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LINKING LANDSCAPE PATTERN TO POPULATION PROCESSES FOR A CARNIVOROUS MAMMAL

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FOR A CARNIVOROUS MAMMAL

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ABSTRACT

As a taxonomic group, carnivores are amongst those with the highest conservation concern due to the combination of wide-ranging behavior, typically slow reproductive rates, and low density. The Pacific marten (*Martes caurina*) is a carnivore species of conservation concern throughout much of its southern range in the U. S. The Pacific marten (marten hereafter) is considered a habitat-specialist, due to its association with late-successional forest habitat which provide specific elements, such as cavities in large-diameter trees for denning, to meet a variety of its life history needs. Across its range, threats to marten persistence range from timber harvest, wildfire and fuels management, and recreational development. Ski areas represent one form of recreation development that involves both the modification of habitat and high concentrations of human activity. My dissertation investigates the influence of landscape pattern from ski area development on population processes to provide insight on the marten's compatibility with this form of recreational development and to develop a sound ecological basis for guiding management.

By comparing 3 pairs of ski and controls areas I found that martens exhibited avoidance behavior in response to winter recreation activities by both reducing the frequency of habitat use and occupancy at ski areas in winter. Females avoided ski areas in winter more strongly than males by also having lower densities at ski areas during winter compared to controls. After winter recreation activity ceased in the spring and summer, habitat use, occupancy rates, and female density at ski areas were no different than at control areas. Both sexes selectively moved

between remnant forest patches with the shortest ski run crossing distances in all seasons at ski areas. Overall the fragmentation of habitat from ski runs reduced the functional connectivity by 41% at ski areas compared to controls.

I found that females were more selective than males for both resources during the denning season and for remnant habitat patches at ski areas. During the denning season females selected for mesic forest habitat in the largest trees size class available and for more of this habitat type than males. Selection for both the largest size class of forest habitat and larger quantities of that habitat types suggests that suitable denning habitat is composed of two resources: suitable denning sites in large-diameter live and dead trees and large amounts of habitat associated with the highest prey abundances. At ski areas females selected for the largest patch sizes of remnant forest while males did not.

Using capture-mark-recapture analysis I found that adult male apparent survival was reduced at ski areas compared to control areas but female survival was not affected. This reduced survival rate was consistent with skewed age structure for males at ski areas suggesting this was largely representative of reduced true survival. Estimates of seniority for sub-adults of both sexes were lower at ski areas, suggesting recruitment of this age class to the adult age class is reduced. Using genetic parentage analysis at 16 microsatellite loci for 53 yearling martens I found that more immigrants were captured at ski areas and the recruitment rate of yearling per adult female was > 4 times lower at ski areas compared to controls.

Overall, my research shows that, considering behavioral responses alone, martens appear compatible with developed ski areas. However, the demographic responses suggest otherwise as the combination of reduced survival of males and reduced recruitment of juveniles suggest martens are just able to maintain persistence at ski areas, but contribute little to the larger

population. Collectively, this suggests ski areas represent ecological traps for martens, where typically reliable sex-specific cues—suitable remnant habitat for denning for females and presence of females for males—are mismatched in landscapes fragmented by ski runs that ultimately reduce individual fitness.

CHAPTER 1

INTRODUCTION AND OVERVIEW

BACKGROUND

The presence and persistence of a species in a landscape is inevitably linked to how important resources and stressors affect demographic processes. Important resources and stressors are rarely distributed evenly across landscapes and this variation can lead to locations where individuals and collectively sub-populations, exhibit variation in demographic performance (Dugger et al. 2005, McLoughlin et al. 2007). Spatial variation in resource quality and stressor intensity can result in source-sink population dynamics (Pulliam 1988, Breininger et al. 1998). Sink habitats may be occupied, but persistence in sink habitats may be entirely or in large part due to immigration from higher quality source habitats elsewhere (Delibes et al. 2001). Human-altered landscapes can introduce novel conditions that can impact a species' fitness by still supporting habitat cues that attract individuals, but due to the types of changes may ultimately support lower rates of reproduction or survival (Battin 2004). Accurately linking resource and stressor conditions to measures of fitness is therefore critical for understanding how these factors influence population persistence and are essential for providing a sound basis for habitat management (Aldredge and Boyce 2007).

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. The most significant declines in distribution have occurred in the southern portions of the Pacific marten range (Zielinski et al. 2001), including in the northern Sierra Nevada mountains of California and Nevada (Zielinski et al. 2005). The Pacific marten is

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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). Outdoor recreational activities are a major factor in the decline of many threatened and endangered species in the United States (Czech et al. 2000). 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. 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). This suggests that ski areas, as high-contrast landscapes, may alter habitat use by martens.

My dissertation research asks the question how does variation in resource quality and stressor intensity affect population processes, including distribution, reproduction, survival, and recruitment, for this species of conservation concern. I address this question by studying marten populations across 3 pairs of landscapes with (treatment) and without (control) developed ski areas. I evaluate the influences that spatial variation in stressor intensity and resource quality have on population processes. The resultant four interlocking studies first documents the

distributional responses to both pulse and press stressors at ski areas; second, identifies how variation in resource quality affects sex-specific density; third, evaluates the influence of ski areas on survival and recruitment of young; and fourth, uses population modeling to quantitatively determine if ski areas represent source or sinks for martens. Finally, in the last chapter I use multi-dimensional habitat modeling to provide blueprints for maintaining and improving portions of the landscape most influential for population persistence.

RESEARCH OBJECTIVES & FINDINGS

Chapter 2: Distributional Responses of Martens to Variation in Stressor Intensity

Ski areas represent a potential stressor for martens due to the combination of a pulse stressor, the direct effects of high intensity human activity in winter, and a press stressor, the indirect effects of habitat modification from development. Development of alpine ski areas involves the modification of habitat by fragmenting previously contiguous forest habitat with high-contrast open areas for ski runs and roads. Both pulse and press stressors have the potential to affect martens. Therefore, in Chapter 2 I asked the following questions:

- *Do ski runs affect marten movement?*

- *Do ski areas affect seasonal or sex-specific occupancy or density?*

I addressed these questions by systematically sampling for the presence of martens at 3 paired ski and control areas from 2009-2011. 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. However, during winter occupancy was significantly lower inside (52%) ski area boundaries than outside

(88%) them. 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. In winter, martens avoided using habitat in ski

operations areas when recreation activity was greatest.

This chapter has been published in *The Journal of Wildlife Management* under the title

"Ski areas affect Pacific marten movement, habitat use, and density" and is co-authored by

William J. Zielinski, and Michael Schwartz.

Chapter 3: Density as a Reliable Sex-specific Indicator of Habitat Quality During the Denning

Season for Pacific Martens

In chapter 2, I showed that variation in two types of stressors at ski areas, press (habitat

fragmentation) and pulse (seasonal recreation activity) affect marten movement, occupancy, and

density. However, variation in resource quality should also have significant influences on the

distribution and density of martens. Therefore, in chapter 3 I asked the questions:

- *How do habitat features affect sex-specific density?*

- *Is density positively correlated with habitat quality?*

I evaluated the influence of habitat features and habitat fragmentation from ski area

development on Pacific martens at 3 pairs of ski and control study areas in the Lake Tahoe

region of California and Nevada from 2009-2011. I captured a total of 96 (63M:33F) individuals

on 843 occasions using live traps during the denning season (May – July) and hair snares during

the non-denning season (January – March). Female density during the denning season was

influenced by both the size class and amount of mesic forest habitat, with females selecting the

largest amounts mesic forest habitat types in the largest size class. Females at ski areas had a

>10 fold greater selection for patch sizes >10 ha.   Male density was influenced by a broader

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range of resource conditions than females, with the amount of medium and large size classes of mesic forest with moderate to dense canopy cover most influencing male density. There was no effect of patch size on male density at ski areas. Pooled sex models masked the importance of female-specific habitat features influencing their density and therefore reproduction, due to the higher numbers of males in the population and more generalized resource needs. Selection for both the size class and quantity suggests that suitable denning habitat is composed of two resources: suitable denning sites in large-diameter live and dead trees and large amounts of habitat associated with the highest prey abundances.

Chapter 4: Pacific Marten Recruitment and Survival is Reduced at Ski Areas

In chapters 2 and 3 I looked at how variation in stressors and resources affected marten distribution and sex-specific density. In chapter 4, I evaluated the influence of ski areas on sex-specific survival, reproduction, and recruitment of young by comparing 3 pairs of ski and controls study areas. To estimate survival, I used the robust-design Pradel model for survival and seniority. Specifically, I estimated stage-specific recruitment using program MARK (White and Garrot 1999). For reproduction, I compared the proportion of females actively lactating annually and the total number of reproductive attempts, whether each female was actively lactating annually, from 2009-2011. To estimate recruitment rates, I first used genetic parentage analysis using 16 microsatellite loci to identify the parents for 53 yearlings captured from 2009-2011 using a combination of exclusion and likelihood methods in program COLONY (Wang 2008). All yearling martens were assigned to an immigrant, emigrant, or local recruit status based in the location of their parents. In this chapter, I addressed the following questions:

- *Do ski areas affect sex-specific survival?*

- *Do ski areas affect reproduction of the recruitment rates of young?*

I found that adult male apparent survival was reduced at ski areas compared to control areas, but female survival was not affected. Estimates of seniority for sub-adults of both sexes were lower at ski areas, suggesting recruitment of this age class to the adult age class is reduced. One or more parent was identified in our study population for 42% of the 53 yearlings. Despite ski areas having more breeding age females (14 versus 10 at controls) and more total reproductive attempts (25 versus 10 at controls), more immigrant offspring were captured at ski areas (24 versus 17). There were only small differences between the number of local recruits (6 at ski versus 10 at controls) or emigrants (3 at ski versus 5 at controls) to other study areas. However, the estimated rate of offspring recruitment per female reproductive attempt to the larger population was >4 times higher for controls versus ski areas. While martens appear to persist at ski areas, they do so with reduced survival rates (males) and reduced recruitment rates of offspring.

Chapter 5: Quantifying the Effects of Landscape Pattern on Population Dynamics

Within this final chapter I evaluated the overall effects of ski areas on population growth by calculating the contribution of marten sub-populations at ski areas (n = 3) and control areas (n = 3) to the overall population. To calculate the contribution of focal subpopulation *r* to the overall population we used the metric C^r, which is the per capita contribution of a member of the focal subpopulation to the overall population (Runge et al. 2006). In Chapter 5, I addressed the following questions:

- *Do ski areas affect the contribution of sub-populations to the overall population?*
- *What areas are the most influential for population growth and persistence in each study area?*

I found that the per capita contribution rates were significantly reduced at ski areas compared to controls. Estimates of C^r for ski areas were close to 1, suggesting that these populations were just able to maintain their abundances but contributed little to the overall marten population. Despite reduced rates of juvenile recruitment and adult male survival, marten density was no different at ski areas compared to controls. This suggests that ski areas represent 'equal preference' ecological traps and that the underlying mechanism for this trap is that ski areas have a resulting reduction in habitat quality, as expressed by recruitment and survival, without a loss in the attractiveness of the habitat conditions for martens. Finally, through the use of density-based habitat models I show that habitat is best viewed and managed hierarchically, to match the relationships that influential vital rates (e.g., production of young) have with particular resource conditions.

SYNTHESIS AND SIGNIFICANCE

The Pacific marten is a species with conservation concern throughout much of its' southern range (Zielinski et al. 2001, Zielinski et al. 2005). There is considerable interest in understanding how to balance marten persistence with other objectives for managing forests in which they occur, including timber harvest, wildfire and fuels management, and recreational development. Understanding how resources and stressors affect demographic processes can provide a sound foundation for management. This understanding can guide the development of strategic management and conservation actions that can improve influential resource conditions or reduce particular stressors that ultimately can increase the likelihood of marten persistence by affect demographic processes.

Developed ski areas involve the combination of both pulse and press stressors for wildlife. Winter recreation activities represented a pulse stressor, where high densities of human

recreation activities occur within ski areas but they only occur over a ~ 4 month period annually. Martens exhibited avoidance responses to the pulse stressor of winter recreation activity by reducing both the frequency of use and occupancy of habitat in the ski areas during the winter recreation season. Females were more sensitive than males to this pulse stressor and also exhibited reduced density in and around ski areas in winter. However, once winter recreation activities ceased in the spring and summer, marten habitat use, occupancy, and female density at ski areas increased and was no different than areas without ski area development.

Ski area development represented a press stressor due to the fragmentation of contiguous forest into remnant patches required to create networks of ski runs, roads, and infrastructure. To access remnant forest habitat at ski areas martens must cross open ski runs and roads where escape cover from predators has been reduced or eliminated. Martens exhibited several behavioral and demographic responses to this form of habitat fragmentation. Both sexes exhibited selection for moving between remnant forest patches with the shortest crossing distances in open ski runs. Females selected for the largest patch sizes of remnant forest while males did not. Selection for larger patch sizes likely reduces the frequency of crossing ski runs. As an apparent consequence of using smaller patch sizes males had a reduced survival rate compared to females at ski areas. Surprisingly, more females reproduced on ski areas than on the paired control areas, however recruitment rates for juveniles per adult female were < 4 times lower at ski areas compared to controls.

