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Research Article

Ski Areas Affect Pacific Marten Movement, Habitat Use, and Density

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ABSTRACT Alpine ski recreation is one of the most popular outdoor winter sports globally but often involves habitat modification and dense human activity, both of which can harm wildlife. We investigated the effects of ski area development and winter recreation activities on movement, occupancy, and density of Pacific martens (*Martes caurina*) in the Lake Tahoe region of California and Nevada, USA by comparing 3 ski and 3 control study areas. We systematically surveyed martens using live traps and hair snares during spring–summer and winter seasons from 2009 through 2011 to identify how martens responded to the year-round effects of habitat fragmentation from ski area development and the seasonal effects of winter recreation activities. Martens selectively moved between remnant forest patches with the shortest crossing distances across open, non-forested ski runs in both seasons, with the effect more pronounced in females. Overall, habitat connectivity was reduced by 41% in ski areas compared to habitat not fragmented by ski runs. During spring–summer, occupancy rates were not different between habitat within or outside of ski operations areas. During winter, however, occupancy was significantly lower inside (52%) ski area boundaries than outside (88%) them. Reduced detection probability in ski areas indicated martens also reduced the frequency of use of operations areas in winter. Using spatially explicit capture-recapture models, we found that marten density did not differ between ski areas and controls during spring, but during winter female density declined at ski areas by 63% compared to spring–summer and was <50% of female density compared to controls. This suggests that females seasonally avoid habitat in ski areas by shifting their habitat use to areas outside ski operations boundaries during winter. Although male marten density did not differ, the lack of resident males >3 years old coupled with higher annual turnover rates suggests male densities at ski areas may be reliant on annual male immigration. In winter, martens avoided using habitat in ski operations areas when recreation activity was greatest. Winter ski recreation may not be incompatible with marten use of habitat in ski areas, but habitat fragmentation from ski areas affects marten movement and recreation activities affect seasonal habitat occupancy and female density. Maintaining functional habitat connectivity, via networks of short ski run crossings that link habitat in and out of ski areas, will be important for maintaining or improving marten use of remnant habitat in developed ski areas. © 2017 The Wildlife Society

KEY WORDS density, marten, *Martes caurina*, movement, occupancy, recreation, ski area, spatially explicit capture recapture.

Outdoor recreational activities are a major factor in the decline of many threatened and endangered species in the United States (Czech et al. 2000). Recreational activities can affect wildlife through 4 primary routes: exploitation, disturbance, habitat modification, and pollution (Knight and Cole 1995). In evaluating the effects of recreational activity on wildlife, it is important to characterize activities with respect to their temporal pattern, spatial extent, and intensity (Knight and Cole 1995). Activities involving exploitation (e.g., hunting, motorized, and non-motorized recreation) are direct effects and when limited to short temporal periods can be classified as pulse stressors (Bender et al. 1984). Activities involving habitat modification or pollution are indirect effects and when permanent or long-lasting can be classified as press stressors (Bender et al. 1984). Species can exhibit different responses to recreational activities representing pulse and press stressors. Common loon (*Gavia immer*) numbers and reproductive success declined with increasing intensity of a press stressor, recreational housing development (Vermeer 1973, Heimberger et al. 1983). Furthermore, the combination of press (e.g., recreational development) and pulse (e.g., boating activity) stressors significantly influence nest site selection and reduce nesting habitat availability in common

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loons (McCarthy and Destefano 2011). The endangered capercaillie (*Tetrao urogallus*) responded to the pulse stressor of ski recreation in Switzerland by avoiding the portions of their home ranges subject to ski recreation but did not establish home ranges to avoid inclusion of ski recreation areas (Thiel et al. 2008).

Alpine ski recreation, including skiing and snowboarding, is one of the most popular winter outdoor recreation activities globally, and is growing. Alpine ski recreation has the potential to affect wildlife because of the combination of a pulse stressor, the direct effects of high intensity human activity, and a press stressor, the indirect effects of habitat modification from development. For example, Patthey et al. (2008) reported that black grouse (*Tetrao tetrix*) abundance was reduced by 36% in spring on ski areas compared to non-ski areas in Switzerland but could not distinguish the relative contributions from disturbance from ski activities versus habitat modification. During the winter recreation season, concentrated human activity, high densities of daytime recreationists, and nighttime activities (e.g., motorized snow surface grooming) represent potential pulse disturbance factors. Although motorized and non-motorized winter recreation activities disturb wildlife (Reimers et al. 2003), their overall effect can range from none (Zielinski et al. 2008) to displacement (Seip et al. 2007). Development of alpine ski areas often involves the modification of habitat by fragmenting previously contiguous forest habitat to create ski runs and infrastructure (e.g., ski lifts, buildings, roads, parking lots). The degree that habitat fragmentation affects wildlife often depends on the level of contrast between the remnant habitat and the habitat resulting from anthropogenic changes. Where the habitat changed is either human-dominated or in high-contrast to remnant habitat (e.g., forest to non-forest) the effects of isolation and patch size of residual habitat on species are strongest (Prugh et al. 2008), suggesting that ski areas, as high-contrast landscapes, may alter habitat use by martens (*Martes* spp.).

The Pacific marten (*Martes caurina*) occurs throughout the higher elevations of mountains in the western United States and Canada where snowfall is common and developed ski areas occur. In the southern portions of the Pacific marten range, the most significant declines in distribution have occurred (Zielinski et al. 2001), including in the northern Sierra Nevada mountains of California and Nevada (Zielinski et al. 2005). The Pacific marten is designated as a sensitive species by the United States Forest Service and a species of special concern by the California Department of Fish and Wildlife. The vulnerability of the marten is largely attributed to the loss and fragmentation of mature and late-successional forest habitat from timber harvest (Moriarty et al. 2011). However, despite the high density of developed ski areas in this region, their effects on marten populations have yet to be evaluated. Martens are highly sensitive to crossing open areas because of the increased predation risk they encounter when away from escape cover (Drew 1995). They travel extended distances to avoid crossing open, non-forested areas (Buskirk and Ruggiero 1994, Cushman et al. 2011). Ski area development involves creating networks of ski runs and roads, leaving residual forest patches only accessible by crossing openings. In addition, after trees are removed, many ski runs are further simplified by removing surface structures (e.g., stumps, downed logs, large rocks; Ries 1996) that martens may perceive as suitable escape cover. Thus, we hypothesized that forest fragmentation from ski resort development may affect marten movement and, where most intense, could result in a reduction in occupancy and population density.

