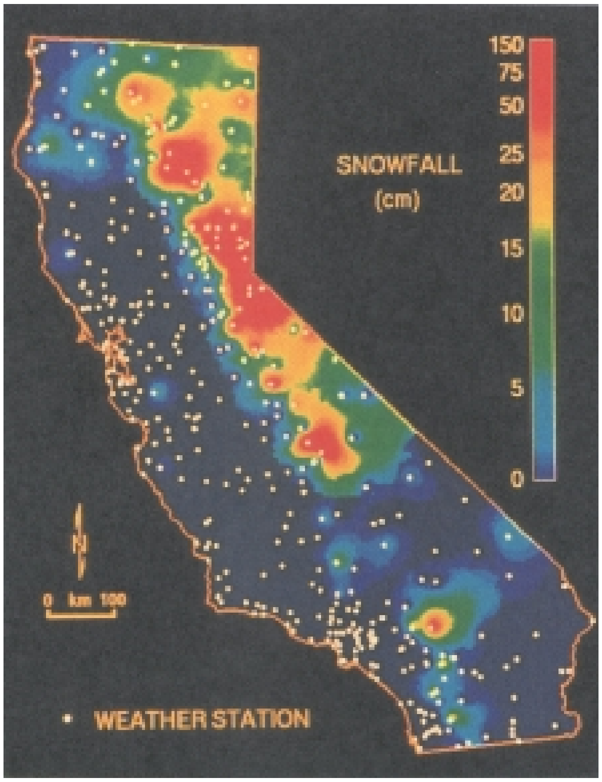

Figure 3. Contours of mean monthly snowfall (in centimeters) for California, based upon means from December to March, 1982-83 to 1991-92. Contours begin at 1.0 cm and are separated by 9.0 cm increments, with the maximum mean monthly snowfall recorded being 173 cm. Based on 390 weather stations with ≥8 years of data.

### Snowfall Distribution

Weather stations were widely distributed across California (Fig. 3), with each station representing an average of 1039 $km^2$. The mean amount of snow falling per winter month varied greatly, with the highest amounts in the northern Sierra Nevada Mountains, and in the southern Cascade Mountains in north-central California (Fig. 3). Because the current distribution of snowfall was closely associated with mountainous areas, and mountains were stable over the time interval of interest, we believe these data represent the approximate distribution of snowfall during the historic period, although we recognize that annual snowfall amounts and distributions are highly variable in California (NOAA records).

The distribution of martens, both in terms of historical data (Fig. 4A; excepting the Humboldt subspecies) and current surveys (Fig. 4B), corresponded closely to the regions of heaviest snowfall. According to current survey data, martens do not occur in the deep snow area in the southern Sierras (Fig. 4B). This area, however, was largely unsampled (Fig. 2). Personal observations (WJZ) and data in Schempf and White (1977) suggest that Group C in Figure 4B should extend to the southern tip of the Sierra Nevada Mountains, corresponding to the southernmost areas of monthly snowfall >23 cm (Fig. 4B). In contrast to martens, fishers occurred mostly in those forested areas with mean monthly snowfalls <13 cm (Fig. 4). Overlap zones occurred in areas of rapidly changing snowfall amounts (13-23 cm per month), specifically at both ends of the Sierra Nevada Mountains and along the western slope of the southern Sierras (Fig. 4). Fishers used areas with significantly ($P < 0.001$) less snowfall than martens in both time periods, but mean snowfall depths did not change ($P > 0.10$) within species between periods (Table 2). Furthermore, snowfall zones and *Martes* groups were spatially related ($P < 0.001$) during both time periods (Table 3). However, because boundaries of the *Martes* groups were hand drawn from non-random data that were incomplete, the spatial relations in Table 3 and Figure 4 are only approximations.