The consideration of only behavioral responses of martens to ski areas suggests that they may be more or less compatible with both the pulse and press stressors present at ski areas. However, the demographic responses suggest otherwise as the combination of reduced survival of males and reduced recruitment of juveniles are unlikely to support persistence of martens at

ski areas without martens immigrating to ski areas from elsewhere. Collectively, this suggests ski areas represent ecological traps for martens, where typically reliable sex-specific cues— suitable remnant habitat for denning for females and presence of females for males—are mismatched in areas modified by ski area development that ultimately reduce individual fitness and the likelihood of population persistence.

DISSERTATION FORMAT

Chapters 2 was formatted and published in accordance with the guidelines of a peer-reviewed scientific journal, *The Journal of Wildlife Management* (Slauson et al. 2017). Chapter 3 was also formatted in accordance with the guidelines of the *Journal of Wildlife Management*. Chapters 4 and 5 are formatted for the *Journal Ecological Applications* and *Journal of Ecology*, respectively. Each one of these chapters is the product of collaboration with other scientists, who are credited at the head of each chapter. It is for this reason that I refer to this collaborative effort by using the collective "we" throughout the remainder of the dissertation.

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CHAPTER 2

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 2009–2011 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.

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 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 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 2,000–3,000 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 and 4.3 degrees C

And an average of 1440mm 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. 2-1). 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 Feb 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. 2-1). 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. 2-1B). 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. 2-1). 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. 2-1). 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.

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 2-1). 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).

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. 2-2A). 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. 2-2B). 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. 2-2B) 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. 2-2). We compared the proportions of used movement paths

between ski areas and non-ski areas (outside operations areas and controls) using Z-tests.

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 McKenzie 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. 2-3).

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. 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. 2-4). 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. 2-3 and 2-4).

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 ($\bar{x} = 20.0$ m, 95% CI = 11.4–28.6 m) versus unused ($\bar{x} = 51.7$ m, 95% CI = 46.6–60.7 m; $t = -4.03$, $P \leq 0.001$) 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 ($\bar{x} = 17.5$ m, 95% CI = 5.4–29.6 m) versus unused ($\bar{x} = 54.8$ m, 95% CI = 42.9–66.5 m; $t = -4.40$, $P \leq 0.001$) 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 ($\bar{x} = 14.0$ m, 95% = 11.7–16.3) versus unused ($\bar{x} = 22.6$ m, 95% CI = 19.5–25.8 m; $t = -4.48$, $P \leq$

0.001) individual ski run crossings. Females moved between forest patches with shorter ski run crossings ($\bar{x}$ = 11.2 m, 95% CI = 9.5–12.8 m) than males ($\bar{x}$ = 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 ($\bar{x}$ = 22.7%, range = 13.6–37.8%) than for males ($\bar{x}$ = 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 2-2). 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 ψ = 0.48 ± 0.05 versus control ψ = 0.29 ± 0.06, Homewood ski ψ = 0.46 ± 0.06 versus control ψ = 0.62 ± 0.06, Sierra ski ψ = 0.60 ± 0.05 versus control ψ = 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 2-2) 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 2-2) 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 2-2). Specifically, stations located in ski areas had lower single-visit probabilities of detection ($p = 0.53 \pm 0.04$) than stations located in controls ($p = 0.75 \pm 0.03$; $Z = 2.94$, $P = 0.003$). Stations located in ski operations areas ($n = 32$) also had lower probabilities of occupancy ($\psi = 0.52 \pm 0.09$) than all stations, ski and control areas combined, located outside of ski operations areas ($n = 126$; $\psi = 0.88 \pm 0.03$; $P < 0.001$). 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 2-3). 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 2-3). 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 $\pm$ 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 2-4). 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 2-3). 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 2-3). 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 2-4).

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 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 2-4). 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 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 1981).

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 2009–2011, 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. 2-4). 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*; Fergeson 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. 2013). 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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Figure 2-1. 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).
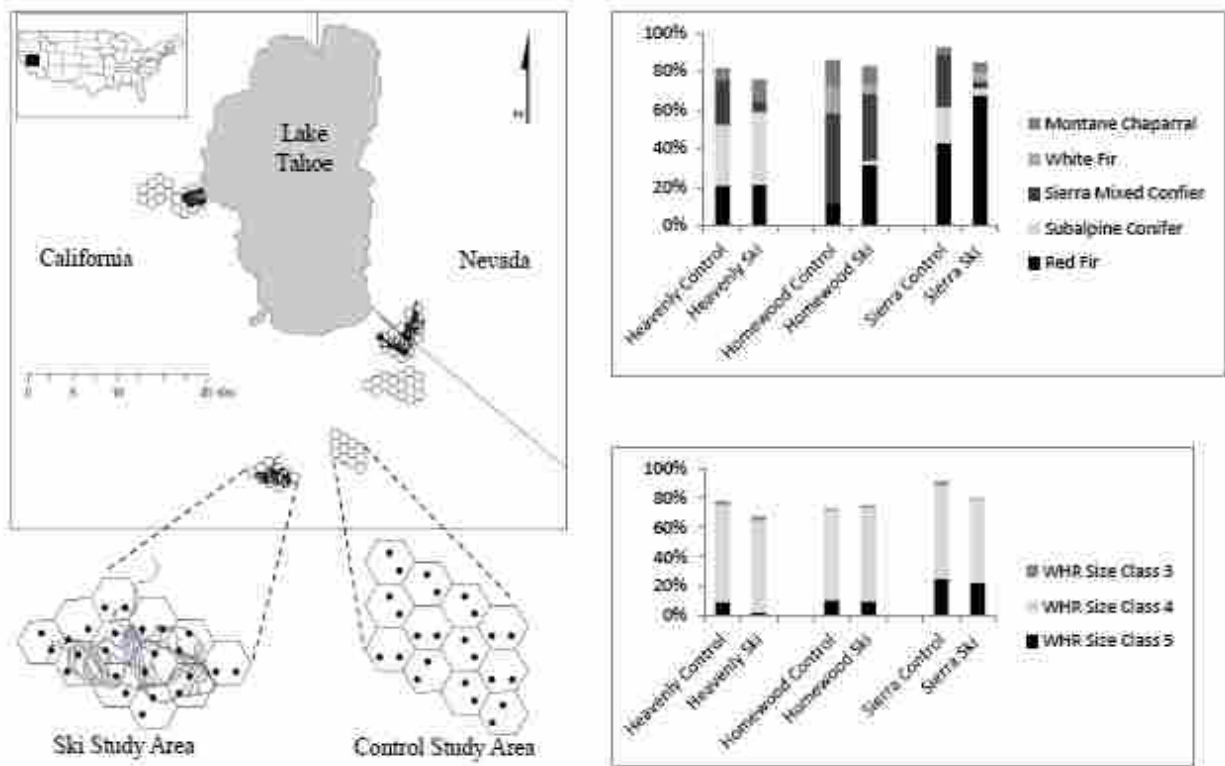
Figure 2-2. Schematic of the methods for identifying and measuring apparent marten movement paths between grid-based survey stations sampled in the spring-summer (2009–2011) and winter (2009) seasons at 3 ski areas in the Lake Tahoe Region of California and Nevada, USA. We present examples of used (solid 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).
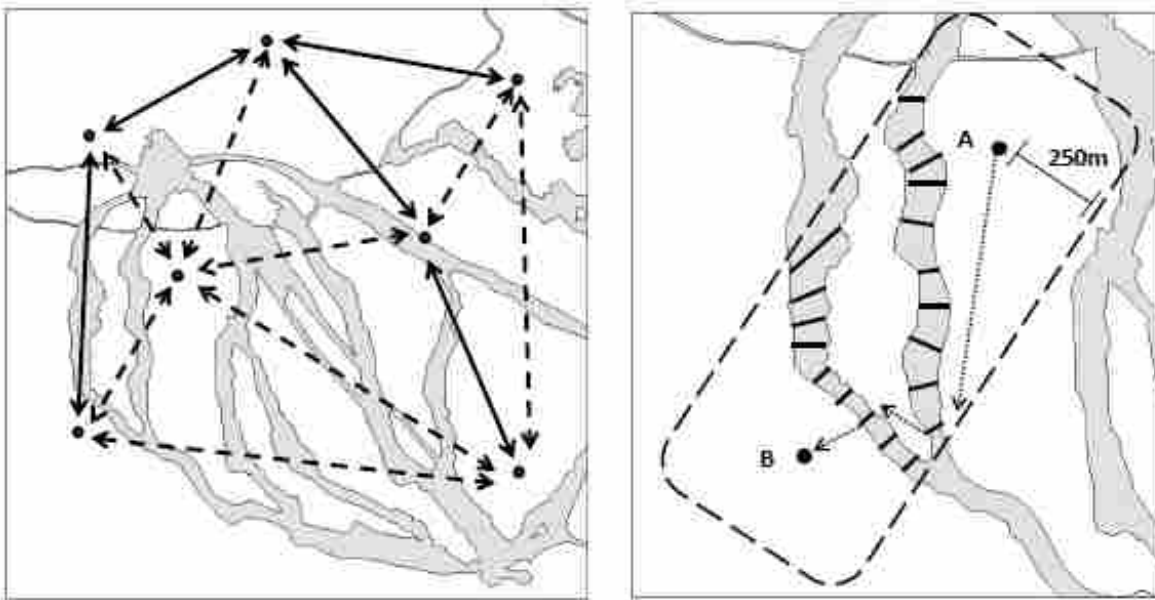
Figure 2-3. Pacific marten detection results at live traps for the 3 ski and 3 control study areas during the spring-summer seasons of 2009–2011 in the Lake Tahoe Region of California and Nevada, USA. Ski operations area boundaries are defined by the outermost extents of the ski runs (gray) in each ski study area; operations area analyses included only stations contained in these boundaries, whereas treatment analyses included all stations at each study area.
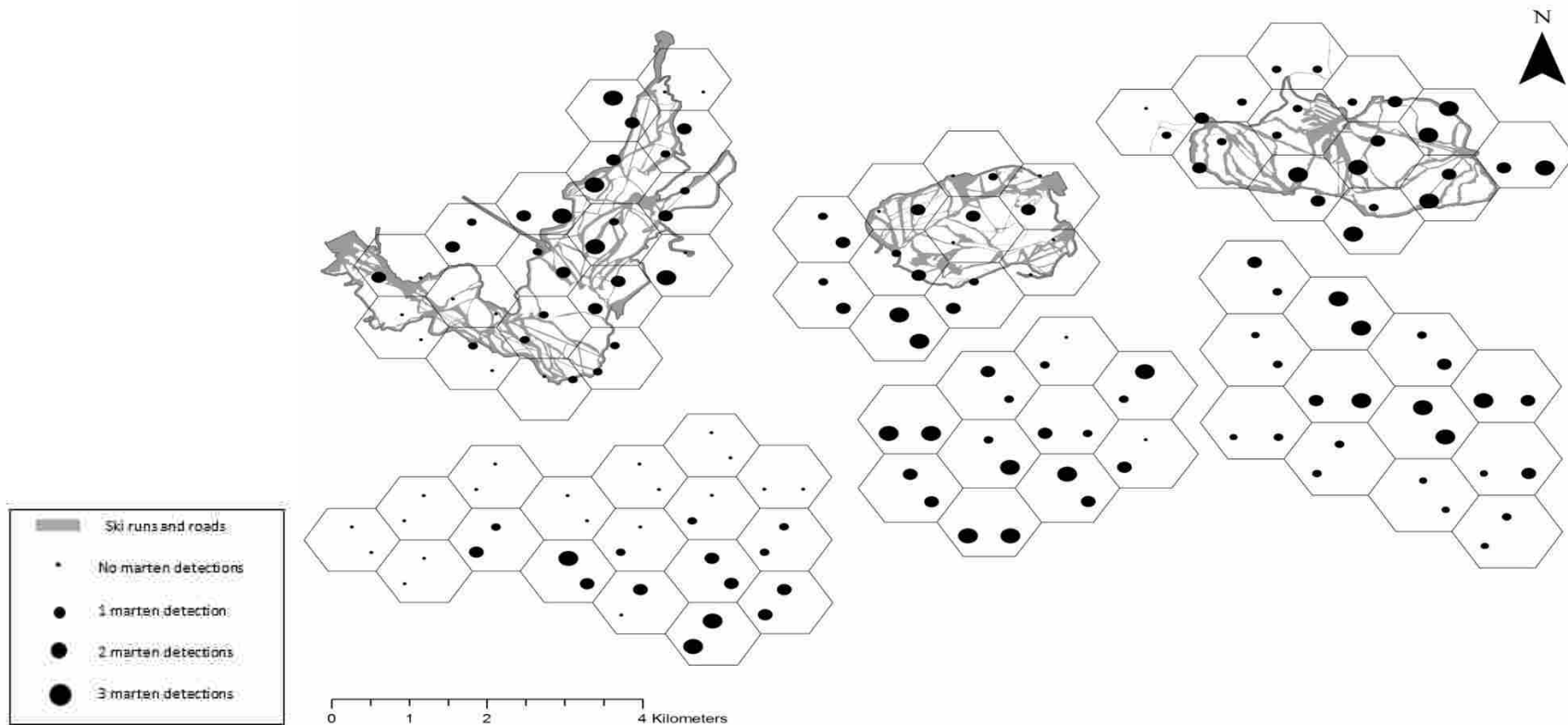
Figure 2-4. Pacific marten detection results at hair snares for the all 3 ski and 3 control study areas during the winter of 2009 in the Lake Tahoe Region of California and Nevada, USA. Ski operations area boundaries are defined by the outermost extents of the ski runs (gray) in each ski study area; operations area analyses included only stations contained in the operations area boundaries, whereas treatment analyses included all stations at each study area.
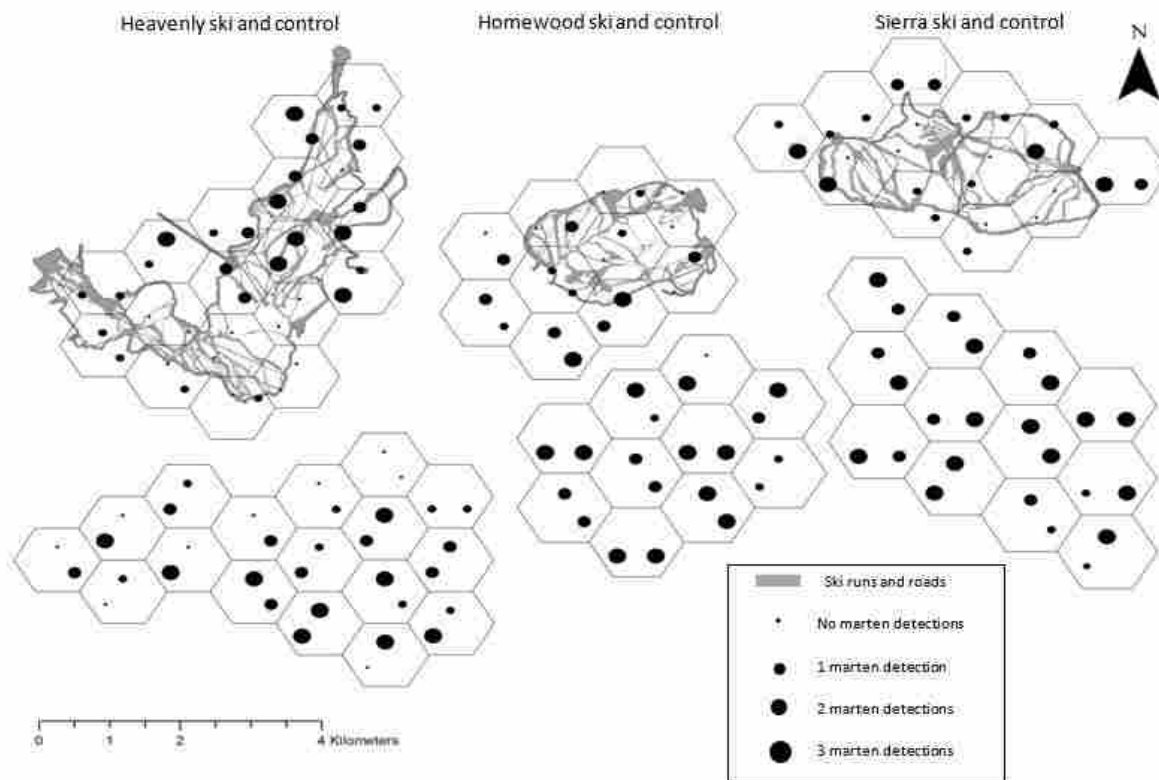
Table 2-1. Month and year in which each of 3 pairs of ski and control study areas were sampled for Pacific martens in the Lake Tahoe Region of California and Nevada, USA.