Our objective was to evaluate the effects of ski areas on marten movement, occupancy, and density. To do so, we systematically sampled marten occurrence using capture-recapture methods at paired ski and control study areas during the seasons when ski recreation activities were and were not present. Because of their sensitivity to crossing open areas, we hypothesized that the high-contrast landscapes of open ski runs and remnant forest patches will alter marten movement in all seasons. Martens appear to tolerate winter motorized recreation when it occurs in small portions of individual marten home ranges and occurs during times of the day martens are inactive (Zielinski et al. 2008), but winter ski recreation may negatively affect martens because of its increased spatial extent and overlap of nighttime recreation activities during times when martens are foraging. If ski recreation negatively affects martens, we predict that 1) habitat connectivity, indexed by marten movement, will be reduced by ski runs; 2) marten activity, indexed by detection probability, will be reduced where ski recreation activity occurs; 3) marten space-use, indexed using occupancy and density estimates, will be reduced where ski recreation occurs and; and 4) if these effects are primarily due to the pulse stressor of winter ski activity, they will be confined to the winter season; if they are primarily due to the press stressor of habitat modification, they will occur independent of time of year. Finally, to evaluate the spatial extent at which any effects may have occurred, we evaluated whether effects on marten activity or space-use extended outside ski area operation boundaries.

STUDY AREA

We conducted our study in the Sierra Nevada mountains of California and Nevada, USA, on the Lake Tahoe Basin Management Unit and El Dorado National Forest, both administered by the United States Forest Service. Elevations ranged from about 2,000 m to 3,000 m and the area was composed largely of forested habitats dominated by red fir (*Abies magnifica*), lodgepole pine (*Pinus contorta*), white fir (*Abies concolor*), western white pine (*P. monticola*), mountain hemlock (*Tsuga mertensiana*), and Jeffrey pine (*P. jeffreyi*). The Lake Tahoe region has a dry-summer continental climate with average temperatures ranging between 25.9° C and 4.3° C and an average of 1,440 mm of precipitation falling predominantly as snow on the mesic western portions of the region where this study occurred. Lake Tahoe is a major tourist attraction and the region is largely managed to support outdoor and winter ski recreation activities.

METHODS

Study Design

We paired 3 treatment areas (Heavenly [18 km^2], Sierra-at-Tahoe [12 km^2], Homewood [10 km^2] ski resorts) with 3 nearby control areas (Fig. 1). We selected controls to match the topographic (i.e., elevation, major aspect) and vegetation characteristics of each ski resort's operations area. We defined ski operations areas as the area enclosed by the collection of ski runs and associated roads and infrastructures. We assessed topographic and vegetative similarity between ski and control areas using digital elevation models and remotely sensed existing vegetation data (U.S. Department of Agriculture, Pacific Southwest Region, Remote Sensing Lab, Updated February 2010, https://www.fs.usda.gov/main/r5/landmanagement/gis). We classified satellite data into vegetation types within the California Wildlife Habitat Relationships system (WHR; Mayer and Laudenslayer 1988). The WHR system classifies forest types based on the dominance of the tree species present and classifies tree size classes based on the average diameter at breast height (DBH) of the largest cohort of trees present. Forested areas composed >75% of each study area and were dominated by red fir, Sierra mixed conifer, and subalpine conifer types in predominantly WHR size class 4 (28–61 cm DBH) with some size class 5 (>61 cm DBH) forest in each area (Fig. 1). We selected control areas with the same forest type and size class distributions present at each ski resort operations area, including habitat lost during their development (Fig. 1B). We reconstructed habitat lost during ski area development by digitizing all ski area development resulting in habitat loss (e.g., ski runs, roads) from high resolution aerial digital ortho-photography (National Agriculture Imagery Program, Updated 2012, https://www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/) and used historical (1940–1969) aerial photography to identify the type of vegetation (e.g., forest, wet meadow) that occurred in each ski area prior to development. Lastly, we used current vegetation types and tree size (diameter at breast height [DBH]) classes in adjacent undeveloped areas (with the same pre-development forest type) to identify the structural characteristics that would be present if ski area development had not occurred.

Marten Sampling

We sampled martens using systematic survey grids that covered the ski operations areas and included areas outside the ski operations areas to determine if marten occupancy or density changed seasonally in habitat located outside versus inside the ski operations areas (Fig. 1). The size and shape of each control area's sampling grid matched that of its paired ski area and was composed of hexagonal cells with an area of 100 ha each, equivalent to the smallest reported sizes of female marten home ranges (Buskirk and McDonald 1989). Two stations were 500 m apart in the center of each grid cell where we used hair snares (winter) and live traps (spring–summer) to determine marten occupancy and density. The number of stations sampled at each ski and control pair was proportional to the size of the each resort's operations area; Heavenly ski and control each had 36 stations, Sierra-at-Tahoe ski and control each had 24 stations, and the Homewood ski and control each had 20 stations (Fig. 1). During station establishment, if a station point either fell in non-forested habitat or fell on the edge of forest habitat we moved it to the nearest forest habitat 50 m in from the edge.

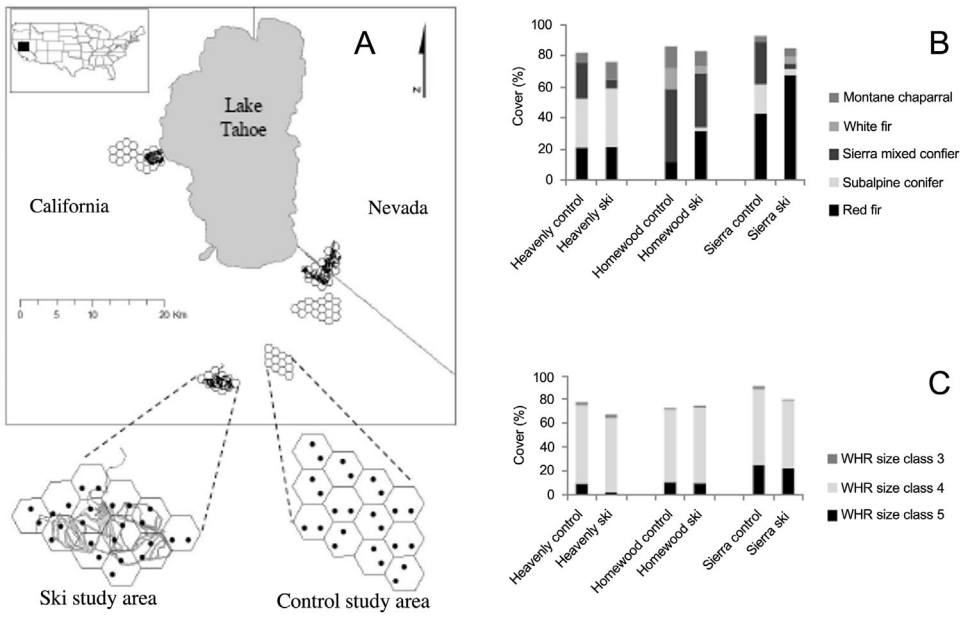

Figure 1. Location of the paired ski and control Pacific marten study areas and their sampling locations (dots) and ski runs (gray lines) in the Lake Tahoe Region of California and Nevada, USA (A). Habitat compositions of each paired ski and control study area (B) using the California Wildlife Habitat Relationships (WHR) classification and remotely sensed data available from the United States Forest Service Pacific Southwest Region Remote Sensing Lab's existing vegetation coverage (updated 2010). The WHR size classes (C) refer to the following tree diameter at breast height classes: 3 (15–28 cm), 4 (28–61 cm), and 5 (>61 cm).