Table 2. Statistical comparisons of monthly snowfall depths (cm) at locations in California where fishers (*Martes pennanti*) and martens (*M. americana*) occurred based on historical harvest (except *M. a. humboldtensis*) and current survey data. Distribution data from Figures 1B and 2B were overlaid on Figure 3 to obtain mean (1982-1991) snowfall amounts for individual locations.

| Monthly snowfall statistics | Historical data (1919-24) | | Current data (1989-93) | |
|---|---|---|---|---|
| | fishers[a] | martens[b] | fishers[c] | martens[d] |
| Mean | 10.5 | 25.9 | 6.9 | 28.3 |
| Standard deviation | 14.5 | 21.5 | 11.9 | 25.5 |
| Range | 0.2-62.6 | 1.8-116.2 | 0.6-66.6 | 1.3-108.3 |
| Sample size | 75 | 78 | 57 | 39 |

[a] *versus* [b] Significantly different; $t = 5.224$, df = 135.8, $P < 0.001$.
[c] *versus* [d] Significantly different; $t = -4.887$, df = 49.4, $P < 0.001$.
[a] *versus* [c] Not significantly different; $t = -1.597$, df = 129.2, $P = 0.12$.
[b] *versus* [d] Not significantly different; $t = 0.502$, df = 65.5, $P = 0.62$.

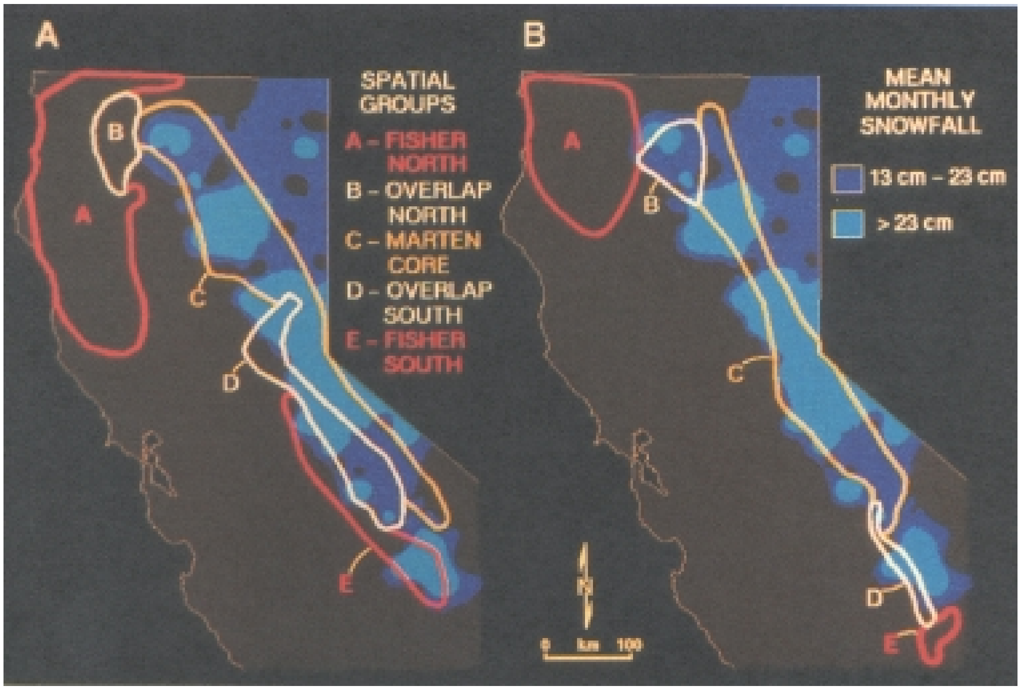

Figure 4. Relationship between the historical (A) and current (B) distributions of *Martes* in California (from Figs. 1, 2) and the current snowfall conditions (from Fig. 3).