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

Table 2-2. 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		ΔAIC_c	w_i	K
ψ	p			
Spring-summer				
Study area*	Year, month*	0.00	0.32	14
Study area*	Year, month*	0.13	0.30	13
Study area, patch size*	Year, month*	1.22	0.17	14
Study area*	Year, month*	2.13	0.11	14
Study area	Year, month	3.56	0.05	13
Winter				
Ski operations*	Treatment*	0.00	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 2-3. 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 x transient response + age + month	Sex x age + month	0.0	0.42	14
Sex x transient response + age + month	Month	2.3	0.13	11
Sex x transient response + age + month	Sex	2.5	0.12	10
Sex x transient response + age + month	Age	2.6	0.11	10
Sex x transient response + age + month	Month + age	3.5	0.07	12
Spring ski areas				
Sex x learned response + operations area + month	Month	0.0	0.72	11
Sex x learned response + operations area + month	Sex + month	2.2	0.24	12
Winter controls				
Sex x transient response + age	Sex	0.0	0.57	8
Transient response + age	Constant	2.2	0.19	5
Sex x transient response	Constant	3.9	0.08	5
Sex + transient response	Constant	4.1	0.07	4
Sex x 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

Table 2-4. 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.

Season	Study area	M			F		
		Density (martens/10 km²)	SE	Effective sample area (ha)	Density (martens/10 km²)	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

Article Summary: 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 a   ities 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.

CHAPTER 3

Density as a Reliable Sex-specific Indicator of Habitat Quality

During the Denning Season for Pacific Martens

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ABSTRACT

We evaluated the influence of habitat features and habitat fragmentation from ski area

development on Pacific martens (*Martes caurina*) at 3 pairs of ski and control study areas in the

Lake Tahoe region of California and Nevada from 2009-2011. Forest habitat at control areas was

in a largely unmanaged condition. Ski area development resulted in the loss of forest habitat and

fragmentation of residual habitat. We captured a total of 96 (63M:33F) individuals on 843

occasions using live traps during the denning season (May – July) and hair snares during the

non-denning season (January – March). We used spatially-explicit capture-recapture analysis to

model season- and sex-specific influences of habitat features and habitat fragmentation on marten density and resource selection in a single integrated framework. Female density during the denning season was influenced by both the size class and amount of mesic forest habitat, with females selecting the largest amounts mesic forest habitat types in the largest size class. This habitat type is associated with both the highest abundance of potential den structures and the most abundant prey resources. The size of remnant forest patch at ski areas influenced female density during the denning season, with females having >10 fold greater selection for patch sizes >10 ha. During the denning season male density was most influenced by a broader range of resource conditions than females, with the amount of medium and large size classes of mesic forest with moderate to dense canopy cover most influencing male density. Remnant patch sizes did not affect male density at ski areas. In winter, male and female density was not well predicted by habitat features, suggesting resource needs and thus habitat use is more general during winter compared to the denning season. Our results suggest suitable denning habitat appears to be limited, occurring in < 20% of the landscape, and is the likely explanation for female density being half that of males. Pooled sex density models for the denning season masked the importance of the limited, but essential, habitat features supporting reproduction and reversed the positive relationship of increasing patch size with female density. For female martens, density was positively correlated with the increasing abundance of habitat features associated with the resources—den sites and abundant prey—necessary to support reproduction. Although males overlapped all females in the population, they occurred in many other areas with less specific resource conditions during the denning season, making models with males or male-only less accurate in identifying the habitat features necessary for supporting reproduction.

Key Words: Pacific marten, denning habitat, winter habitat, spatially-explicit capture-recapture, ski area, recreation, fragmentation, occupancy, habitat importance

INTRODUCTION

Identifying the habitat features supporting critical life-history stages is essential for understanding how habitat influences population persistence. Ultimately, habitat features affecting individual fitness—survival and reproduction—can have an important influence on population growth and persistence. Empirical evidence for most species indicates that there is spatial variation in individual fitness in most populations (e.g., McLoughlin et al. 2007) and that it is due to variation in the habitat features affecting survival and reproduction (e. g., Dugger et al. 2005), although variation in environmental conditions can also be influential (e.g., Mosser et al. 2009). Distinguishing how variation in habitat features affects measures of fitness allows for an assessment of habitat quality. Accurate assessments of habitat quality are needed to advance our understanding of habitat-performance relationships (Galliard et al. 2010) and for providing sound foundations for guiding habitat management for species of conservation concern.

Habitat quality is best assessed using measures of individual performance, survival and reproduction, which drive population growth and persistence. However, when the amount of resources influencing one or more measures of fitness vary across vegetation types, this can result in variation in both individual performance and population density. While the case for not using animal density as the only proxy for assessing habitat quality has been well justified (e.g., Van Horne 1983, Mosser et al 2009), where performance, density, and the amount of resources influencing performance positively co-vary in a particular vegetation type, their combined effects can greatly increase the relative contribution of that vegetation type to population growth. This suggests that using a performance metric in combination with density can provide a more rigorous evaluation of habitat quality than using a single performance metric. In addition, for

species where the roles in raising of young are sex-specific, such as in polygynous carnivores, the relationships between habitat features important for supporting the raising of young and their influence on density may be sex-specific (Aronsson et al. 2016). Therefore, for assessing habitat quality for species with sex-specific roles in raising of young, including both measures of resource use during the period when young are raised and density, can be important for identifying the sex-specific influences of habitat features may have on supporting all phases of the successful production of young. We assessed the habitat quality for Pacific martens (*Martes caurina*), 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, using one proxy for fitness, reproduction, and density in a single integrated analytical framework. Our assessment of habitat quality was conducted in a landscape consisting of both unmanaged forest habitat and forest habitat developed for ski areas. We developed our assessments of habitat quality by season (reproductive and non-reproductive) and by sex to contrast the influence of habitat features and fragmentation effects for these two factors. We use the 'structural' definition of habitat (Gaillard et al. 2010) to describe the vegetation types that are associated with resources (e.g., den and rest sites, prey) important to meet seasonal and sex-specific life history needs as this definition most closely relates to how habitat for martens is typically studied and managed.

Female martens are solely responsible for raising of young and therefore have several resource requirements, such as suitable den structures and abundant prey resources nearby dens, to support reproduction that males do not. There have been few studies investigating the resource and environmental conditions that influence reproduction in North American martens despite the importance of reproduction for population persistence (reviewed in Thompson et al. 2012). Prior estimates of the density of female martens in the Lake Tahoe region were 50-67%

lower than males, suggesting that suitable habitat conditions to support female home ranges and therefore reproduction in this region may be limited (Slauson et al. 2017). Martens are obligate cavity users for reproduction, with females giving birth to young in dens that are typically aerial cavities in large-diameter live or dead trees (Ruggiero et al. 1998). The characteristics of suitable den structures, typically limited to cavities early in the denning period (Raphael and Jones 1997, Ruggiero et al. 1998, reviewed in Thompson et al. 2012), are likely to be more limited than those of daily resting sites used by males or by females in the non-denning season. Once females give birth to their kits, they become central-place foragers, returning to the den site frequently in-between foraging bouts to feed kits and assist them with thermoregulation. If female martens are similar to other mustelids, they may require more than double the daily energy intake of the larger-bodied males during the denning season (e.g., fisher [*Pekania pennanti*, Powell 1993). Consequently, during the denning season females should select habitat types providing both of these critical resources, suitable den structures and abundant prey resources, as has been shown for marten den sites in Wyoming (Pearson and Ruggiero 2001). Males should exhibit strong spatial overlap with females to increase mating opportunities during the period of the denning season when mating occurs (June-August; Mead 1994). However, their overall resource needs are less stringent than females during the denning season, limited to daily resting sites and prey necessary to meet daily energetic demands (15-25% of body mass, Gilbert et al. 2009). As a result, males should be expected to use a broader range of resource conditions than females during the denning season. In the non-denning season, use of habitat types by the sexes should be similar because during this season their resource needs, rest sites and prey, are similar (Sandell 1989).

Habitat loss and fragmentation is one of the primary threats to species conservation. For many species, spatial variation naturally exists in the quantity and quality of resources and environmental conditions that affect survival and reproduction. Therefore, the degree of impact that habitat loss and fragmentation can have on a species will often depend on whether important resources are impacted and how their modification leads to changes in vital rates. Ski area development is a unique form of habitat fragmentation where habitat is removed to create ski runs and roads and the remaining forest habitat is fragmented into smaller patches by the run and road networks. This type of habitat fragmentation results in high contrast between residual forest habitat and the open ski runs and roads, which affects Pacific marten movement (Slauson et al. 2017) and tends to affect species most where the contrast between altered and residual habitat is high (Prugh et al. 2008). There is a growing awareness of the effects of ski area development and recreation on wildlife species of conservation and management concern (Ferguson and Keith 1982, Hamr 1988, Patthey et al. 2008, Thiel et al. 2008, Slauson et al. 2017).

In the Lake Tahoe region of the Sierra Nevada, martens continue to use much of the habitat at ski areas, especially in the denning season, but they avoid or reduce their use of habitat when ski recreation activities are present (Slauson et al. 2017). To use remnant habitat patches at ski areas, martens must cross open runs and roads. Remnant habitat patches range from ~1 ha to ~40 ha in size (K. Slauson unpubl. data), representing ~2% to ~ 13% of the average marten home range in the region (Spencer et al. 1983). Martens can traverse their entire home range in as little as a day in winter (Moriarty 2014). Smaller patches will require martens to leave the patch to forage elsewhere. Patch size will ultimately be important to martens if selecting resources in areas that minimizing the frequency of crossing ski runs is important. However, sex-specific differences in the selection of patch sizes may be observed during the denning season if the use

of dens in small patches increases the predation risk of frequently crossing ski runs or with

moving kits across open ski runs to alternative den sites over the course of the denning season.