Spring–summer sampling occurred from May through July for 3 years (2009–2011), with a single ski and control pair sampled each month. To control for any temporal effects on capture probability, each ski area-control pair was rotated through each sampling month such that each study area was sampled once in May, June, and July (Table 1). At each station, we trapped martens using a single wire mesh live trap (model 105; Tomahawk, WI, USA), modified with plywood cubby boxes on the ends to provide security for captured animals. We baited traps with chicken and tied a sponge soaked with olfactory lure (Gusto, Minnesota Trapline Products, Pennock, MN, USA) to the nearest tree branch. Once established, we checked traps at least once daily for 13–15 consecutive days. We chemically immobilized martens, examined them to determine their sex, marked them with a uniquely numbered passive integrated transponder (PIT) tag for individual identification (12.5 mm; Biomark, Boise, ID, USA), and collected genetic samples via hair to compare to winter marten detections. Use of PIT tags facilitated scanning and individual identification of martens in traps, allowing for immediate release of recaptured martens. We captured and processed martens using methods approved by the California Department of Fish (SC-4683) and Wildlife and Nevada Department of Wildlife (S-31799) Scientific Collecting Permit Programs.

We sampled martens at pairs of ski and control study areas simultaneously, from January to March in 2009. We surveyed the 2 stations in each hexagonal cell during 2 separate 15-day survey periods, such that each study area was sampled over 30 days. At each station, we used a hair snare attached to the bole of a large diameter tree and composed of a corrugated plastic (Coroplast, Vanceburg, KY, USA) snow shield with 2 hair snares attached, 2 chicken drumsticks nailed to the tree as bait, and a Coroplast collar with 3 hair snares attached, located below the bait. Each hair snare was a 0.30-caliber gun-cleaning brush (Hoppe's, Bushnell Outdoor Products, Overland Park, KS, USA). We hung a sponge soaked in olfactory lure on a nearby tree branch. We checked each station 3 times at 5-day intervals. We collected hair samples and stored them in silica desiccant prior to DNA analysis. We extracted DNA and the National Genomics Center for Wildlife and Fish Conservation (Missoula, MT, USA) conducted individual identification of martens using microsatellite variation at 9 loci (Schwartz et al. 2012). To ensure high quality genotypes, technicians analyzed each sample multiple times, then screened the genotype database for genotyping errors using Microchecker (Van Oosterhout et al. 2004) and DROPOUT (McKelvey and Schwartz 2004) as implemented in Schwartz et al. (2006).

Table 1. Month and year in which each of 3 pairs of ski and control study areas were sampled for Pacific martens in the Lake Tahoe Region of California and Nevada, USA.

Yr	May	June	July
2009	Homewood	Sierra-at-Tahoe	Heavenly
2010	Sierra-at-Tahoe	Heavenly	Homewood
2011	Heavenly	Homewood	Sierra-at-Tahoe

Marten Movement

To evaluate whether ski runs and roads have altered the ability of martens to move between remnant forest patches (i.e., functional connectivity), we compared the proportion and characteristics of used versus unused movement paths. Used movement paths were those between adjacent stations where an individual marten was captured (via either live trap or hair snare) on sequential captures 3 days apart in spring–summer and 5 days apart in winter. We used the limited temporal periods to reduce the chance of including sequential captures at adjacent stations that were less likely to involve direct movement between those stations. Unused movement paths were those between 2 adjacent stations that were not observed to be used by any individual marten.

We refer to movement paths as putative movement paths that inferred marten movement between adjacent stations because we did not have actual path data, which methods using global positioning system (GPS) collars or snow tracking can yield. We predicted martens would use the shortest ski run crossings based on the well-documented behavior of martens minimizing travel in open areas, and evaluated 6 ski run crossing metrics (min., max., mean, and the lower, middle, and upper mean quartile distances) for their ability to explain marten occurrence in remnant forest patches at ski areas. Of the 6 metrics evaluated, the minimum ski run crossing distance explained 3–23 times the variation in detection at remnant patches compared to the other candidate metrics (see Table S1, available online in Supporting Information); therefore, we used this metric for all subsequent analyses. We estimated the putative movement path between adjacent stations that minimized the distance of open ski run to cross and compared these minimum crossing distances between pairs of stations where individual martens were and were not detected. Martens move using gaits that typically span 1 m, and to measure movement paths at a comparable fine scale, we developed a vector-based approach in a geographic information system (GIS) to measure movement paths.

The first step of our vector-based approach was to digitize all ski runs. Next, we used our station grid to identify the ski runs that martens would need to cross to move between adjacent stations and to reach contiguous forest at the closest edge of the ski operations boundary (Fig. 2A). Next, we constrained the search area for movement paths between adjacent stations by buffering the direct line of travel between station pairs by 250 m, half of the average distance between adjacent stations, and used this search area to identify all possible ski run crossing locations between station pairs (Fig. 2B). For every ski run crossing in the search area that involved moving between a unique pair of remnant forest patches, we measured the shortest crossing distances at 5-m intervals at all locations in the 250-m buffer (Fig. 2B) and calculated the minimum crossing distance. Finally, to identify the putative movement path between any station pair, we selected the single path that minimized the distance a marten would have to move in an open ski run (Fig. 2). We compared the proportions of used movement paths between ski areas and non-ski areas (outside operations areas and controls) using *Z*-tests.

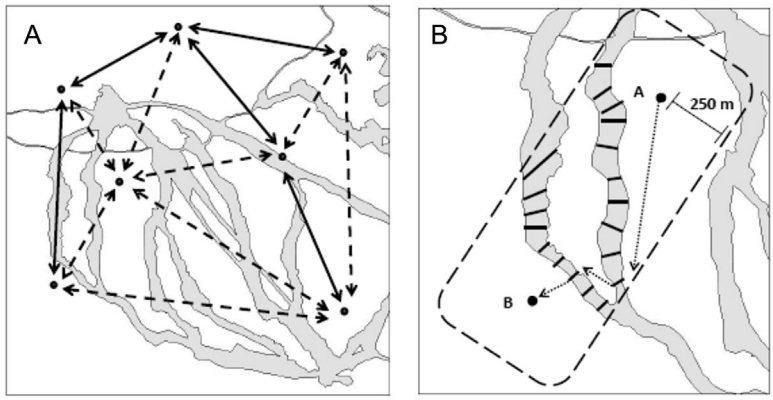

Figure 2. Schematic of the methods for identifying and measuring apparent marten movement paths between grid-based survey stations sampled in the spring–summer (2009–2011) and winter (2009) seasons at 3 ski areas in the Lake Tahoe Region of California and Nevada, USA. We present examples of used (solid lines) and unused (dashed lines) movement paths between stations (A) and measurement rules for determining likely ski run crossings (B). To determine likely crossings, we buffered the direct line of travel between station pairs (dots) by 250 m and identified the putative movement as the single path (dotted) that minimized the distance a marten would have to move in an open ski run (gray) based on widths measured at 5-m intervals (solid lines).