Table 3. Proportions, and areas in 1000 km$^2$ in parentheses, of *Martes* spatial groups relative to snowfall zones.

| Mean snowfall (cm) per winter month | Historical distributions[a] | | | Current distribution[b] | | |
|---|---|---|---|---|---|---|
| | fishers | overlap | martens | fishers | overlap | marten |
| <13 | 0.88<br>(36.2) | 0.42<br>(6.95) | 0.14<br>(4.41) | 0.99<br>(21.22) | 0.16<br>(1.16) | 0.07<br>(1.90) |
| 13 to 23 | 0.04<br>(1.74) | 0.28<br>(4.65) | 0.35<br>(11.23) | 0.01<br>(0.32) | 0.57<br>(4.19) | 0.35<br>(8.78) |
| >23 | 0.08<br>(3.05) | 0.30<br>(4.81) | 0.51<br>(16.25) | 0.00<br>(0.00) | 0.27<br>(1.98) | 0.58<br>(14.78) |

[a] Areas calculated from Figure 4A. Snowfall and distribution significantly related; $x^2 = 41.2$, df = 2, $P < 0.001$.

[b] Areas calculated from Figure 4B. Snowfall and distribution significantly related; $x^2 = 44.9$, df = 2, $P < 0.001$.

## Forest Types

Despite the presence of suitable habitat types in the southern Cascades and northern Sierra Nevadas (Fig. 5A), the historical view of fisher distributions (Grinnell et al. 1937) suggests that fishers may have been less common in these areas than elsewhere in California. Whether this distribution was the historic condition or reflects human effects on forests and fishers prior to their assessment is unknown. Habitat for the Humboldt marten was apparently available in the North Coast ranges in historic times (Fig. 5B), but today this subspecies is either at very low population density or extirpated (Kucera et a1.1995; Fig. 2B).

Currently, fishers are at very low densities or absent from the southern Cascades through the central Sierra Nevada, despite the presence of apparently suitable habitat types (Fig. 6A). In addition, martens were detected by surveys as far north as the interior part of northern California where, according to forest types present, habitat should be unavailable for martens (Fig. 6B). We also note that no martens were detected in northwestern California, despite the occurrence of suitable habitat types (Fig. 6B) and the historic use of the west side of this area by the Humboldt marten (Fig. IA).

Using the sizes of the spatial groups defined by the harvest and survey data as indices to occupied ranges, significantly more than half of the presumably suitable habitats for fishers ($P < 0.10$) and martens ($P < 0.01$) appeared unoccupied