Our objective was to assess the influence of habitat features and habitat fragmentation from

ski area development on habitat quality for martens using a proxy for fitness, reproduction, and

sex-specific density. We evaluated three hypotheses. Females require two resources for raising

kits, suitable denning structures and reliably abundant prey resources. Therefore, we

hypothesize that females should select for and their density be positively associated with both the

forest structural size class with suitable den structures and larger amounts of the forest type(s)

supporting the most abundant prey resources. If suitable den structures are important, we predict

that females will select for forest structural class that is assumed to have the highest availability

of suitable den structures (i.e., stands with large-diameter live and dead trees). If prey abundance

is essential, we predict females will also select for higher amounts of forest structural conditions

most closely associated with high abundances of important prey. Second, we hypothesized that

the effects of fragmentation of forest habitat from ski resort development would be greatest on

females during the denning season, when resource demands and avoiding predation risk are

likely greatest. If development affects martens, we predict that females will both exhibit stronger

selection for larger forest patch sizes during the denning season and that selection for larger

patch sizes will be stronger for females than males. Our third hypothesis is that the habitat

features most important for supporting reproduction would only positively co-vary with female

density and only during the denning season due to different sex- and season-specific resource

demands. If true for sex, we predict that the habitat features most closely associated with density

of females will represent a narrower range of resource conditions during the denning than those

associated with male density. If true for season, the habitat features most closely associated with

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female density during the denning season will represent a narrower range of resource conditions than those associated with the density of either sex during the non-denning season.

METHODS

Study Design and Site Selection

The study was conducted in the Sierra Nevada Mountains of California and Nevada, on the Lake Tahoe Basin Management Unit and El Dorado National Forest, both administered by the U.S. Forest Service. Elevations range from about 2000 – 3000 m and the area is 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*). Precipitation is primarily snowfall and averages >1000 cm annually, with >125 cm falling on average monthly from November through March.

Our study design assesses habitat quality at 3 pairs of treatment (ski resorts) and control study areas and included the Heavenly, Sierra-At-Tahoe, and Homewood ski areas (Figure 3-1). Control areas were selected systematically to be representative of ski areas in the Lake Tahoe region and to match the topographic (elevation range and major aspect) and vegetation characteristics of each ski resort's operations area. The ski operations area is defined as the outer perimeter of habitat modification from the outermost run or road at each ski area. We assessed topographic and vegetative similarity using digital elevation models and remotely sensed existing vegetation data (USDA, Pacific Southwest Region, Remote Sensing Lab, Updated Feb 2010) based on California Wildlife Habitat Relationships system (hereafter CWHR, Mayer and Laudenslayer 1988) vegetation types in a geographic information system (GIS). Vegetation types were classified by the combination of the dominant plant species (e.g., red fir, *Abies*

magnifica) and both the mean diameter at breast height (dbh) and percent canopy closure. Control areas were selected with equivalent forest type and size class distributions as occurred at each ski resort operations area, including habitat lost during their development (Figure 3-1). Collectively the study areas were dominated by red fir (43%), Sierra mixed conifer (29%), and subalpine conifer (25%) CWHR habitat types and medium (CWHR size class 4 = 11-23 in dbh, 81%) and large tree (CWHR size class 5 = >24" dbh, 16%) tree size classes. Apart from the removal of forest habitat to create ski runs and ski area infrastructure, residual forest habitat at ski areas and forest habitat in control areas was largely unmanaged with little alteration from logging (Lindström et al. 2000).

Study Design

To test our hypothesis we used a study design that jointly estimates density and resource selection using a spatially-explicit capture-recapture (hereafter, SCR) framework. SCR models provide a mechanism for modeling second- and third-order resource selection using capture-recapture data alone to estimate resource selection parameters (Royle et al. 2013, Royle et al. 2014). We investigated second-order selection in this study because Pacific martens typically exhibit stronger patterns of second-order habitat selection than at other scales and decisions at this scale most likely influence individual fitness (Thompson et al. 2012). To model the effects of resources on marten density we used SCR models with inhomogeneous point process models that allow resource covariates that are defined systematically across all study areas to influence the estimated location of each individual's home range or activity center. This design for resource selection, comparing used versus available resources where available resources was defined by their prevalence across all study areas, conforms to sampling design II (Manly et al. 2007).

Marten Sampling Design

We sampled martens using systematic grids overlaid on control and ski areas to determine how individual martens used habitat both in and adjacent to each ski area (Figure 3-1). At ski areas, each grid included the entire extent of the developmental footprint of the ski area, hereafter called the ski operations area, as well as additional habitat adjacent to the ski operations area (Figure 3-1). The size and shape of each control area's sampling grid matched that of its paired ski area. Each grid was composed of hexagonal sample cells with an area of 100 ha, equivalent to the size of the smallest reported female marten home ranges (Buskirk and McDonald 1989). In each grid cell, two marten sampling stations were established 500 m apart in the center of each cell. The number of sample cells and, therefore the number of stations sampled at each ski area 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 (Figure 3-1). We sampled martens during the early portion of the denning season (May-July) and later portion of the non-denning season (January-March).

Marten Sampling: Denning Season

Denning season sampling occurred from May through July for 3 years (2009-2011), with a single matched ski and control study area 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. Martens were trapped at each sampling station using wire mesh live traps (Tomahawk Co, Tomahawk, WI, USA, Model #105), modified with plywood cubby boxes on the ends to provide security for trapped animals.

Traps were baited with chicken and a sponge soaked with olfactory lure (Gusto, Minnesota Trapline Products, Pennock, MN) was tied to the nearest tree branch. Traps were checked at least once daily for 13-15 consecutive days.

We chemically immobilized captured martens to determine their sex and age class. One upper first premolar was removed and sent to Matson's Laboratory (Manhattan, MT) to be aged by counting cementum annuli (Poole et al. 1994). For individuals missing all pre-molars, or when poor tooth samples could not be accurately aged, tooth wear was used to estimate age class based on similarity to known age individuals of the same sex. All individuals received uniquely numbered passive integrated transponder (PIT) tags for individual identification (12.5mm; Biomark, Boise, ID). Use of PIT tags facilitated scanning and identifying individual martens in traps, allowing for immediate release of recaptured martens. Hair and blood (taken by swabbing tooth extraction sites) samples were collected to provide DNA samples for comparing individuals detected at hair snares during the non-denning season (see next section). Martens were captured and processed using methods approved by the California Department of Fish and Wildlife and Nevada Department of Wildlife Scientific Collecting Permit Programs and followed the American Society of Mammalogists guidelines for the use of wild mammals in research (Sykes 2016).

Marten Sampling: Non-denning Season

We sampled martens at pairs of ski and control study areas simultaneously, from January to March in 2009. The 2 sampling stations in each hexagonal cell were surveyed during 2 separate 15-day survey periods, such that each study area was sampled over a total of 30-days. We did not use traps during this season because we would put martens at risk due to the more extreme

weather conditions in winter. Instead, each sampling station consisted of a hair snare attached to

the bole of a large-diameter tree and each consisted of a corrugated plastic (coroplast^{TM}) snow

shield with 2 hair snares attached, 2 chicken drumsticks as bait, and a coroplast collar below the

bait with 3 hair snares attached. Each hair snare was a 30-caliber gun-cleaning brush (Hoppe's,

Bushnell Outdoor Products, Overland Park, KS). A sponge soaked in olfactory lure was hung on

a nearby tree branch. Each station was checked 3 times, every 5 days, for a total of 15 days.

Hair samples were collected and stored in desiccant prior to DNA analysis. DNA was extracted

and individual identification of martens was conducted using microsatellite variation at 9 loci

(Schwartz et al. 2012) by the National Genomics Center for Wildlife and Fish Conservation

(Missoula, MT) following the methods described in Slauson et al. (2017).

Assigning Age Class and Denning Status

We assigned age class based on the combination of age and reproductive status (females) to all

martens captured in the spring-summer season only because this was the season when we had the

animals in hand to assess these demographic characteristics. Individuals were captured ~1.5 to 4

months after their birthdays, so we assigned age class based on their estimated age – 1 year to

represent their ages coming into the capture season. Slauson et al. (2017) found that 100% of

females >1 year of age were reproductively active annually from 2009-2011. Therefore, we

classified females >1 year of age as adults and sub-adult females as those 1 year old. Males do

not typically reproduce until at least 2 years old, due to reaching sexual maturity at age 1 and

typically requiring social dominance for access to females in estrus (Sandell 1986, Mead 1994),

so males $\geq$2 were classified as adults and males < 2 as sub-adults. We determined the

reproductive status of each female by examining the teat condition of females captured during

spring-summer.   A female was considered to have given birth that season if she exhibited at

least one of these characteristics: (1) at least one teat that expressed milk, (2) at least one sucking ring present, or (3) enlarged teats, with ≥ 3 mm width on at least one teat.

Modeling the Encounter Process

Before we could estimate density, it was necessary to estimate the encounter or observation sub-model to account for the detection process in spatially-explicit capture-recapture (SCR) analysis. We developed spatial capture histories for each individual where a "1" indicates an individual was captured during a 1-day (denning) or 5-day (non-denning) sampling interval and a "0" indicates no capture. A spatial capture history for an individual takes the form of a matrix, where each capture is a vector, which identifies the individual, the day of the capture, and the location of the trap or hair snare. These individual matrices were then joined into a detection matrix where each capture of each individual was georeferenced to a trap location. In both denning and non-denning seasons, not all sampling locations in each study area were surveyed simultaneously, representing spatial-temporal heterogeneity in sampling effort. To account for this, each hair snare or live trap was identified as being available or unavailable over the entire 21-occasion (denning) or 9-occasion (non-denning) sampling durations. Thus, any capture history is a combination of structural and sampling zeroes that are accounted for in the model (Royle et al. 2009).

We used SCR analysis to estimate density with the package SECR version 2.10 (Efford 2015) in program R (version 3.2.4, R Core Development Team 2009). In SECR, the probability model for spatial detection histories comprises an 'observation' sub-model for detection or capture of animals (e.g. half-normal function of distance between a range center and a trap) and a 'state' sub-model for the distribution of home-range centers (e.g. 2-D Poisson) (Efford et al. 2009).

Each model was fitted by maximizing the full likelihood on the number of animals observed. The spatial model of the detection process relates the probability of detecting an individual at a particular station (g0, hair snares; lambda0, traps) to the distance (d) of that station from each animal's home range center and is estimated by:

$$g(d) = g0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$$

where the effect of distance from home range center on detection probability is conditional on the movement scaling parameter (σ) of animals exhibited during the survey period. The distribution of home-range centers is a derived density estimate (D) that takes into account the effective sampling area estimated from spatial capture recapture data (Royle et al. 2009; Efford 2015).

For the denning season, live traps were identified as 'single' detectors and we used the hazard half normal detection function (Borchers and Efford 2008) and for the non-denning season analysis we identified hair snares as 'proximity' detectors and used the half normal detection function. We define the denning season home range as the area used by an individual marten during our 3 15-day May to July survey periods from 2009-2011. For individuals caught in a single year there was a minimum of 15 days of survey effort and for individuals caught in >1 year there was from 30-45 days of survey effort to determine their home range. During the non-denning season, all individuals were exposed to 30-45 days of survey effort from January to March in 2008.

In SCR analysis, the home range centers are unobserved random effects, modeled using a Poisson point process (Royle et al. 2014). Conceptually, the detection model is the composite of 2 processes: 1) movement and habitat use of an individual about its' home range 2) detection of

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individuals at stations conditional on habitat use in the vicinity of each station. As detections of

individuals accumulate over space and time, the detection probability model equates a

conditional distribution of points, a utilization distribution of points, from which the effective

home range area that contains some percent (e.g., 95%) of all space used by an individual can be

estimated. The estimate of movement scaling parameter (σ) is the radius about the home range

center that was used to calculate the area that encloses any specified percent of movements

within the home range under the detection model. We then used the movements of individuals to

calculate the effective sampling area (ESA), which we used to derive a density estimate of the

total number of observed and unobserved individuals in the ESA.

We used a hierarchical modeling process to develop models for each component of the

observation and state sub-models. First, we evaluated sources of heterogeneity in the two

components of the observation model, detection (g0) or capture (lambda0) probability and the

movement scaling parameter (σ). Candidate models were developed that evaluated the following

covariates for detection/capture heterogeneity on the detection function: sex, age, survey month

(spring-summer only), trap response (e.g., 'trap shy or trap happy'), and transient response

(Markovian response, the detection response depends on detection the prior occasion). In

addition, for evaluating potential effects of ski areas on observation model parameters we

included covariates for ski study areas (treatment effect) and whether the station was located in

or out of the ski operations area combined with controls (operations area effect). For each sex

and season, we developed between 10 (denning) and 8 (non-denning) candidate observation sub-

models representing alternative hypothesis about how the two components of the observation

process are affected by the covariates.

Modeling Resource Influences on Density

The second step of the SECR modeling process was to develop candidate sub-models for estimating density. We modeled the influence of resource and stressor covariates on marten density at the home range scale (second order selection, Johnson 1980). Using a spatially explicit capture-recapture model (SECR; Efford et al. 2009), we evaluated the influence of covariates on the distribution of home range centers by modeling their effects on the density parameter (D). Underlying the SCR models is a spatial point process that describes the distribution of marten home range centers. To model the influences of covariate on density, we used an inhomogeneous Poisson point process model (Borchers and Efford 2008), where the intensity parameter μ is allowed to vary spatially and is a function defined at each point s on the habitat mask using spatially referenced covariates and a vector of regression covariates (β); a function denoted as μ(s, β). Therefore any candidate model describing the influence of covariates on density will take the form of:

$$\mu(s, \beta) = \exp{(\beta o + \beta_1 Covariate_1 + \beta_2 Cvoariate_2 \ldots\ldots)}$$

To test our predictions we modeled the influence of habitat on density for each sex and season. We were limited to including age class as a covariate in the detection model because SECR does not allow the use of individual covariates. Grouping covariates can be used as sessions in SECR, however we decided to model survey month using the session option due to the high levels of heterogeneity on capture probability and movement observed by month in prior analyses (Slauson et al. 2017). To model the influence of resource and stressor covariates on D we used a habitat mask, where each point on the mask represents a grid cell of potentially occupied habitat. The habitat mask is a systematic grid of points (n = 4450) attributed with resource and stressor covariates, with 250 m spacing between mask points and extending 2 km beyond the outermost station locations sampled in each study area (Figure 2).