We evaluated the potential effects of ski areas on martens at 2 spatial scales: the treatment level, which compared the ski and control study areas, and the operations area level, which compared the habitat found in and out of each ski areas' operational boundary. Operations areas were an average of 58% (range = 50–65%) of each ski study area. Comparing areas at the operations area level accounts for the fact that some stations within ski study areas occur outside the operational boundary and are not directly affected by ski area development and are substantially less affected by seasonal ski recreation activity. Importantly, we grouped habitat sampled outside ski operations boundaries at ski study areas with control areas for the operations area analysis. Use of these 2 scales of analysis allowed us to examine whether the effects of ski areas were limited to operations areas or extended beyond them.

Marten Occupancy

We used multiple-season (spring–summer 2009–2011) and single-season (winter 2009 only) occupancy modeling in program PRESENCE, version 2.4 (Hines and Mackenzie 2006) to evaluate whether ski areas affected the distribution of marten populations. For the spring–summer analysis, station detection histories were composed of 13–15 survey occasions, where each survey occasion represented the 1-day interval between trap checks. For the winter analysis, station detection histories were composed of 3 survey occasions, each occasion representing the 5-day intervals between checking hair snares.

For each analysis, we used a hierarchical modeling approach based on guidelines for occupancy modeling (MacKenzie et al. 2006). First, we developed multiple candidate models of detection heterogeneity to account for variation due to either temporal or spatial variation in the sampling protocol's performance or hypotheses on how potential ski area stressors may affect marten detectability. During both seasons, we evaluated the following effects on detection probability: treatment, operations area, sex, remnant forest patch size, survey month, and year. Then, we used the detection model with the lowest Akaike's Information Criterion (AIC) value for developing candidate occupancy models representing multiple hypotheses of how marten occupancy may be affected by potential ski area stressors. During both seasons, we evaluated the following effects on occupancy: treatment, operations area, study area, remnant forest patch size, and a general 2-group variable to detect other significant sources of heterogeneity. For each season, we modeled occupancy using a single analysis that included all ski area and control study areas. We compared occupancy estimates from models with the lowest AIC values, for the spring–summer and winter seasons, both between ski areas and controls (treatment level) and between stations in and outside of ski operations areas (operations area level). We did not use model averaging because our candidate model sets were not orthogonal. All comparisons of occupancy estimates used McNemar's chi-square test.

Marten Density

We used spatial capture-recapture models to evaluate the effect of ski areas on marten density at the treatment and operations levels (Efford 2015). We developed spatial capture histories for each individual where 1s indicated an individual was captured during a 1-day (spring) or 5-day (winter) sampling interval and 0s indicated no capture. A spatial capture history for an individual takes the form of a 3-dimensional matrix, where each capture is a vector that identifies the individual, the day of the capture, and the location of the trap or hair snare. We then joined these individual matrices into a detection matrix where we georeferenced each capture of each individual to a trap location. Because we did not survey all sampling locations in each study area simultaneously, there was spatial-temporal heterogeneity in sampling effort. To account for this, we identified each hair snare or live trap as being available or unavailable over the entire 21-occasion (spring) or 9-occasion (winter) sampling duration. Thus, any capture history is a combination of structural and sampling zeros that are accounted for in the model (Royle et al. 2009).

We conducted spatially explicit capture-recapture analysis using the package SECR version 2.9 (Efford 2015) in

program R (R Core Development Team 2009). In SECR, the probability model for spatial detection histories comprises a sub-model for the distribution of home-range centers (e.g., 2-D Poisson) and a detection sub-model (e.g., half-normal function of distance between a range center and a trap; Efford et al. 2009). The model may be fitted by maximizing either the full likelihood or the likelihood conditional on the number of animals observed. The spatial model of the detection process relates the probability of an individual being detected at a particular station (g0) or probability of capture at an individual trap (lambda0) as the magnitude (intercept) of the detection function, conditional on the distance of that station from each animal's home range center. The effect of distance from home range center on detection probability is conditional on the movement distances (σ) of animals exhibited during the survey period. The distribution of home-range centers is a derived density estimate that takes into account the effective sampling area estimated from spatial capture recapture data (Royle et al. 2009, Efford 2015). Effective sample area is the explicit area sampled by the marten survey grids and is dependent on the spatial extent of the survey grids and the movement scaling parameter (σ) estimate, which accounts for the extent of marten movement during the survey periods.

We modeled ski areas and control study areas separately in our SECR analysis and separately for winter and spring–summer seasons. We calculated maximum likelihood density estimates independently for the spring–summer and winter seasons and independently for the ski and control study areas. We identified the spring–summer live traps as single detectors and used the hazard half normal detection function (Borchers and Efford 2008) and identified the winter analysis hair snares as proximity detectors and used the half normal detection function. For each analysis, we developed candidate models that evaluated the following covariates on the detection function: sex, age, survey month (spring–summer only), learned response (where the recapture or detection probabilities change after the first encounter with a trap or hair snare), Markovian transient response (where the detection probability depends on detection state during the previous survey period), and time trends. In addition, for ski area analyses we also evaluated whether traps located in or out of the ski operations area influenced the detection function. For model selection, we used the same AIC approach as previously described for evaluating occupancy models.

RESULTS

Capture of Martens

Over the 3 spring–summer seasons, we captured 96 individual martens (63 M:33 F), 51 on ski areas (33 M:18 F) and 49 on control areas (34 M:15 F); we recorded 587 captures. No marten mortalities or injuries due to live trapping or processing occurred during the 3 years of live trapping effort. Initial captures (66% M:34% F) and recaptures (78% M:22% F) were male-biased. We captured individual males an average of 7.9 1.5 (SE) times (range = 1–37) at an average of 3.3 0.5 stations (range = 1–9) and captured individual females an average of 4.5 1.0 times (range = 1–15) at an average of 2.2 0.4 stations (range = 1–5). We captured martens at all 6 study areas, with 19–25 individuals captured on ski areas and 17–21 individuals on control areas annually (Fig. 3).

From January to March of 2009, we collected 256 marten hair samples, representing 38 unique individuals (26 M, 12 F). Samples were male-biased with 204 (80%) from males and 52 (20%) from females. No samples contained DNA from >1 individual, probably because we analyzed only 1 brush/snare, unless DNA amplification failed.