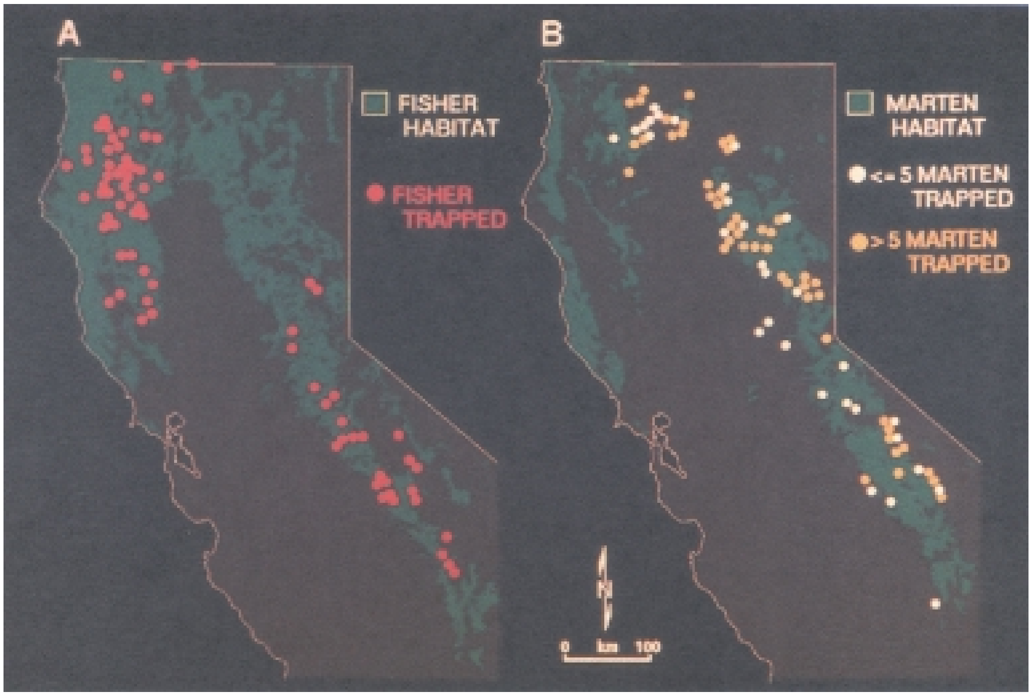

Figure 5. Spatial relations between historical harvest of fishers and martens and habitats used by fishers (A) and martens (B). Forest cover types are listed in Table 1, and are derived from California Vegetation Map (Matyas and Parker 1980).

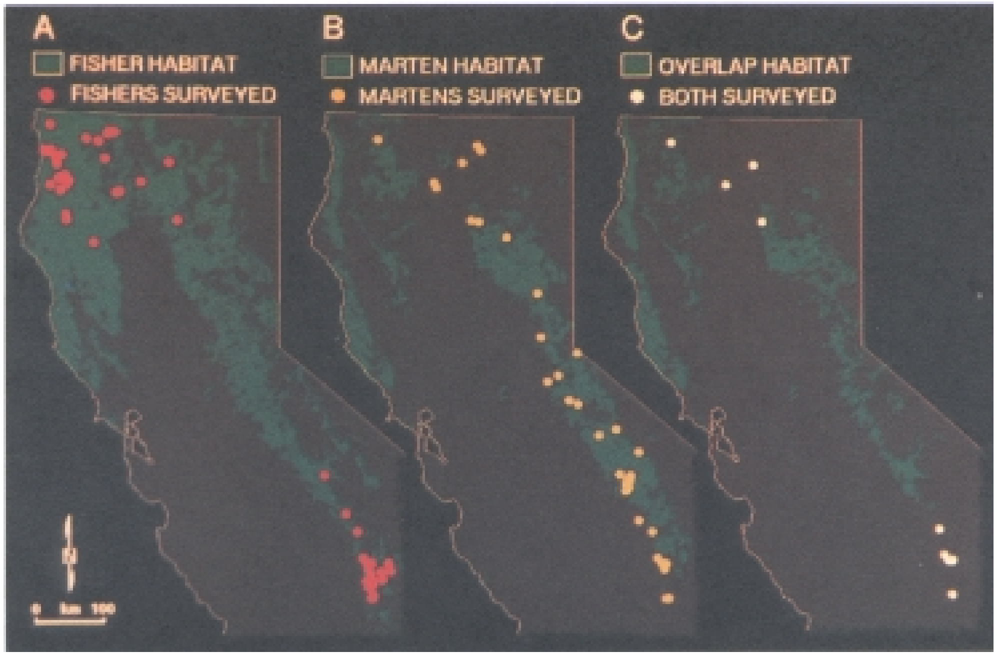

Figure 6. Spatial relations between current surveys of fishers and their habitats (A), martens and their habitats (B), and both *Martes* species and shared habitats (C). Forest cover types used by fishers, martens, or both are listed in Table 1, and are derived from California Vegetation Map (Matyas and Parker 1980).

Table 4. Proportions, and areas in 1000 km$^2$ in parentheses, of *Martes* spatial groups relative to forest types that are suitable habitats for fishers, martens, and both species.

| Suitable habitats[a] | Historical distribution[b] fishers | overlap | martens | Current distribution[c] fishers | overlap | martens |
|---|---|---|---|---|---|---|
| Occupied by spatial group(s) | 0.44<br>(22.10) | 0.16<br>(3.91) | 0.39<br>(5.28) | 0.27<br>(13.45) | 0.02<br>(0.46) | 0.48<br>(6.44) |
| Unoccupied by spatial group(s) | 0.56<br>(28.62) | 0.84<br>(20.78) | 0.61<br>(8.11) | 0.73<br>(37.26) | 0.98<br>(24.24) | 0.52<br>(6.96) |

[a] Forest types documented to have been used in California by fishers, martens, or both species (Table 1).