Each point on the habitat mask was attributed with 10 resource and stressor covariates that represented the structure and composition of vegetation (Table 3-1), including CWHR system vegetation types, tree size classes, and canopy cover class, from the Existing Vegetation (EVEG) polygon coverage developed by the USDA Forest Service Pacific Southwest Remote Sensing Lab (http://www.fs.fed.us/r5/rsl/clearinghouse/gis-download.shtml; accessed December 2015). Multiple covariates were developed form the CWHR coverage to represent combinations of mesic forest types, those typically supporting more prey and den structures than xeric types, in a reduced (R) subset of CWHR types (RWHR: i.e., red fir, white fir, sierra mixed conifer, lodgepole pine, subalpine conifer) and either size class 4 (RWHR4: 11-24" dbh trees) or size class 5 (RWHR5: >24" dbh trees) or the combination of these two. See Table 3-1 for all other variable descriptions. In addition to these categorical CWHR variables we used continuous tree diameter and tree cover values estimated from satellite imagery in EVEG were used to create the tree diameter and tree cover covariates to represent different ranges than the CWHR classes (Table 3-1). Riparian habitat was represented from two sources of GIS data. The first was stream density as derived from a digital line graph coverage representing USGS 7.5 minute quadrangle map information on streams for the Lake Tahoe region (http://tahoe.usgs.gov/DLG.html). We also digitized the locations of riparian vegetation patches, largely composed of thin leaf alder (*Alnus incana*), from digital ortho-photos. We used elevation measured at 10 m resolution re-sampled from a USGS 1-m resolution digital elevation model for the study area (http://nationalmap.gov/elevation.html).

We evaluated our predictions about how fragmentation from ski area development affected marten density by developing additional covariates for ski areas. To represent the cumulative fragmentation effects of ski area development we digitized a polygon representing the ski

operations boundary, defined by the outermost ski runs or roads that contained all landscape

modification from resort development. We digitized all remnant forest patches in each ski area

and calculated each patch's total area. Correlation was assessed between all candidate variables

and in cases where two variables had an $r^2 > 0.6$, the variable of the pair most correlated with

other variables was removed from the analysis.

To select the scale at which each resource covariate was measured we evaluated the spatial

scale that maximized the statistical fit of the each resource covariate separately for male and

female martens (Shirk et al. 2012). Each candidate resource covariate was measured at 4 spatial

scales at each point on the habitat mask, starting with 1,000 m representing the average radius of

a typical marten home range (~300 ha; Spencer et al. 1983) and then sequentially smaller areas

750, 500, 250, representing smaller core areas within home ranges. Resource covariates were

measured at each spatial scale with circular moving windows using the FOCALSUM function in

ArcGIS (ESRI, Redlands CA, 92373). Each resource covariate was modeled independently

using a univariate model for each of the 4 spatial scales in SECR and the scale with the lowest

AICc score was retained for inclusion in the final model development step (e.g., Shirk et al.

2012). The final step involved creating an orthogonal set of multivariate models using all

resource covariates with w_i values >0.05 (see below) from the univariate model evaluation. The

final model set for each sex by season analysis included all univariate models with each variable

represented at its' optimal scale and the orthogonal multivariate model set. This resulted in from

20 to 30 models per sex for each season. Finally, a key goal of our work was to compare

inferences about habitat on density between single-sex and pooled-sex models. Our final step

was to pool the data for both sexes and to evaluate each of the models in the 95% confidence set

for each sex.

Models were ranked using Akaike's Information Criterion for small sample size, (AIC_c; Burnham and Anderson 2002) and were interpreted by the comparison of ΔAIC_c values, providing a measure of strength of evidence (Anderson et al. 2000). Akaike weights (w_i) were calculated using ΔAIC_c values and w_i were used to create a 95% confidence set of models whose cumulative weights equaled 0.95 (Burnham and Anderson 2002). Model fit was evaluated using the secr.test function in SECR to conduct a Monte Carlo test of the scale deviance (Borchers and Efford 2008). We calculated odds ratios from coefficients from the top ranked model(s) to determine how covariates affected the detection and density estimates of sub-models. To test for resource selection, we calculated resource selection ratios (Manly et al. 2003) using the R package adehabitatHS, version 3.5. We calculated strength of selection (Boyce et al. 2002) for habitat covariates by comparing the values of habitat covariates at home range centers to their availability across the habitat mask.

RESULTS

Captures in the Denning Season

Over the 3 denning seasons, we captured 96 individual martens (63M:33F), 51 on ski areas (33M:18F) and 49 on control areas (34M:15F), a total of 587 times. No marten mortalities or injuries due to live trapping or processing occurred. We captured males an average of 8.4 times (SE = 1.2) and females an average of 4.5 times (SE = 0.7; Figure 3). Initial captures (0.66 M:0.34F) and recaptures (0.78M:0.22F) were male-biased. During the denning season we captured martens at all 6 study areas, capturing between 19 - 25 at ski areas and 17- 21 at control areas annually.

We captured 29 females on 43 occasions to assess reproductive status. All reproductive age females (>1) captured (28/28) showed evidence of lactation. As expected, yearling females rarely showed evidence of lactation (20%, 3 of 15). Only 2 of 12 (17%) of the reproductively active females in ski operations boundaries maintained use areas exclusively inside the ski operations area boundary during the denning season, despite the fact that the operations areas averaged 43% of the total ski areas.

Detections in the Non-Denning Season

From January to March of 2009 we collected 256 marten hair samples, representing 38 unique individuals (26M, 12F). Twenty-four (0.63; 16M:8F) of these individuals were recaptured in one or more of the subsequent denning seasons. Overall, hair samples were male-biased with 204 (0.80) from males and 52 (0.20) from females. No samples contained DNA from >1 individual, probably because we analyzed 1 brush per snare, unless DNA amplification failed. Thirty-three of 38 individuals (0.87) were represented by >1 hair sample and individuals were captured an average of 7.5 times (SE = 1.1) for males and 4.2 times (SE = 0.9) for females. Martens were detected on all 6 study areas, 23 individuals (14M:9F) at control areas and 17 individuals (13M:4F) at ski areas.

Movement and Detection Models

During the denning season, detection and movement for males and females was affected by capture month, with capture probability variable by month and movement decreasing from May to July (Table 3-2). The sexes responded differently to initial capture, with males having a trap happy response to re-capture and females a trap shy response (Table 3-3). The top capture sub-models for males (month-specific and positive trap response) and females (slight negative linear

trend in month) were >13 ΔAIC_c and <2 ΔAIC_c units lower than other candidate capture models, respectively. Other highly competing covariates for female capture probability included an negative operations area effect, transient effect, and month-specific estimates, however for simplicity we used the single top covariate—linear trend in month—only. The top movement sub-model for males (negative linear trend) and females (month-specific, declining from May to July) were >10 ΔAIC_c and >5 ΔAIC_c units lower than other candidate movement models, respectively. From May to July, movement of males and females declined by an average of 230 m and from 179-241 m monthly for males and females, respectively (Table 3-3).

In the non-denning season, encounter probabilities increased for females, but were similar for males during both seasons. The top encounter probability sub-model for males (positive Markovian dependence on prior detection state [transient response]) and females (constant encounter probability) were both >7 times more likely that all other candidate models. The top movement sub-models for males (age-specific movement rates) and females (treatment effect) were only 1.4 to 1.6 and 2.6 times more likely than the next candidate models, respectively. Highly competing models for males included negative operations area effects and no effects (null) on movement. Overall, there appeared to be less heterogeneity in capture and movement within and between the sexes during the non-denning season compared to denning seasons.

Influence of Habitat on Density in the Denning Season

Optimizing Scales for Habitat Covariates--Overall comparisons between the 4 spatial scales resulted in relative differences of 0.3 to 5.2 $\Delta AICc$ units for each variable evaluated (Figure 3-4). Overall, the strongest association of influential habitat covariates on martens occurs at larger spatial scales, those proportional to half or the entire area of their home ranges (Figure 3-4).

Between the sexes, scale-specific relationships between influential variables and martens were generally similar, however the magnitude of differences differed (Figure 3-4).

Males—During the denning season density was best modeled by the combination of stream density and either the forest structural variable RWHRmd or RWHR5. Five state models were in the 95% confidence set (Table 2), however only the top 2 were highly competing (<2ΔAICc units). Each model contained stream density at the 750m scale and one variable representing forest structure, RWHRmd (see Table 3-1 for variable definitions) at the 750m scale and RWHR5 at the 1-km scale. The 2 forest structure and composition variables had larger effect sizes and positively affected male density compared to stream density (Table 3-4). A 20 ha increase in RWHRmd and RWHR5 resulted in 18.3% and 19.3% increases in the odds of a male home range occurring after accounting for the effect of stream density, respectively. An increase of stream density of 200 m within 750 m resulted in a 7.2% decrease in the odds of a male home range occurring after accounting for the effects of forest structure and composition (Table 3-4). Male home range centers occurred in nearly all stream density categories and occurred in larger amounts (>60 ha) of RWHRmd and RWHR5 habitat 1.4 and 1.6 times greater than expected, respectively (Figure 3-5).

Females— During the denning season female density was best modeled by the combination of the amount of RWHR5 at the 1-km scale, mesic forest types in the largest tree size class, and stream density (Figure 3-6). Five state models were in the 95% confidence set (Table 3-2), however only the top 2 were highly competing (≤ 2 ΔAICc units) and each model contained stream density at the 750m scale, with the addition of RWHR5 at the 1-km scale and size of the remnant forest patch size at ski areas included in 2 of the highly competing models. Remnant forest patch size was the variable that had the largest effect size on female density, but this only

affected the 10 females (30%) that occurred in ski operations areas and this likely accounts for its lower relative variable importance weight (Table 3-4).

Females selected for the largest forest patch sizes at ski areas >10 times greater than expected (Figure 3-5). Amount of RWHR5 at the 1-km scale influenced female density. Every 20 ha increase in this variable increased the odds home range occurrence by 19.4% after accounting for stream density and remnant forest patch size. RWHR5 (1-km) had a stronger relationship to female home ranges than males, with > 60 ha included in female home ranges 2.1 times greater than expected (Figure 3-5). Similar to males, stream density at the 750 m scale had a slightly negative effect on female density (Table 3-4). However, female home range centers occurred with a narrower range of stream densities than males, 82% had < 2km stream/km, 1.4 times greater than expected (Figure 3-5).

Pooled-sexes—During the denning season, both top single-sex models were within 0.6 ΔAICc units and accounted for 85% of the model weight (Table 3-2). Adjusted variable importance weights were nearly identical for RWHR5-1km, RWHRmd-750m, and stream density-750m (Table 3-4). Effect sizes were overall similar to those from the single-sex models, but importantly the effect sizes for RWHR5-1km and RWHRmd-750m were nearly equal, suggesting that both habitat covariates have the same effect on the density of both male and female marten home ranges during the denning season. In addition, the size of the remnant habitat patch at ski areas had a similar variable importance weight as in the female only analysis, however the relationship changed from a positive effect of increasing patch size on density in the female-only analysis to a negative effect of increasing patch size on density for the combined male and female analysis (Table 3-4).

Influence of Habitat on Density in the Non-denning Season

Males—During the non-denning season none of the habitat covariates we evaluated explained the density of males better than the null model, suggesting either there are much weaker relationships to habitat conditions we evaluated during the non-denning versus denning seasons or that alternative resources we did not measure are important in the non-denning season. Fourteen state models were in the 95% confidence set for males in winter and 6 were highly competing and were within <2 ΔAICc units and had 10-17% of model weight (Table 3-2). The top state model was the null model suggesting that males were equally using the major habitat types, size classes, canopy cover classes, and remnant patch sizes in proportion to their availability across the study areas during the non-denning season. The habitat covariates in the highly competing models included negative responses of male density to areas with sparse tree cover (TCOV20-750m) , patch size, and operations areas at ski areas, This model also had a positive relationship between male density and the most widespread size class of mesic forest types (RWHR4-750m).

Females—Similar to males the null model was most supported in explaining density during the non-denning season, suggesting either much weaker relationships between the habitat characteristics we measured or that alternative resources we did not measure more influence density during the non-denning season. Six state models were in the 95% confidence set for females in winter and the top model had 74% of w_i and was >12 times more likely than the next candidate model (Table 3-2).

Pooled Sexes—After pooling for both sexes, no habitat covariates collectively explained density in the non-denning season. Three models were in the 95% confidence set and the top

model (null for density) had 91% of the w_i (Table 3-2). There was little difference between the pooled and un-pooled results during the non-denning season, supporting our predictions that resource selection will be both more generalized and will differ least between the sexes during the non-denning season.

DISCUSSION

We found that marten density was affected by habitat characteristics and fragmentation from ski areas, but that these effects differed by season and sex. Consistent with our third prediction, both sexes of martens selected for a narrower range of habitat conditions during the denning season. Forest structural conditions and streams, measured at the home range scale (1,000 m radius), had strong effects on marten density during the denning season, but not during the non-denning season.