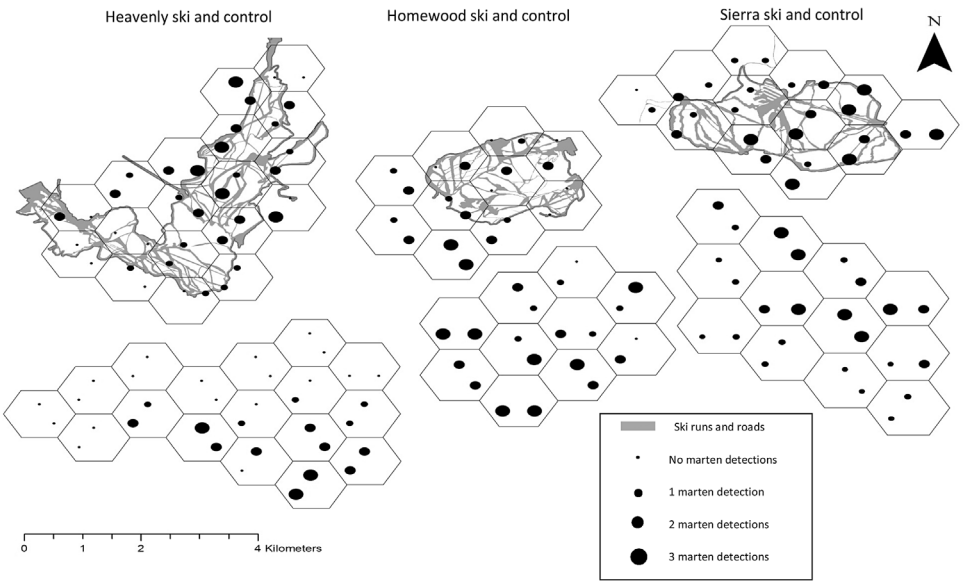

Figure 3. Pacific marten detection results at live traps for the 3 ski and 3 control study areas during the spring–summer seasons of 2009–2011 in the Lake Tahoe Region of California and Nevada, USA. Ski operations area boundaries are defined by the outermost extents of the ski runs (gray) in each ski study area; operations area analyses included only stations contained in these boundaries, whereas treatment analyses included all stations at each study area.

Thirty-three of 38 individuals (87%) were represented by >1 hair sample. Overall, during winter, we detected 38 individuals 252 times, with individual males detected an average of 7.5 0.9 times (range = 1–12) at an average of 4.7 0.7 stations (range = 1–14) and individual females detected an average of 4.2 0.9 times (range = 1–12) at an average of 3.2 0.8 stations (range = 1–9). We detected martens on all 6 study areas, with 17 (13 M:4 F) individuals detected on the ski areas and 23 (14 M:9 F) on the control areas (Fig. 4). We detected 9 females on controls versus 4 on ski areas and detected females at 64% more stations at controls ($n = 23$) than at ski areas ($n = 14$). Seventy-six percent of winter marten detections in ski operations areas occurred in remnant forest patches bordering the ski operations area boundary compared to 55% of spring marten detections (Figs. 3 and 4).

Marten Movement

During the spring–summer seasons from 2009–2011, we identified 39 used and 82 unused putative movement paths. Cumulative ski run crossing distances were shorter at used ($x = 20.0$ m, 95% CI = 11.4–28.6 m) versus unused ($x = 51.7$ m, 95% CI = 46.6–60.7 m; $t = -4.03$, P 0.001) movement paths. During the winter season we identified 36 used and 75 unused putative movement paths between adjacent stations. Minimum cumulative ski run crossing distances were shorter at used ($x = 17.5$ m, 95% CI = 5.4–29.6 m) versus unused ($x = 54.8$ m, 95% CI = 42.9–66.5 m; $t = -4.40$, P 0.001) putative movement paths. There were no differences between the mean cumulative crossing distances between males and females during winter ($t = -0.75$, $P = 0.23$). For the operations area analysis, the proportion of used movement paths was less within the operations areas (37%) compared to outside the operations areas and in the controls combined (63%; $Z = 4.05$, $P < 0.01$). This suggests the fragmentation of forest habitat from ski area development has reduced functional habitat connectivity by 41% compared to the surrounding undeveloped forest landscape.

During the spring–summer seasons, we identified 56 used and 182 unused individual ski run crossings and during the winter season we identified 44 used and 177 unused individual ski run crossings. Ski run widths used only in the winter did not differ compared to those used only in the spring–summer season ($t = 1.46$, $P = 0.07$). Therefore, we pooled all used ski run crossings (used in 1 or both seasons) and all unused ski run crossings (not used in both winter and spring–summer seasons) for this analysis. The pooled ski run crossing widths were shorter at used ($x = 14.0$ m, 95% CI = 11.7–16.3) versus unused ($x = 22.6$ m, 95% CI = 19.5–25.8 m; $t = -4.48$, P 0.001) individual ski run crossings. Females moved between forest patches with shorter ski run crossings ($x = 11.2$ m, 95% CI = 9.5–12.8 m) than males ($x = 15.1$ m, 95% CI = 12.8–17.3 m; $t = 2.83$, $P = 0.002$). The proportion of all available ski runs across all 3 ski areas with crossing widths within the 95% confidence intervals for females was smaller ($x = 22.7\%$, range = 13.6–37.8%) than for males ($x = 32.9\%$, range = 24.8–46.8%; $Z = -2.27$, $P = 0.02$).

Seasonal Occupancy

We developed 17 candidate models to estimate marten spring–summer occupancy (ψ) and detection probability (p). Several models were well-supported, but all top models showed p was best modeled using a year and survey month covariate to account for detection heterogeneity from temporal variation (Table 2). Occupancy (ψ) was best modeled separately for each study area, suggesting variation between each study area explained more variation than any other covariate: Heavenly ski $\psi = 0.48$ 0.05 versus control

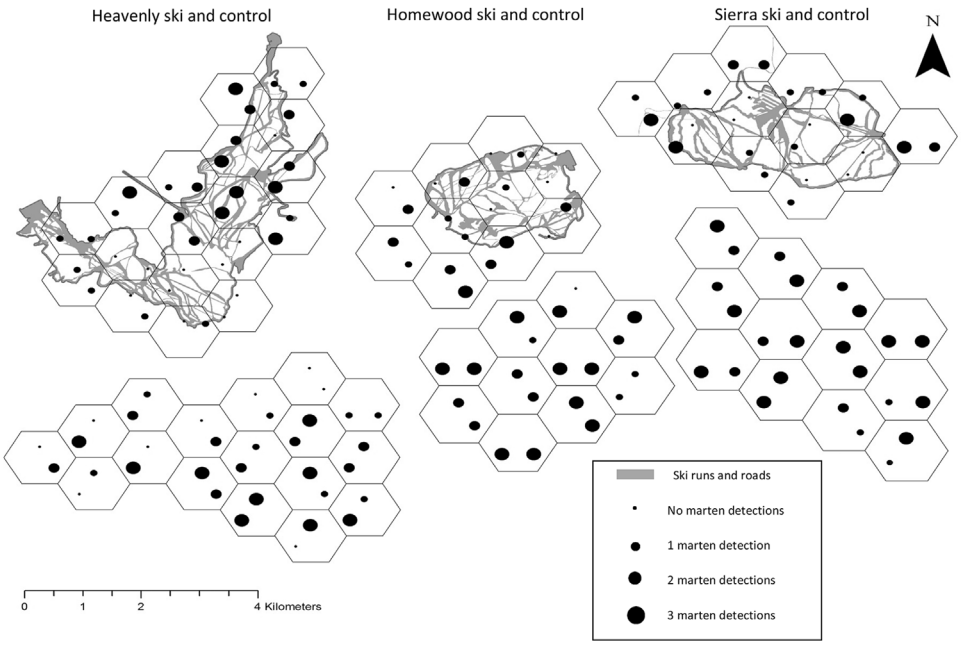

Figure 4. Pacific marten detection results at hair snares for the all 3 ski and 3 control study areas during the winter of 2009 in the Lake Tahoe Region of California and Nevada, USA. Ski operations area boundaries are defined by the outermost extents of the ski runs (gray) in each ski study area; operations area analyses included only stations contained in the operations area boundaries, whereas treatment analyses included all stations at each study area.