[b] Areas calculated from an overlay of spatial groups in Figure 1B on presumably suitable habitats in Figure 6. Significantly more habitat unoccupied than occupied; $x^2$ = 5.72, df = 2, $P < 0.10$.

[c] Areas calculated from an overlay of spatial groups in Figure 2B on presumably suitable habitats in Figure 6. Significantly more habitat unoccupied than occupied; $x^2$ = 11.37, df = 2, $P < 0.01$.

during both time periods (Table 4). Overall, small-scale maps of forest types known to be used by fishers and martens in California were poor predictors of the occurrence for both species (Figs. 5, 6).

## Discussion

Grinnell et al. (1937:25) stated that fishers ranged ". . . south from Mount Shasta and Lassen Peak throughout the main Sierra Nevada to Greenhorn Mountain, in north central Kern County." Although the map of fisher distribution in Grinnell et al. (1937), on which our Figure lA is based, gives the impression that fishers may have been less common in the southern Cascades, northern Sierra Nevadas, and east side of the southern Sierra Nevada, than in the rest of their range, these results must be interpreted with caution. Figure 1 is based on only 1 5-year period, prior to which there was already concern that trapping had decreased the population of fisher in California to a point where season closings were recommended (Dixon 1925, Grinnell et al. 1937). In terms of current distribution patterns, if the west side of the central Sierras was under-sampled, and fishers were more common here than suggested by Figure 2, then the boundaries of Overlap South and Fisher South could be similar to the historic pattern (Fig. 1B).

Because neither the historic nor the current data on *Martes* distributions were based on uniform sampling effort (or even known effort in the case of the historical data), we did not assess temporal changes in the distribution of *Martes.* Furthermore, boundaries of the various spatial groups may be wrong, as specifically noted above for the current occurrence of martens on the east side of the southern Sierras. However, even though both distribution datasets probably do contain errors caused by over- and under-sampling, we believe that both datasets do provide an adequate small-scale representation of the major distribution patterns of *Martes* in California.

### Fisher/Snow Hypothesis

In the historical and current data on distributions, fishers were clearly associated with areas of low snowfall across a wide range of forest types. Furthermore, forest types known to be used by fishers in California appeared to be used less when located in deep snow areas. Forested areas inhabited by both fishers and martens occurred in areas of intermediate snowfall, across a wide range of forest types, and in topographic breaks where snowfall amounts changed greatly over a small area. These patterns are consistent with the hypothesis that deep snow can limit fisher populations.

A logical question is how can snow, which restricts the travel of fishers for less than 4 months out of a year, determine the year-long distribution? Krohn et al. (1995) proposed an ultimate mechanism based on energetics and fitness. A more proximate mechanism could involve the animal's dispersal and spacing patterns. Because most juvenile fishers disperse during the snow season (Arthur et al. 1993), and because adult females seem to have territories that are more or less fixed for life (Arthur et al. 1989), the initial selection of the home range may exclude deep snow where travel is impaired. Although some adult males shift territory locations after the spring breeding season (Arthur et al. 1989), it is unlikely that, even if unimpaired by snow, males would establish a territory in an area devoid of resident females. Of course, because energetic balance varies not only with snow conditions (i.e., depth, frequency, hardness), but also with such factors as prey abundance and availability, we suspect that there is no absolute line between suitable and unsuitable habitats, but instead an ever-shifting zone of varying degrees of suitability relating to energy inputs versus outputs.