We hypothesized that this seasonal difference in the influence of habitat on density is likely influenced by 3 factors: 1) changes in prey availability between the two seasons 2) recruitment of dispersing young of the year into the population and 3) kit-rearing activities of females during the denning season. The denning season is coincident with the peak in prey resources, when all prey species are present and most of them are producing young. During the non-denning season prey resources decline as migration (non-resident birds), hibernation (ground-dwelling sciurids: *Tamias* sp., *Spermophilus lateralis*) and the formation of a deep snow pack reduces access to fossorial prey (e.g., Montane gophers [*Thomomys monticola*] and moles [*Scapanus* sp.]). In response to this seasonal change in prey resource availability, martens prey on fewer taxa and shift their foraging activity to better overlap with the available prey (Zielinski et al. 1983). However, when prey resources are less dense, predators must forage more widely and perhaps in

other habitat types, a response that has been exhibited by martens elsewhere (Thompson and Colgan 1987). In our prior analysis (Slauson et al. 2017) and here we found that marten movement was approximately 2-6 times greater in the non-denning season compared to the denning season (Table 3-4) and we attribute this seasonal change in large part to an increase in the area individuals are using for foraging in the winter portion of the non-denning season.

During the non-denning season dispersing young of the year are present and are searching for areas to establish home ranges. Numerically, marten populations are at their greatest during this period, with some individuals provisionally occupying habitat as they disperse, while other juveniles do not survive. Our previous estimates of occupancy in habitat outside of ski operations areas was 88% in the non-denning season versus 29-62% in these same areas during the denning season (Slauson et al. 2017). The combination of increasing the extent of foraging by residents and presence of dispersing young means that habitat use, expressed across all martens in the population, in the non-denning season is likely to be most extensive and most general (Zielinski et al. 2015).

Our second prediction was that female density was influenced by a narrower range of habitat conditions than male density during the denning season, the period of the year when resource requirements of each sex are the most disparate. This was highly supported. Densities of both sexes were influenced by forest structural conditions and stream density, however females selectively used a narrower range of stream densities and selected for larger amounts of the largest tree-size class (WHR size 5) of mesic forest vegetation types (Figure 3-3). Although both male and female top model sets included largest tree-size class of mesic forest vegetation types at the 1-km scale, for males this variable had a nearly equivalent effect size to the much more

widely distributed combination of medium (WHR size 4) and large tree-size classes of mesic forest types (RWHRmd) measured at the 750m scale.

Resource requirements are most dissimilar between the sexes during the denning season. However, the mating season overlaps with the denning season. To have the best opportunity for mating and siring young, males compete for home ranges that overlap adult females (Powell 1994). We expected that this overlap would result in some homogenization of habitat selection between the sexes during the denning season. We didn't see homogenization because males overlapping adult female home ranges used a broader range of habitat conditions and roughly half of the males we captured did not overlap female home ranges. The forest structural conditions best explaining male density, the amount of mesic forest types in size class 4 and 5 (RWHRmd), is weakly correlated with the conditions best explaining female density, the amount of mesic forest types in size class 5 (RWHR5) ($r^2 = 0.25$). Furthermore, RWHRmd is far more common—occurring in 68% of the study areas—whereas RWHR5 is uncommon—occurring in 24% of the study areas. Without the need to find suitable den structures or find the additional prey resources to raise kits, males can utilize a broader range of habitat than females and RWHRmd appears to represent this range of habitat suitable for males during the denning season. The majority of actively denning females (72%) had ≥ 40 ha of RWHR5 within 1-km of their estimated home range center, with the strength of selection increasing as the amount of RWHR5 increases (Figure 3-3). In sum, the best female model differed from the best male model by identifying a narrower range of habitat conditions. The use of sex-specific models allows for the identification of habitat conditions most important for supporting reproduction and they can be used to emphasize the importance of these limited conditions for management and conservation.

Pooling introduces the additional issue of unequal sample sizes for males and females. The number of martens captured during the denning season was nearly 2:1 (63M:33F) and the number of overall captures was >3:1 (456M:131F). The overwhelming influence of males in the pooled-sex model reduced the statistical importance of the amount of RWHR5 at the 1-km scale, and switched the relationship of increasing patch size at ski areas from positive in the female-only models to negative in the pooled-sex models. The end result is that the pooled sex model gives a misleading view of the amount, location and composition of suitable denning habitat. The female denning season model identifies that suitable denning habitat occurs in < 20% of the study area and occurs in the largest residual patches at ski areas while the pooled sex model suggests suitable habitat during the denning season is much more widespread—> 60% of the study area—and is not associated with large patch sizes.

Denning habitat is composed of two critical resources: suitable denning structures and abundant prey. Martens are obligate cavity users for denning, most often requiring cavities in large diameter live and dead trees to give birth to and raise young (reviewed in Thompson et al. 2012), and these structures may require more than two centuries to develop (Ruggiero et al. 1998). During the denning season, females were most selective for the largest size class of mesic forest habitat where the availability of these types of structures for denning is greatest (e.g., North et al. 2010). While suitable denning structures for martens are clearly an important component of denning habitat, less attention has been given to the habitat conditions providing abundant prey during the denning season. Pearson and Ruggiero (2001) found that martens used dens in habitat with the most abundant prey resources, suggesting an important relationship between the proximity of suitable den structures to abundant prey resources.

Female martens typically move kits to new dens several times over the course of the denning season, with some evidence suggesting they may use up to 10 dens over the course of a denning season (K. Slauson unpubl. data). In largely unmanaged forest habitat this number of den structures can be found in a relatively small amount of mesic forest habitat in the largest size class (e.g., North et al. 2010). However, during the denning season the quantity of forest in the largest size class was important, with females selecting for the largest patches of late-successional forest (RWHR5) habitat and against small patches (<40 ha). This suggests that RWHR5 habitat also contains the most abundant prey resources. In the Sierra Nevada, the abundances of several of the most important prey species available to females during the early portion of the denning season, including Douglas and Northern flying squirrels (Zielinski et al. 1981, K. Slauson unpubl. data), are most abundant in mesic late-successional forests (Waters and Zabel 1995, Hallet et al. 2003, Smith et al. 2003). Therefore the importance of mesic forest habitat in the largest size classes during the denning season is associated with both resource needs during the denning season: suitable den structures and abundant prey resources. This supports our third and fourth predictions that denning habitat quality (mesic forest habitat in the largest size class with abundant prey) and quantity (suitable numbers of den structures and amounts of habitat with abundant prey) are important elements of suitable denning habitat for martens.

Female marten density was best explained by RWHR5 habitat at the 1-km scale, however not all females followed this pattern. Eleven females (38%) had estimated home range centers with <29 ha of RWHR5 at the 1-km scale and appeared to respond to alternative habitat conditions s during the denning season. Seven of these 11 (64%) females denned in ≥1 year and occurred in 2 less commonly used forest types and structural conditions. Three of these 7 females used small

amounts (7-21 ha) of RWHR5 combined with large amounts of RWHRmd (108-138 ha) within 1-km and the other 4 females used large amounts of CWHR size class 4 subalpine conifer habitat (167-241 ha) with spatially extensive surface rocks and boulder piles. Spatially extensive surface rocks and bounder piles provide alternative horizontal structural complexity that can influence marten foraging efficiency (Andruskiw et al. 2008) and alternative den structures (interstitial spaces in boulder piles; Ruggiero et al. 1998) typically provided by large downed and standing trees in older forests. The characteristics of surface rock were not available in any GIS resources we were aware of and therefore we could not include it in our analysis. Finally, four of the 11 females were non-denning sub-adults, that occupied home ranges with relatively small amounts (56-86 ha) of RWHRmd or subalpine habitat with extensive surface rock cover. Although 73% of all denning females exhibited home range scale selection with large amounts of RWHR5 habitat, there are exceptions to this pattern but they tend to occur in alternative habitat types and compositions much less than expected based on their availabilities.

We previously identified two effects of ski areas on martens in the same study area: 1. martens, especially females, avoid using habitat in ski operations during winter when ski recreation activities occur 2. ski runs affect marten movement, with martens only observed moving between remnant forest patches with short crossing distances (< 20m; Slauson et al. 2017). In this study we evaluated the influence of patch size on density and hypothesized that the fragmentation of habitat into patches ranging from 1 to >100 ha would have the greatest effect on females during the denning season. Patch size only influenced female marten density during the denning season, and is consistent with our predictions that females would exhibit stronger selection for patch size during the denning season and selection for large patch sizes would be greater for females than males. We were somewhat surprised patch size did not affect

male density, however this was consistent with the overall pattern of male martens being less sensitive to stressors from ski areas, including crossing wider ski runs than females and males showing less avoidance of ski areas than females during winter (Slauson et al. in press). For males, the ultimate outcome of these behaviors, whether using smaller patches and crossing wider ski runs affects survival, has yet to be evaluated and remains an important research question to address.

Ski runs create a high contrast, structurally simplified open areas, compared to residual forest and can create isolation effects, where the use of residual forest patches depend on whether the width of the ski runs martens must cross to reach them is <13 m for females and <18 m for males (Slauson et al. 2017). Martens respond to habitat isolation in this case similarly to other species that live in highly fragmented landscapes with high contrasts between residual forest patches and altered habitats (Prugh et al. 2008). However, the patch size or area effect we observed on density was sex-specific. It affected females positively during the denning season, and negatively when males were included in the pooled-sex analysis. This suggests that habitat fragmentation can have differential effects on groups within-species, such as sex (as demonstrated here) but also potentially on age or dominance classes. Although female martens did not avoid establishing home ranges in ski areas, they required larger home ranges and positioned them to include the largest remnant forest habitat patches in ski areas, moved between patches with the shortest available distance to cross open ski runs, and included habitat outside ski areas so as to avoid habitat affected by ski recreation activities in winter (Slauson et al. 2017). Collectively, the effects on home range placement and movement from habitat alteration from ski area development and seasonal avoidance of habitat when winter ski recreation activities occur place female martens in an intermediate impact level from ski areas compared to

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other wildlife species. Complete avoidance of ski areas has been exhibited by mountain goats (*Oreamnos americanus*; Richard and Cote 2015) and spatial avoidance of areas where recreation activies occur within ski areas has been exhibited by the Capercaillie (*Tetrao urogallus*; Thiel et al. 2008).

Linking the results of habitat selection to their survival and reproduction outcomes is essential for demonstrating the importance of habitat for individual fitness and for overall population persistence (Franklin et al. 2000, Jones 2001, Aldridge and Boyce 2007). The presence of individuals alone in a forest type is no guarantee that particular forest type is positively related to habitat quality (Van Horne 1983, Pulliam 1988). In this study we found that the identification of the habitat conditions supporting reproduction by martens was only revealed by measuring sex-specific relationships to habitat during the denning season. The habitat conditions used by females were a subset of those used by males and were far more spatially limited (< 20% of study area) than the conditions males used during the denning season. The limited amount of suitable denning habitat in the study area is a likely explanation for the extremely skewed sex ratio, nearly 2:1, of males versus females. Although others have emphasized the importance of evaluating group and individual habitat selection patterns (e.g., Thomas and Taylor 1990), our results reinforce this approach. We demonstrate the importance of linking patterns of habitat selection to fitness outcomes—reproduction or survival—to provide an explicit understanding of how habitat influences the population processes critical for persistence.

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Table 3-1. Candidate resource covariates and their hypothesized relationships with marten home range centers at 3 ski areas and 3 paired control areas in the Lake Tahoe Region of California and Nevada, USA. CWHR is the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) that classifies forest vegetation types based on the dominance of tree species, size classes, and canopy cover.

Resource Covariate	Variable Name	Source GIS Dataset	Description	Hypothesized Relationship to Martens
Patch Size	PATCH	Digitized	Size of remnant forest patch in ski ops area, each pixel gets that patch's area value	Martens select the largest available remnant forest patches
Operations Area	OPS	Digitized	In or out of operations areas	Martens minimize their use of habitat in ski areas seasonally (adult females) and year-round (adult males)
Stream Density	STREAM	USGS DLG	Index of linear distance of perennial stream	Martens select habitat with streams due to its higher productivity for prey
Riparian Habitat	RIPHAB	Digitized	Amount of riparian habitat	Martens select areas with more riparian vegetation due to its higher productivity for prey
Elevation	ELEV	DEM	Elevation	Martens minimize their use of lower elevation habitat where encounters with larger-bodied predators not adapted for efficient travel in deep snow is more likely
Overstory Tree Diameter	TREEDIAM25	EVEG	Overstory tree quadratic mean diameter $\geq 20"$	Martens select for the largest tree size classes that have more den structures and prey
Total Tree Cover From Above	TREECOV20	EVEG	Total tree cover from above $\leq 20\%$	Martens avoid open and sparse tree cover habitats due to increased predation risk
Select CWHR Habitats with med-large dbh and mod-high canopy cover	RWHRmd	EVEG	LPN (4-6), RFR (4-6), WFR (4-6), SMC (4-6), SCN (size classes 4-6) with Canopy cover classes M - D	Martens select for medium and large tree size classes in mesic forest types with moderate to dense canopy cover

Select CWHR Habitats with med dbh	RWHR4	EVEG	LPN (4), RFR (4), WFR (4), SCN (3-4)	Martens select for medium tree size classes in mesic forest types with fewer potential den structures and less abundant prey
Select CWHR Habitats with large dbh	RWHR5	EVEG	LPN (5-6), RFR (5-6), WFR (5-6), SMC (5-6), SCN (size classes 5-6)	Martens select for the largest tree size classes in mesic forest types that have den structures and higher prey abundance

Table 3-2. Models in the 95% confidence set for maximum likelihood spatially-explicit capture-recapture analysis of Pacific martens during: 1. spring-summer season and 2. during the winter at 3 ski areas and 3 paired control areas in the Lake Tahoe Region of California during 2009-2011 and Nevada, USA. Symbols: detection/capture probability ($g0$), movement (σ), difference in Akaike's information criteria score (ΔAIC_c), relative model weight (wi), number of parameters in model (K). See Table 3-1 for covariate descriptions.