$\psi = 0.29$ 0.06, Homewood ski $\psi = 0.46$ 0.06 versus control $\psi = 0.62$ 0.06, Sierra ski $\psi = 0.60$ 0.05 versus control $\psi = 0.52$ 0.07. Covariates for treatment or operations area effects on ψ or p were not included in the top models for the spring–summer season (Table 2) indicating that detection probability and occupancy rates were not significantly affected by the press stressor of ski area development during the spring–summer season. The overall single-station probabilities of detection, which considered the entire 13–15-day survey period, for spring–summer were >0.90 in all years and months except for July of 2009, when it was 0.74.

We developed 13 candidate models to estimate marten winter occupancy and detection probability. One model (Table 2) was superior to all others and received 99% of the Akaike weight (w_i). This model contained covariates related to the effect of treatment versus controls on detection probability and the effect of being in or out of the ski operations areas on winter occupancy but unlike the spring–summer results, no study area specific effects (Table 2). Specifically, stations located in ski areas had lower single-visit probabilities of detection ($p = 0.53$ 0.04) than stations located in controls ($p = 0.75$ 0.03; $Z = 2.94$, $P = 0.003$). Stations located in ski operations areas ($n = 32$) also had lower probabilities of occupancy ($\psi = 0.52$ 0.09) than all stations, ski and control areas combined, located outside of ski operations areas ($n = 126$; $\psi = 0.88$ 0.03; $P < 0.001$). The overall single-station probability of detection, which considered the entire 15-day survey period with 3 visits, for the winter hair snare protocol was 0.90 for ski areas and 0.98 for controls.

Marten Density

We developed 21–27 candidate SECR models to estimate marten density for ski and control areas for each season. Sex-specific effects on detection (g0) and capture probability (lambda0) were present in most highly competing models (<2 ΔAIC) and also on the movement parameter, σ, but only in control areas (Table 3). For the spring–summer control area analysis, the top models all contained sex-specific Markovian (transient) responses and the effects of month and age class on capture probability (Table 3). Sub-adults had higher capture probabilities (g0[sub-adult] = 1.03 0.41) than adult base probability and males typically had higher initial capture probabilities (g0[M] = 0.57 0.54) compared to the female base probability. Survey month affected capture probability, June having the lowest capture probability (g0[Jun] = − 1.38 0.39) compared to July (g0[Jul] = 0.78 0.48) or the May base probability. The movement parameter was influenced by the combination of sex and age classes and by month. Males typically moved more (σ[M] = 0.22 0.16) than the female base rate of 647.1 m 14.1, but sub-adult males moved farther (σ[sub-adult M] = 0.49 0.17) than adult males, whereas sub-adult females moved the shortest distances (σ[sub-adult F] = − 0.78 0.17). Movement distances were shortest in July (σ[Jul] = − 0.28 0.10) compared to June (σ[Jun] = 0.26 0.12) or the May base probability. Density estimates for males ranged from 3.29/10 km^2 to 2.31/10 km^2 from May to June, respectively (Table 4). Female density was less than male density, ranging from 1.73/10 km^2 to 0.71/10 km^2 from May to July, respectively (Table 4).

The top model(s) for spring–summer ski area analysis all contained sex-specific learned responses (e.g., trap happy, see below) and effects of month and whether the station was in a ski operations area (Table 3). Males typically had a higher initial capture probability (g0[M] = 0.55 0.46) than the female base probability and males exhibited a trap happy response, increasing the probability of re-capture after initial capture (g0[M trap] = 0.88 0.48) compared to the female base recapture probability. Stations in the ski operations areas had a lower probability of capture (g0[operations] = − 0.43 0.22) than the base probability of those outside ski operations boundaries. The movement parameter was significantly reduced from the May average of 639.3 m 12.4 by 89.6% to 66.4 m in June 13.3 and by 40.9% to 377.8 m in July 16.2. Male density was only slightly lower at ski areas than controls, ranging from 2.66/10 km^2 to 1.97/10 km^2 from May to July, respectively (Table 3). Female density was similar to somewhat higher at ski areas compared to controls, ranging from 1.99/10 km^2 to 1.57/10 km^2 from May to July, respectively (Table 4).

For the winter-control area analysis, the top model contained a sex-specific Markovian (transient) response and an age class effect on encounter probability and an effect of sex on movement distance, with males moving on average 37.8% farther than the female base rate of 617.4 m 58.7 m. The top model for the winter ski area analysis contained sex-specific detection effect on probability, with male encounter probability (g0[M] = 1.15 0.50) higher than female encounter probability, and a study area effect on movement, with the Sierra (σ[Sierra] = − 0.26 0.15) and Homewood (σ[Homewood] = − 0.45 0.15) study areas having lower movement rates than the Heavenly ski area. Density for males was similar at control areas (2.26/10 km^2) and at ski study areas (2.00/10 km^2), whereas density of females was >2

Table 2. Multiple-season occupancy modeling results for Pacific martens during spring–summer seasons of 2009–2011 and single season results for winter season of 2009 at 3 ski areas (treatment) and 3 paired control areas in the Lake Tahoe Region of California and Nevada, USA. We modeled occupancy (ψ) and detection probability (p) and ranked models by difference in Akaike's Information Criterion (ΔAIC_c), relative model weight (w_i) and number of parameters in the model (K). Only the top 5 ranked models are presented and asterisks identify the models that are included in the 95% confidence set, calculated by summing the w_i.

Model parameters				
ψ	p	ΔAIC_c	w_i	K
Spring–summer				
Study area	Year, month	0.0	0.32	14
Study area	Year, month	0.1	0.30	13
Study area, patch size	Year, month	1.2	0.17	14
Study area	Year, month	2.1	0.11	14
Study area	Year, month	3.6	0.05	13
Winter				
Ski operations	Treatment	0.0	0.99	4
Constant	Treatment, patch size	10.8	0.00	4
Constant	Treatment	10.9	0.00	3
Ski operations	Ski operations	13.2	0.00	4
2-groups	Constant	21.0	0.00	4

Table 3. Models in the 95% confidence set for spatially explicit capture-recapture analysis of Pacific martens during the spring–summer season (2009–2011) and during winter (2009) at 3 ski areas and 3 paired control areas in the Lake Tahoe Region of California and Nevada, USA. We modeled detection and capture probability (g0) and movement (σ) and ranked models based on difference in Akaike's Information Criterion (ΔAIC_c), relative model weight (w_i), and number of parameters in the model (K).