### Fisher/Marten Hypothesis

Were martens present during both time periods in the northern Sierras and southern Cascades because of low fisher populations, presence of deep snow, or other factors? Because we have no data directly bearing on fisher/marten interactions or other possible factors, we cannot answer this question. It appears that the martens inhabiting the coastal forests of northwestern California in the early

1900s did not persist (Schempf and White 1977; Kucera et al. 1995), probably due to the rapid loss of original redwood forest habitat in the region at the turn of the century (Fox 1989, Buskirk and Ruggiero 1994). Fishers have never been common in the redwood forest along the coast (Grinnell et al. 1937; Zielinski et al. 1995), but competition with fishers may also have contributed to the decline in the Humboldt marten. Studies of large numbers of radio-collared fishers and martens living sympatrically are needed to clarify an issue that has been the subject of comment in the technical literature throughout North America for almost nine decades (Table 5).

### Alternative Hypotheses

Although the above findings are consistent with the 2 hypotheses of interest, we recognize that other factors affect the distributions of both *Martes* species. For example, CALUEG did not include information on the current developmental stage and timber harvest history of each polygon, nor was the suitability of landscapes surrounding survey locations assessed (e.g., Rosenberg and Raphael 1986). Statewide data on these features will rarely, if ever, be available for the historical period. Moreover, there are other sources of information on the distribution of vegetation in California (e.g., Griffin and Critchfield 1976, Airola 1988) that in some cases disagree with CALVEG (e.g., in the north-central area where CALUEG has no suitable marten habitat). Thus, the lack of agreement between forest types and *Martes* distributions may be because snow is a better explanatory variable, or because the CALUEG data excluded important habitat variables.

In a review of the habitat ecology of fishers and martens, Buskirk and Powell (1994) argued that habitat structure is important to both species. Although these authors did not specify the kind of structure needed, Powell and Zielinski (1994:53) stated that ". . . vertical and horizontal complexity created by a diversity of tree sizes and shapes, light gaps, dead and downed wood, and layers of overhead cover. . ." are important to fishers. Similarly, Buskirk and Ruggiero (1994) emphasized the importance of forest structure, including coarse woody debris and large-diameter trees, to martens. Unfortunately, the available habitat data lacked subcanopy structural characteristics.

Approximately 8 fishers were reportedly taken within the range of the now extinct Humboldt marten between 1919 and 1924 (Fig. 1A). During this same 5-year period, 43 Humboldt martens were trapped (Grinnell et al. 1937). The low number of fishers relative to martens is consistent with the hypothesis that high fisher populations can limit martens. However, because this area currently receives little snowfall (Fig. 3), and probably did so historically, the low fisher population in this area is inconsistent with the notion that deep snow limits fishers. However, we have no basis to argue that snowfall is the only factor that can limit fisher populations. We note that there are other areas in California where snowfall

Table 5. Literature comments on the interaction between fishers *(Martes pennanti)* and martens (*M. americana*).

| Location | Comments | Citation |
|---|---|---|
| Maine | Noted an apparent inverse pattern between the numbers of fishers and martens trapped. | Hardy (1907) |
| California | Cited an experienced trapper who believed that fishers preyed upon martens, but found ". . . little first-hand confirmation. . ." Cited a letter stating that "Old hunters say they [martens] will not live where there are fishers." | Grinnell et al. (1937:200, 210) |
| Ontario | Reported an inverse relation between fisher and marten harvests, but noted enough exceptions to reject the idea that ". . . one species might suppress the level of the other." | de Vos (1952:29) |
| New Hampshire | Documented instances of fishers killing martens in traps, and stated that ". . .there is some evidence that fisher also prey on marten . . ." and cited Piper who felt that ". . .fisher are partially responsible for the depletion of marten in the White Mountains National Forest." | Silver (1957:262) |
| Ontario | Reported marten remains in the stomach of a fisher. Apparently the fisher came from an area open to fur-trapping, so the marten(s) may have been trapped. | Daniel (1960) |
| Ontario | Believed that fishers and martens competed for den sites and food. | Clem (1977) |
| Manitoba | Reported *2* cases, in an area without fur trapping, of martens eaten by fishers. | Raine (1981) |
| Ontario | An inverse relation (see de Vos 1952) noted between fisher and marten harvests. Acknowledged the possibility of ". . .a fisher-marten interaction. . ." | Douglas and Strickland (1987:519) |