		Variables			Model Ranking		
Season	Model #	Capture (lambda0) / Detection (g0)	Movement(σ)	Density	ΔAIC_c	*wi*	K
Denning Season Males							
	1	Month + trap response	Month	RWHRmd-750m + Stream Density-750m	0	0.58	10
	2	Month + trap response	Month	RWHR5-1km + Stream Density-750m	1.2	0.32	10
	3	Month + trap response	Month	RWHR5-1km	4.7	0.06	9
	4	Month + trap response	Month	Stream Density-750m	6.9	0.02	9
	5	Month + trap response	Month	RHWRmd-750m	7.4	0.01	9
	8	Month + trap response	Month	Null	9.9	0	8
Denning Season Females							
	1	Month	Month	RWHR5 1-km + Stream Density 750m	0	0.51	9
	2	Month	Month	Stream Density 750m	1.7	0.22	8
	3	Month	Month	Stream Density 750m + Patch	2.2	0.17	11
	4	Month	Month	Stream Density 750m + RWHR 1km + Patch	5.0	0.04	12
	5	Month	Month	Patch	6.5	0.02	10
	7	Month	Month	Null	8.1	0	7
Denning Season Males and Females							
	1	Month + trap response	Month	RWHR5 1-km + Stream Density 750m	0.0	0.49	10
	2	Month + trap response	Month	RWHRmd-750m + Stream Density-750m	0.6	0.36	10

			RWHR5-1km + Stream Density-750m +			
3	Month + trap response	Month	Patch	2.7	0.13	11

Non-Denning Season Males

1	Transient response	Age Class	Null	0	0.17	6
2	Transient response	Age Class	Tree Cover <20% 750m	0.5	0.14	7
3	Transient response	Age Class	RWHR4 750m	0.8	0.12	7
4	Transient response	Age Class	Remnant Patch Size	0.9	0.11	7
5	Transient response	Age Class	Operations Area	1.1	0.10	7

Non-Denning Season Females

1	Constant	Treatment	Null	0	0.74	5
3	Constant	Treatment	Treatment	5.1	0.06	5
4	Constant	Treatment	RWHR4 250m	5.7	0.04	5
6	Constant	Treatment	TDIAM25 250m	6.0	0.03	5
7	Constant	Treatment	Tree Cover <20% 1-km	6.4	0.03	5
8	Constant	Treatment	RWHR5	6.9	0.02	5

Non-Denning Season Males and Females

1	Transient Response	Constant	Null	0	0.91	5
2	Operations Area	Constant	Null	5.6	0.06	6
3	Constant	Constant	Null	6.7	0.03	4

Table 3-3. Coefficients for observation sub-model parameters and derived estimates of density and effective sampling area for models in the 95% confidence set for spatially-explicit capture-recapture analysis of Pacific martens during: 1. spring-summer season and 2. during the winter at 3 ski areas and 3 paired control areas from 2009-2011 in the Lake Tahoe Region of California and Nevada, USA.

Season	Sex		Encounter Probability	Movement (σ) m	Density Martens / 10 km2	Effective Sampling Area (ha)	95% Utilization Distribution (ha)	Goodness of Fit Observed	p
Denning Season	Male								
		May	0.24 (0.06)	585 (52)	1.73 (0.30)	21,249	149.1	0.19	0.18
		June	0.14 (0.04)	456 (45)	2.46 (0.32)	14,456	93.7	0.37	0.65
		July	0.26 (0.08)	355 (50)	2.21 (0.34)	14,894	65	0.26	0.42
	Female								
		May	0.16 (0.04)	542 (88)	1.39 (0.32)	15,117	162	0.33	0.73
		June	0.15 (0.04)	301 (66)	1.25 (0.45)	8,004	58.9	0.4	0.52
		July	0.14 (0.06)	363 (96)	1.16 (0.36)	12,364	96.8	0.33	0.46
Non-Denning Season	Male		0.25 (0.05)	1501 (87)	1.22 (0.15)	22,018	881.4	0.17	0.45
							734.5		
	Female		0.20 (0.03)		0.54 (0.15)			0.19	0.45
	Ski			2,032 (87)		24,344	1528.8		
	Control			1,363 (87)		16,855	742.2		

Table 3-4. Adjusted variable important weights (wi) for habitat covariates influencing the density from the 95% confidence

set of spatial capture-recapture models for Pacific martens in the Lake Tahoe Region of California and Nevada, 2009-2011.

| Season | Sex | Variable | Adjusted wi | Odds Ratio | 95% Confidence | | Unit of Measure | Effect Sizes of Changes | |
					Lower	Upper		10-unit	20-unit
Denning Season	Male	Stream Density 750m	0.35	0.996	0.994	0.999	10 meters of stream	-3.6%	-7.2%
		RWHR-MD 750m	0.34	1.009	1.003	1.015	1- ha of habitat	9.1%	18.3%
		RWHR-5-1km	0.22	1.010	1.003	1.016	1- ha of habitat	9.7%	19.3%
	Female	Stream Density 750m	0.31	0.994	0.991	0.998	10 meters of stream	-5.6%	-11.2%
		RWHR-5-1km	0.15	1.010	1.001	1.018	1- ha of habitat	9.7%	19.4%
		Remnant Patch Size	0.10	1.051	1.017	1.087	1- ha of habitat	51.4%	102.8%
	Male & Female	Stream Density 750m	0.41	0.997	0.995	1.089	10 meters of stream	-3.2%	-6.4%
		RWHR5-1km	0.42	1.010	1.005	1.246	1- ha of habitat	9.7%	19.3%
		RWHRmd-750m	0.40	1.008	0.992	1.774	1- ha of habitat	8.4%	16.7%
		Patch	0.09	0.991	0.947	3.006	1- ha of habitat	-9.0%	-17.9%

Figure 3-1. Location of the 6 paired ski and control Pacific marten study areas 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 classification and remotely sensed data available from EVEG (updated 2010).

A. Study Area Locations

B. Study Area Habitat (top) and Tree Size Compositions (bottom)
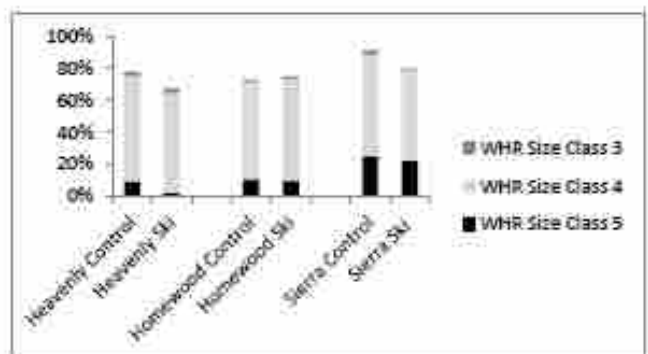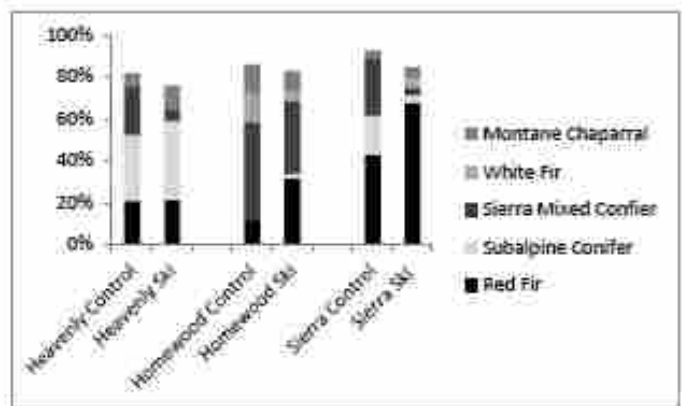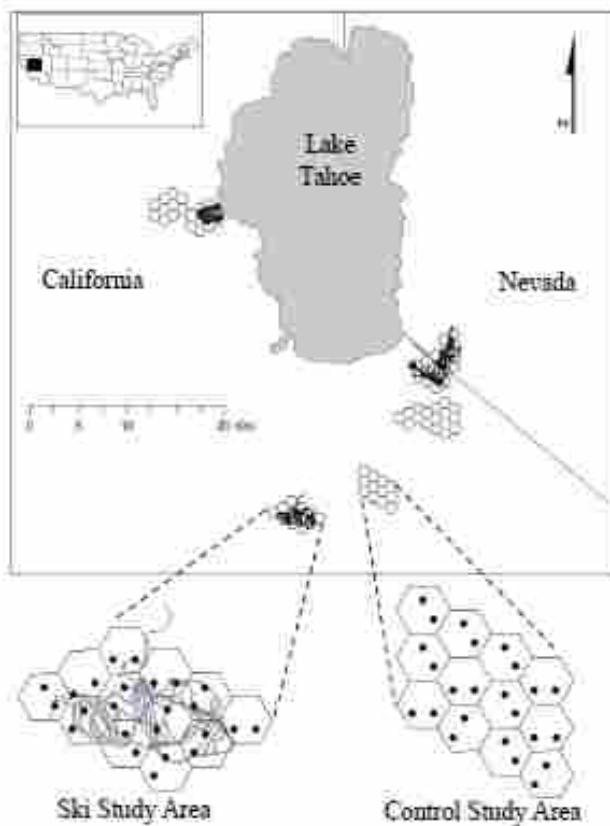
Figure 3-2. Estimated home range centers from a spatially explicit capture-recapture analysis using SECR for female Pacific Martens (*Martes caurina*) on 3 pairs of ski and control study areas in the Lake Tahoe region of California and Nevada.
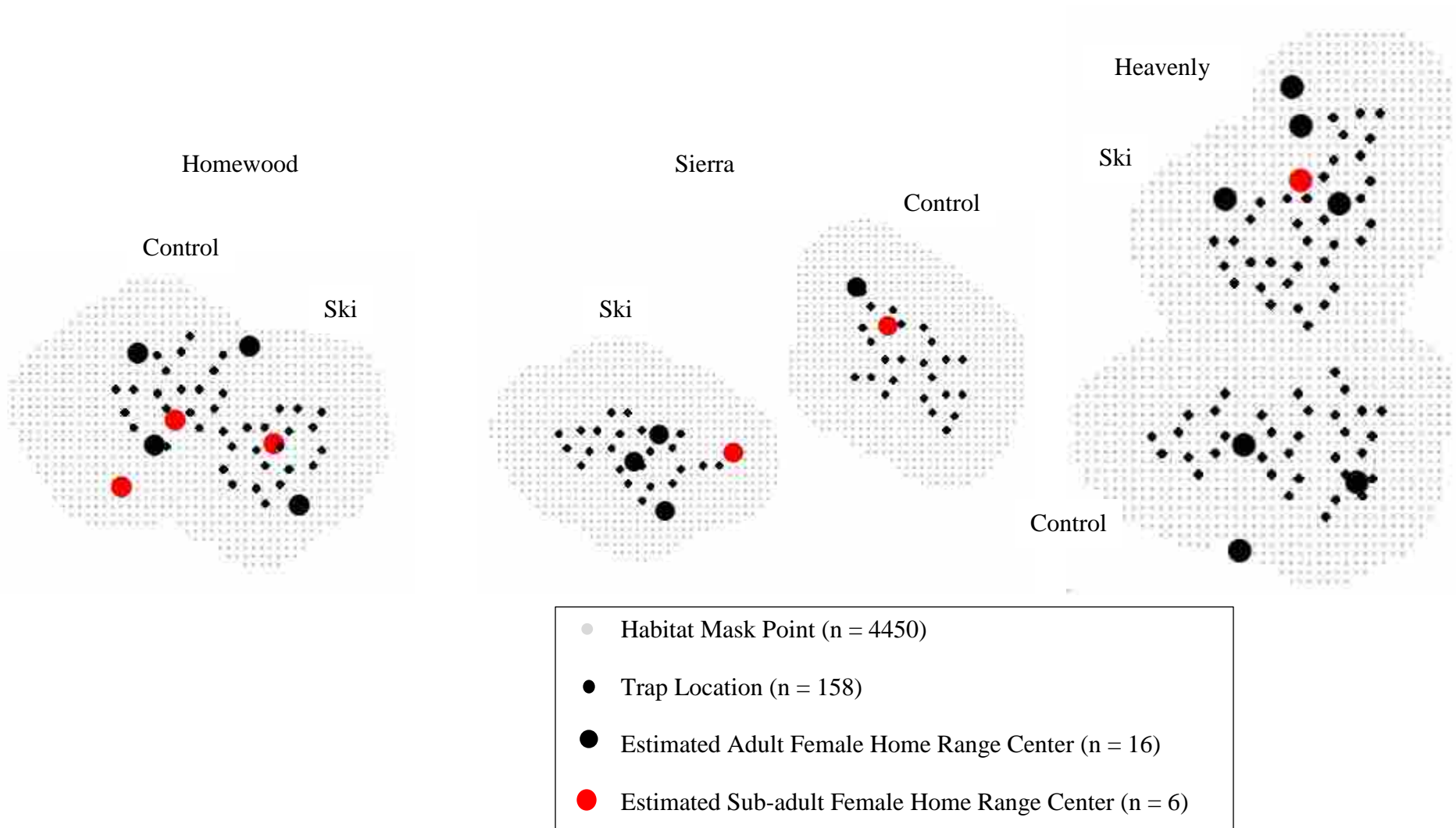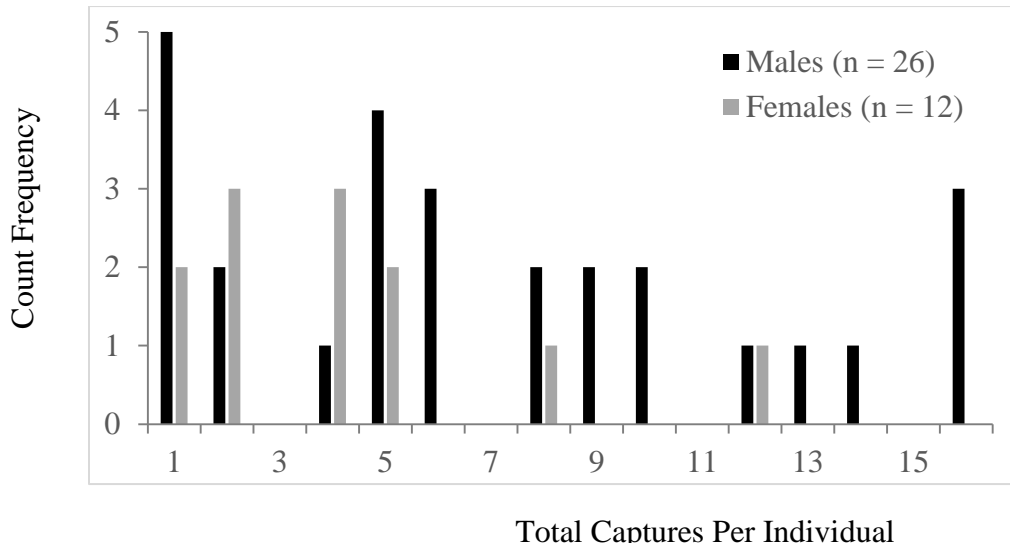
Figure 3-3. Frequency distribution of individual Pacific marten (*Martes caurina*) captures from 2009-2011 at 6 paired ski and control Pacific marten study areas in the Lake Tahoe Region of California and Nevada, USA.