Model parameters				
g0	**σ**	**ΔAIC_c**	**w_i**	**K**
Spring controls				
Sex transient response + age + month	Sex age + month	0.0	0.42	14
Sex transient response + age + month	Month	2.3	0.13	11
Sex transient response + age + month	Sex	2.5	0.12	10
Sex transient response + age + month	Age	2.6	0.11	10
Sex transient response + age + month	Month + age	3.5	0.07	12
Spring ski areas				
Sex learned response + operations area + month	Month	0.0	0.72	11
Sex learned response + operations area + month	Sex + month	2.2	0.24	12
Winter controls				
Sex transient response + age	Sex	0.0	0.57	8
Transient response + age	Constant	2.2	0.19	5
Sex transient response	Constant	3.9	0.08	5
Sex + transient response	Constant	4.1	0.07	4
Sex transient response + age	Sex + study area	5.3	0.04	10
Winter ski areas				
Sex	Study area	0.0	0.42	5
Sex	Time	1.5	0.19	4
Sex	Constant	1.6	0.18	3
Sex + transient response	Constant	4.0	0.06	4
Sex	Sex	4.5	0.05	4

times higher at control areas (1.41/10 km^2) than at ski study areas (0.66/10 km^2; Table 4). Effective sampling areas were equivalent between May and winter months, when snow cover was continuous (Table 4). However, the effective sampling area declined from 21% to 38% for males and 7% to 29% for females from June to July, respectively. Overall, the effective sampling area ranged between 1.03 and 1.66 times larger than the actual sampled area for spring–summer and winter, respectively, and was not significantly different between males and females (Table 4).

DISCUSSION

We found that both the press stressor of habitat fragmentation from resort development and the pulse stressor of winter ski recreation activities affected martens in different ways. Collectively, the effects of habitat fragmentation and winter ski recreation were not severe enough to completely preclude use of much of the remnant habitat within ski operations areas. Our prediction that habitat connectivity would be reduced from the creation of ski runs and road networks that require martens to cross open areas to reach remnant habitat patches was supported by the significant reduction in functional connectivity and the relatively small threshold distances (<20 m) beyond which we did not observe them moving between remnant forest patches at ski areas. Our predictions that both marten activity and space use would be reduced in habitat where and when ski recreations activities were occurring were also supported; martens avoided and made less frequent use of remnant habitat in ski operations areas during the winter recreation season. Martens responded to the press stressor of habitat fragmentation from resort development year-round, by selectively moving between forest patches with the shortest distances required to cross open ski runs and roads in all seasons. In response to the pulse stressor of ski recreation activity, martens exhibited both temporal and spatial avoidance behaviors. In our study, the pulse stressor of human activity reduced the amount of available habitat in

Table 4. Derived density estimates from top spatially explicit capture-recapture models for Pacific martens during the spring–summer season (2009–2011) and during winter (2009) at 3 ski areas and 3 paired control areas in the Lake Tahoe Region of California and Nevada, USA. Effective sample area is the explicit area sampled by the marten survey grids.

		Males			Females		
Season	**Study area**	**Density (martens/10 km^2)**	**SE**	**Effective sample area (ha)**	**Density (martens/10 km^2)**	**SE**	**Effective sample area (ha)**
Spring	Controls						
	May	3.29	0.70	6,710	1.73	0.60	5,201
	June	3.32	1.28	4,134	0.99	0.62	3,015
	July	2.31	0.66	5,632	0.71	0.36	5,632
	Ski areas						
	May	2.66	0.65	6,382	1.99	0.58	6,038
	June	2.57	0.83	4,272	1.87	0.70	4,272
	July	1.97	0.66	5,081	1.57	0.58	5,081
Winter	Controls	2.26	0.59	6,629	1.41	0.53	5,692
	Ski areas	2.00	0.55	6,481	0.66	0.33	6,044

winter, especially for females, more than the reduction of functional connectivity by the press stressor of habitat fragmentation.

In all seasons, martens moved between remnant habitat patches with the shortest distances to cross in open, non-forest habitat. This finding was consistent with the established pattern of martens avoiding natural (Buskirk and Ruggiero 1994) and human-created (Cushman et al. 2011) open areas where escape cover in the form of vertical tree boles and complex physical structure near the ground is reduced or absent. However, in most previous studies on marten movement relative to openings, study landscapes were not composed of true habitat islands as in our study. Thus, our findings more directly evaluate the conditions under which marten will cross open areas rather than measuring their avoidance behaviors to minimize their use of openings. We inferred ski run crossing behavior using individual movements about our survey grids; more direct measurements using snow tracking or GPS collars are possible. However, snow tracking in this study would be difficult because of daytime weather conditions (i.e., direct sun and temperatures) that render the snow surface unable to reliably record marten tracks to a few days after fresh snowfall, nightly grooming activities that reduce the ability to detect tracks crossing ski runs, the need to find tracks before recreational skiers degrade them, and the limitation of this technique to the winter season. At the time of this study, GPS collars of suitable weight for martens were only being piloted on males (Moriarty 2014), and combined with the costs per collar, would preclude use on a large sample of male and female martens. Given these constraints for other methods, use of movement about our sampling grids to characterize ski run crossing behavior gave us a more complete sample from both sexes and year-round measurement of movements.

Our findings expand the types of human-created openings to which martens show behavioral responses to include linear features, ski runs and roads (Frouin 2011). Tigner et al. (2015) evaluated the effects of seismic exploration lines on marten movement behavior and reported that line width and revegetation state affected their crossing frequency, with the greatest effect on movement from the combination of width (>6 m wide) and reduction in structural complexity (unvegetated). Our study expands on the types of unvegetated linear features that affect marten movement to include ski runs and roads. Ski runs present challenges for crossing openings if they are, on average, >18 m (M) and >13 m (F). We also observed apparent sex-specific thresholds for crossing open ski runs and roads of <18 m and <13 m, for males and females, respectively, that when exceeded precluded observable movement by martens between remnant forest patches in either winter, spring, or summer. Although martens may be capable of crossing larger open ski run distances, these apparent distance thresholds limited marten movements about our sampling grids. This avoidance behavior for entering areas with reduced escape cover by martens appears adaptive; the majority of sites where martens have been reported to have been killed by predators have been in areas where escape cover had been reduced (Thompson 1994, Ellis 1998, Bull and Heater 2001). This was also consistent with the overall pattern reported by Prugh et al. (2008) that species tend to show stronger responses to isolation of habitat where the remnant patches and matrix are highly contrasting.

Despite a 41% reduction in functional habitat connectivity and only an average of 33% (M) and 23% (F) of the available ski run crossing widths falling within the ranges of acceptable widths, the fragmented habitats in the ski areas were inhabitable. We did not detect significant differences in occupancy or density comparing ski and control areas in the spring–summer. That the densities were no different suggests that although martens adapted their movements in the fragmented ski areas to minimize travel in open areas, they still used much of the remnant forest habitat. We are reminded, however, that density and occupancy measures are only indices of population performance and, compared to demographic rates, can be misleading indicators of habitat quality (Van Horne 1983).

Survival is the demographic characteristic with the most influence on population growth in North American martens (Buskirk et al. 2012). Male martens traverse their home ranges every few days and travel >5 km/day when foraging (Moriarty 2014). This makes them vulnerable to predators. If occupying home ranges with ski runs ultimately reduces survival, because of the increased risk of predation from frequently crossing ski runs, then these areas may be occupied but represent low-quality or sink habitat. We have some cause for concern in this regard because only 2 (18%) of the males >3 years of age were resident within ski operations areas from 2009 to 2011, whereas 9 (82%) were residents outside operations areas and in controls. It is currently unclear if females move as far and as frequently as males, but adult females >3 years of age were present in ski operations areas in the spring–summer. Determining if crossing ski runs influences survival for males or females will be an important question for future research.