Table 5. Continued.

| Location | Comments | Citation |
|---|---|---|
| Maine | Reported an inverse relation between the statewide harvests of fishers and martens, 1980-1987. Formally proposed that high fisher populations could limit marten populations. | Krohn et al. (1995) |
| Maine | Of 13 radio-collared martens killed by predators in north-central Maine, 3 were attributed to fishers, 6 to other known predators, and 4 to unknown predators. | Hodgman et al. (this volume) |

is low and forest types typically used by fishers occur, and yet fishers are seemingly absent today. Specifically, the west side of the central and northern Sierra Nevada Mountains apparently do not now support fishers. It's possible that mining and timber harvesting in the Sierras reduced habitat quality, possibly through fragmentation and the reduction of structural diversity.

### California-Maine Comparison

Krohn et al. (1995) proposed that in regions with more mountainous terrain than Maine, transitions between fisher and marten areas (i.e., overlap zones) would occur over shorter distances. Clearly, overlap zones were smaller and more distinct in California (for both time periods) than Maine. In addition, differences in the distributions of the 2 *Martes* species in Maine were subtle, being largely based on differences in density, whereas in California spatial groups were classified solely by species composition. In Maine the 48-cm snowfall contour (mean monthly, December to March) corresponds to the center of overlap between the distribution of the 2 *Martes* species (Krohn et al. 1995), whereas data for California suggest a threshold around 18 cm (see Snowfall Data in Methods). We speculate that the more open coniferous forests of California have less effect on snow structure than the more closed-canopy coniferous forests of Maine, and thus the level at which mean monthly snowfall affects fishers is lower in California than Maine. However, snowfall frequencies and snow structure (i.e., crusting conditions), which could also affect the mobility of fishers and martens (Raine 1981), probably also differed between the 2 states.

## Conclusions

The small-scale analyses reported here do not prove that deep snows limit fishers, nor that high fisher populations limit martens. With the exception of the now-extinct Humboldt marten, however, both hypotheses explain the *Martes* distribution patterns in 2 California datasets. Thus, we encourage others to consider the ramifications of these 2 hypotheses and to carefully design and conduct tests of the 2 relations proposed by Krohn et al. (1995).

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## Literature Cited

Airola, D. A. 1988. A guide for the California Wildlife Habitat Relationships System. California Department of Fish and Game, Wildlife Management Division, Sacramento, California.

Arthur, S. M., W. B. Krohn, and J. R. Gilbert. 1989. Home range characteristics of adult fishers. Journal of Wildlife Management 53:674-679.

Arthur, S. M., T. F. Paragi, and W. B. Krohn. 1993. Dispersal of juvenile fishers in Maine. Journal of Wildlife Management 57:868-874.

Buck, S. G. 1982. Habitat utilization by fisher *(Martes pennanti)* near Big Bar, California. M.S. Thesis, California State University, Arcata.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283-296 in. S: W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York.

Buskirk, S. W., and L. F. Ruggiero. 1994. American marten. Pages 7-37 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. The scientific basis for conserving forest carnivores - American marten, fisher, lynx, and wolverine in the western United States. General Technical Report RM-254. US Department of Agriculture Forest Service,

Clem, M. K. 1977. Interspecific relationship of fishers and martens in Ontario during winter. Pages 165-182 *in* R. L. Phillips, and C. Jonkel, eds. Proceedings of the 1975 Predator Symposium, Montana. Forestry Conservation Experiment Station, University of Montana, Missoula.

Daniel, M. 11960. Porcupine quills in viscera of fisher. Journal of Mammalogy 41:133.

de Vos, A. 1952. The ecology and management of fisher and marten in Ontario. Technical Bulletin (Wildlife Series) 1, Ontario Department of Lands and Forests.

Dixon, J. 1925. A closed season needed for fisher, marten, and wolverine. California Fish and Game 11:23-25.

Douglas, C. W., and M. A. Strickland. 1987. Fisher. Pages 510-529 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, Ontario Ministry of Natural Resources, Toronto.

Fox, L. 1989. A classification, map, and volume estimate for the coast redwood forest in Califomia. Final Report. Forest Rangelands Resources Assessment Program, California Department of Forestry and Fire Protection, Sacramento, California.

Griffin, J. R., and W. B. Critchfield. 1976. The distribution of forest trees in California. General Technical Report PSW-87, US Department of Agriculture Forest Service, Pacific Southwest Research Station, Berkeley, California.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing mammals of California. Volume 2. University California Press, Berkeley.

Hardy, M. 1907. The fisher. Forest and Stream 68:692-693.

Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. Journal of Wildlife Management 48:140-146.

Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. This volume. Survival of American marten in an untrapped forest preserve in Maine.

Katnik, D. D. 1992. Spatial use, territoriality, and summer-autumn selection of habitat in an intensively harvested population of martens on commercial forestland in Maine. M.S. Thesis, University of Maine, Orono.

Krohn, W. B., K. D. Elowe, and R. B. Boone. 1995. Relations among fishers, snow, and martens: Development and evaluation of two hypotheses. The Forestry Chronicle 71:97-105.

Kucera, T. E., W. J. Zielinski, and R. H. Barrett. 1995. Current distribution of the American marten, *Martes americana,* in California. California Fish and Game 81:96-103.

Lewis, J. C., and W. J. Zielinski. 1996. Historical harvest and incidental capture of fishers in California. Northwest Science 70:291-297.

Martin, S. K. 1987. The ecology of pine marten (*Martes americana*) at Sagehen Creek, California. Ph.D. Thesis, University of California, Berkeley.

Matyas, W. J., and I. Parker. 1980. CALVEG - Mosaic of existing vegetation of California, 1979. US Department of Agriculture Forest Service Regional Ecology Group, San Francisco, California.

Phillips, D. M. 1994. Social and spatial characteristics, and dispersal of marten in a forest preserve and industrial forest. M.S. Thesis, University of Maine, Orono.

Powell, R. A., and W. J. Zielinski. 1994. Fisher. Pages 38-73 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. The scientific basis for conserving forest carnivores - American marten, fisher, lynx, and wolverine in the western United States. General Technical Report RM-254. US Department of Agriculture Forest Service.

Raine, R. M. 1981. Winter food habits, responses to snow cover, and movements of fisher *(Martes pennanti)* and marten *(Martes americana)* in southeastern Manitoba. M.S. Thesis, University of Manitoba, Winnipeg.

Rosenberg, K. V, and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison.

Schempf, P. F., and M. White. 1977. Status of six furbearer populations in the mountains of northern California. US Department of Agriculture Forest Service, Region 5, California.

Self, S. E., and S. J. Kerns. 1992. Pine marten-Pacific fisher study. Phase II Report. Final report from wildlife resource managers to Sierra Pacific Industries, Redding, California.

Silver, H. 1957. A history of New Hampshire game and furbearers. New Hampshire Fish and Game Department, Concord, New Hampshire.

Simon, T. L. 1980. An ecological study of the marten in the Tahoe National Forest, California. M.S. Thesis, California State University, Sacramento.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1181-I 186.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

Zielinski, W. J. 1981. Food habits, activity patterns and ectoparasites of the pine marten at Sagehen Creek, California. M.S. Thesis, University of California, Berkeley, California.

Zielinski, W. J. 1991. A survey protocol for the detection of forest carnivores in proposed management activity areas. US Department of Agriculture Forest Service, Pacific Southwest Experiment Station, Arcata, California.

Zielinski, W. J., T. E. Kucera, and R. H. Barrett. 1995. Current distribution of the fisher, *Martes pennanti,* in California. California Fish and Game 81:104-112.

Zielinski, W. J., R. L. Truex, C. V Ogan, and K. Busse. This volume. Detection surveys for fishers and American martens in California, 1989-1994: summary and interpretations.