During the spring–summer in ski and control study areas, male marten density was 2.1–3.3 times higher than female density. Sex-biases are expected in mustelids, when home ranges are sexually dimorphic, sampling is arranged in grids, and when rates of travel are higher in males (Buskirk and Lindstedt 1989). Our study design accounted for this bias in 2 ways. First, average trap spacing of 500 m ensured that there were multiple traps in each of the female's smaller home ranges. Second, an explicit incorporation of sex-specific detection and capture probabilities and movement rates in SECR helped address the sex bias. The differences in density estimates between the sexes appear to reflect behavioral differences in territory packing and by extension habitat selection. In control study areas, males were detected at 1.75 and 2.65 times more stations than females during the spring and winter seasons, respectively. Across all study areas and seasons, female martens were detected at 35% of stations compared to 71% by males. This suggests that males may have a broader range of habitat conditions they make use of and that habitat conditions suitable for use by females, and thus reproduction, may be more limited and possibly represent a limiting factor for marten populations in this region. Accordingly, an increased emphasis should be put on

understanding and managing habitat capable of supporting females, because they are solely responsible for raising young, and the habitat they occupy directly supports reproduction.

With the addition of the pulse stressor of winter ski recreation activities, martens avoided significant portions of forest habitat and reduced their spatial and temporal use of habitat in operations areas, increasing the degree of impact from habitat fragmentation alone. The majority of detections of martens in ski operations areas during the winter were in habitat patches near the edge of the operations boundaries (Fig. 4). Female density showed a larger decline from spring to winter than males at ski areas compared to controls. This suggests females are more sensitive to winter ski recreation activities and exhibit stronger seasonal avoidance responses than males. Martens responded to winter ski recreation as a pulse disturbance, temporarily altering their spatial and temporal use of habitat exposed to this disturbance. Once winter recreation activities had ceased, martens resumed their use of habitat in ski operations areas to levels similar in areas without ski recreation activity. Occupancy in ski operations areas was equivalent to controls in the spring–summer season, but the proportion of new individuals captured on ski areas in the spring–summer season was more than double that of controls. This suggests a potential mixture of avoidance and apparent survival effects, or potentially source-sink dynamics, from the combination of the press stressor of habitat fragmentation and pulse stressor of winter ski recreation. The seasonal shift away from operations areas in winter by martens was similar to how several other relatively wide-ranging species, including capercaille (Thiel et al. 2008), chamois (*Rupicapra rupicapra*; Hamr 1988), and moose (*Alces alces*; Ferguson and Keith 1982) respond to the pulse stressor of winter ski recreation.

To shift their spatial and temporal use of habitat away from ski operations areas, martens must have access to additional nearby habitat. Habitat avoided in ski operations areas represents a temporary direct loss of the available habitat to support the marten population. One way to view the net loss is to consider the loss of occupied area as a result of the presence of ski operations areas. The estimate of winter occupancy outside the operations areas was 88%, whereas only 52% of the area inside the operations area was estimated to be occupied. Given the actual areas of our study areas, this represents a temporary loss of 36% (i.e., 88–52%) which translates to 600.4 ha of habitat lost in the 3 ski areas combined during winter. In other studies where habitat (Thompson et al. 2012) or prey populations (Thompson et al. 1994) have been degraded, martens responded by increasing their home ranges to compensate for the degradation in resources. The rate of home range increase was typically proportional to the amount of home range degraded (Potvin et al. 2000). If the same phenomenon occurs in ski areas, the combination of habitat lost during ski area development plus the amount of area avoided during winter represents as much as 37% of the ski study area.

Our spring–summer occupancy models contained study-area-specific effects, suggesting that additional variation in habitat conditions were affecting marten occupancy patterns during that season but not winter. Martens have been shown to exhibit population-level differences in the characteristics of habitats they occur in during winter and summer, occurring in a broader range of habitat during winter when populations are at their peak and prey resources are most limited and more limited range of habitat during summer when reproduction occurs (Zielinski et al. 2015). Despite attempting to control for variation in habitat conditions during the study design, it appears additional variation in habitat conditions is influencing density, especially for female martens, during the spring–summer. In addition, although we found that ski runs affect the movement behavior of martens similar to other linear features including seismic lines, the effects of linear features also have been reported to reduce individual home range occupancy (Tigner et al. 2015). Collectively, this suggests sex-specific home range scale analysis of habitat features influencing density and the influence of linear features on home range fidelity and survival will be important areas for future research.

Habitat fragmentation from development of the 3 resorts in this study largely involved the fragmentation of contiguous forest with no appreciable further degradation of habitat conditions in remnant forest patches. Our ski study areas did not include habitat modification to remnant forest patches that occur elsewhere in ski area development, such as thinning or glading of trees to improve conditions where skiers are allowed and encouraged to ski between trees. These additional habitat modifications have the potential to increase effects on martens because martens typically respond negatively to similar changes in forest structure from silvicultural treatments (Thompson et al. 2012). Variation in the quality of habitat in remaining forest patches was, therefore, due to natural variation in structural and compositional characteristics and the degree of isolation from fragmentation. It appears that martens are able to move in and out of ski operations areas to use remnant forest habitat during the non-ski recreation periods of the year and that there may be little overall effects on population distribution or density. However, if increased mortality is occurring, due to necessity of crossing ski runs, some portions of ski areas may be functioning as sinks or ecological traps (Schlaepfer et al. 2002). Additional research will be necessary to determine if any sensitive vital rates (e.g., survival) are being affected before conclusions about population-level impacts from ski area recreation can be made.

MANAGEMENT IMPLICATIONS

Much of the conflict between ski area development and protecting marten habitat is because the areas that marten select as their favored habitat are the same types of areas ideal for ski area development. Mesic topographic positions such as north-facing slopes that favor the accumulation and persistence of snow are good for ski activities and also support the most productive and structurally complex forest habitats favored by martens. There are actions, however, that can foster coexistence. We think that marten populations can be maintained on developed ski areas if sufficient functional

habitat connectivity exists to permit movement between remnant habitat patches within ski operations areas and to habitat outside the operations boundaries. Habitat connectivity at ski areas can also be improved by evaluating the widths of ski-runs to identify those that are narrow enough to encourage both sexes to cross (i.e., <12 m). The next step would be to determine how these runs are distributed relative to the remnant habitat patches in the operations areas. The goal would be to maintain or enhance the proportion of ski runs that are narrow enough to encourage crossing to and from the operations areas and between the largest and most suitable remnant forest habitat patches. Finally, we suspect that nighttime activities on the ski areas may be a likely explanation for why martens avoid ski areas during winter. Skiing run grooming activities typically occur at the same time of day (nighttime) that martens are active and foraging in winter (Zielinski et al. 1983, 2008). If this is indeed the case, ski run grooming activities could be conducted during periods of the day that minimize their overlap with times of peak marten foraging activity to reduce this seasonal impact during winter.

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