A. Winter Captures at Hair Snares

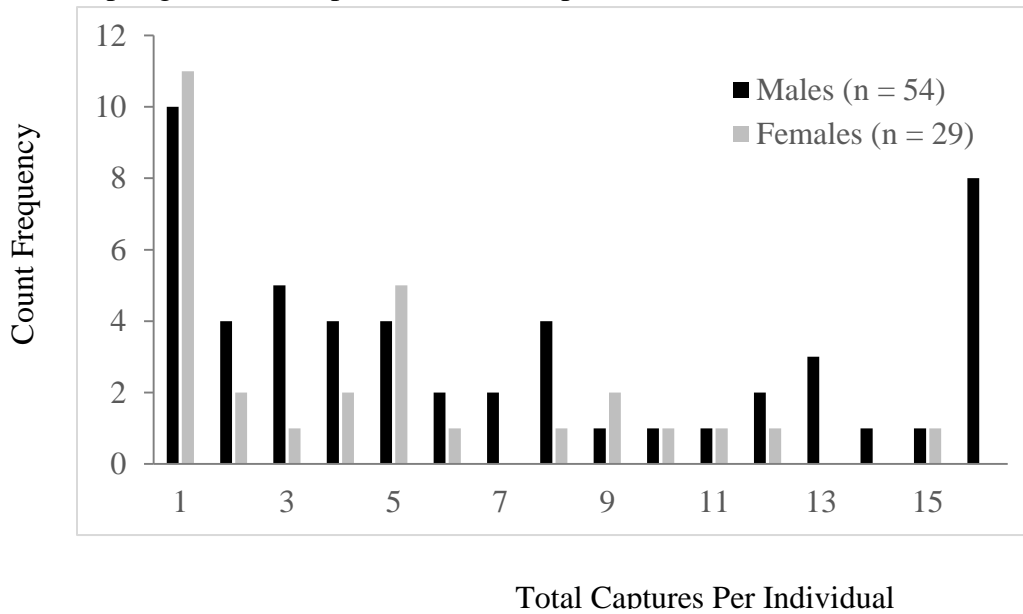B. Spring-summer Captures in Live Traps

Figure 3-4. Seasonal and sex-specific spatial scale relationships for Pacific martens (*Martes caurina*) and habitat covariates in the Lake Tahoe region of California and Nevada, 2009-2011. RWHR5 is the amount of mesic forest types in size class 5 (>24" dbh).
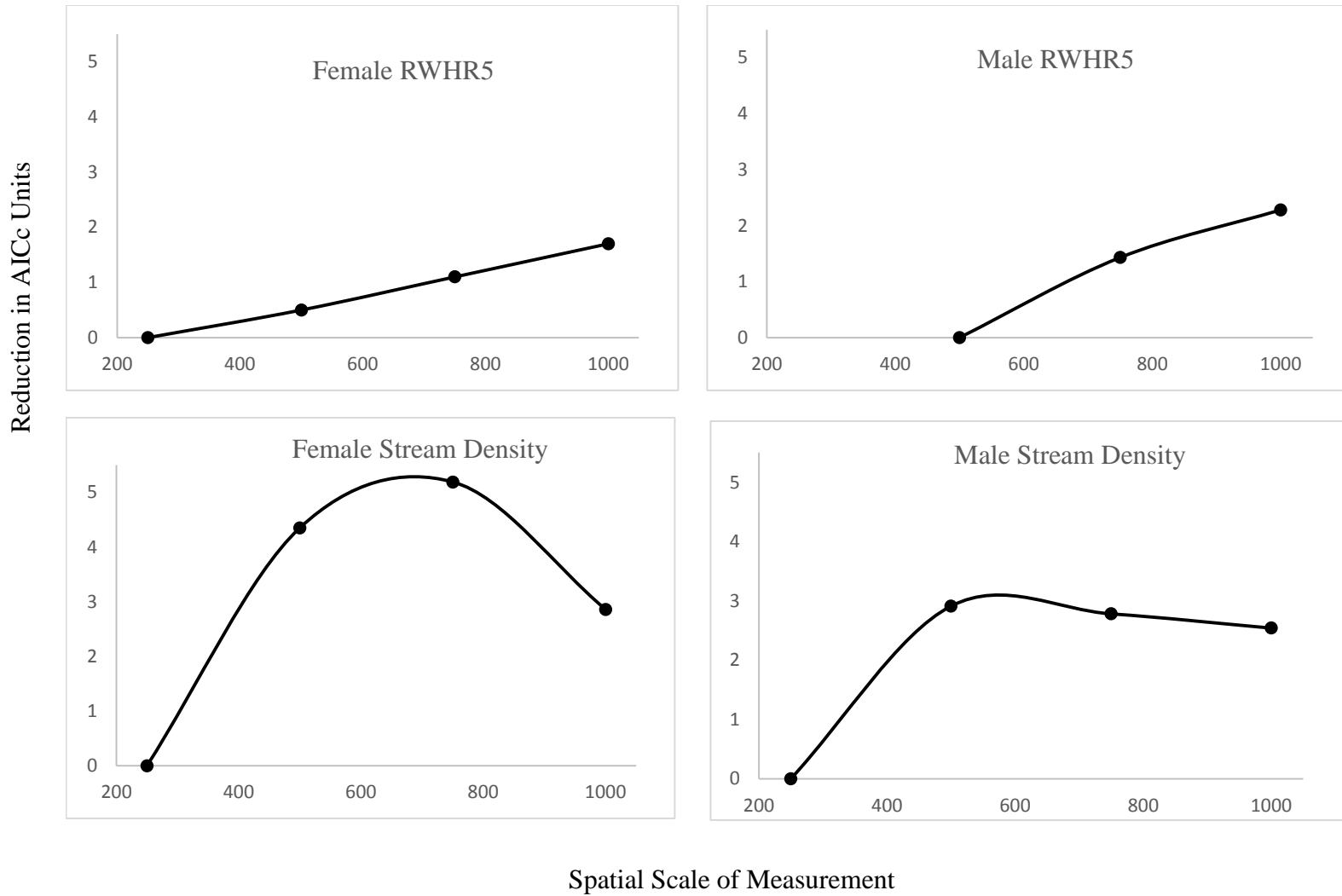
Figure 3-5. Manly's selection ratios for the most influential resource variables influencing the density of female martens during the denning season in the Lake Tahoe Region of California and Nevada, 2009-2011. Resource variables for the home range centers for males (n = 54) and females (n = 29) were compared to their availability across the study area using the 4450 points spaced at 250 m intervals in the habitat mask.
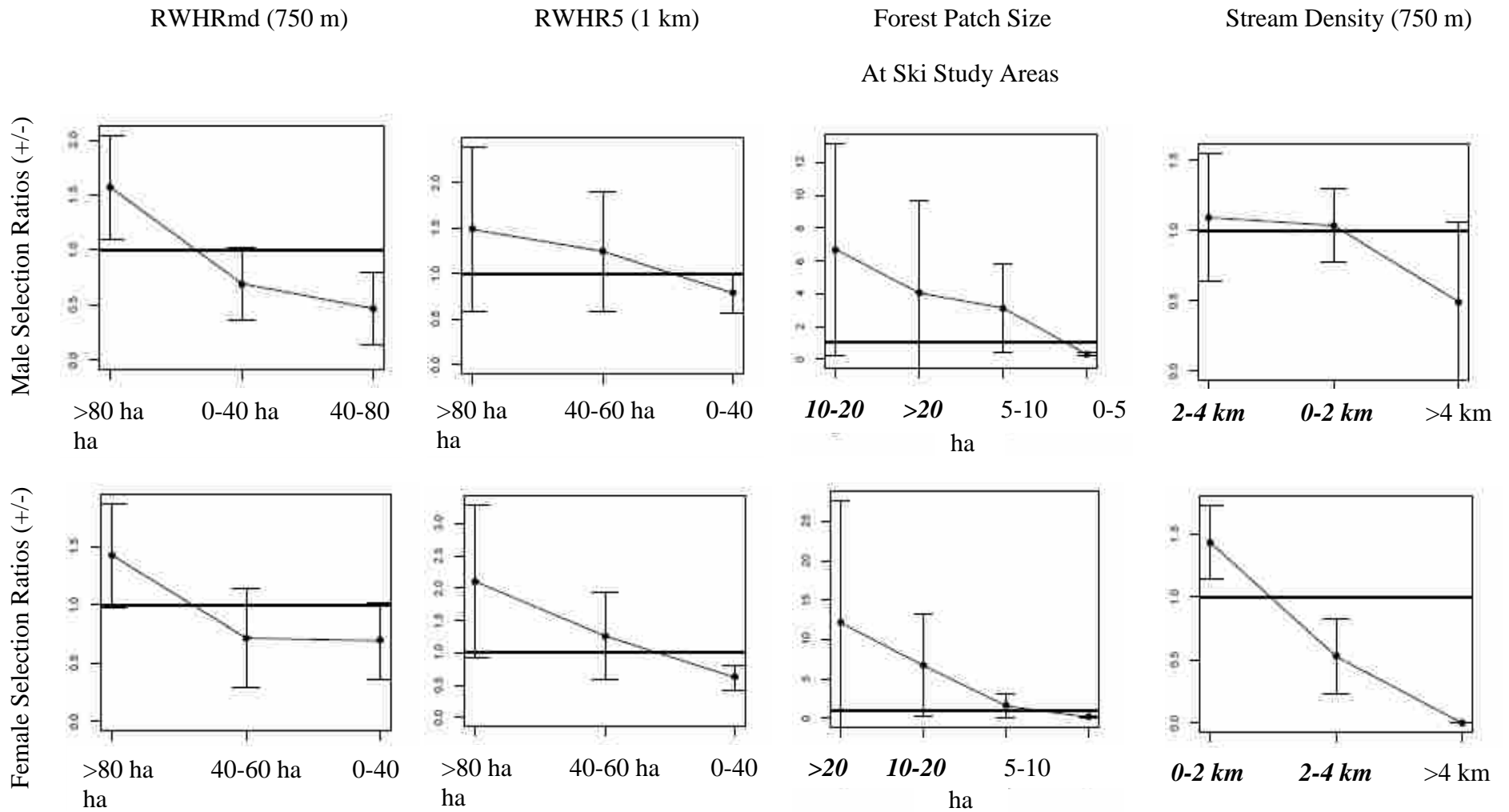
Figure 3-6. Predicted density of female Pacific martens during the denning season on 3 pairs of ski and control study areas in the Lake Tahoe region of California from 2009-2011 using spatially explicit capture-recapture analysis. The top model included the amount of California Wildlife Habitat Relationships mesic forest habitat types (red fir, white fir, Sierra mixed conifer, subalpine conifer, lodgepole pine) in size class 5 (>24" dbh) within 1-km radius of the home range center and the density of perennial streams within 750 m of the home range center.

CHAPTER 4

Pacific Marten Recruitment and Survival is Reduced at Ski Areas

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ABSTRACT

Survival and reproduction are essential for the persistence of wildlife populations and understanding how habitat and stressors affect these vital rates is needed to contribute to sound management. We investigated the effects of developed ski areas on the survival, reproduction, and recruitment of offspring of Pacific martens (*Martes caurina*) in the Lake Tahoe region of California and Nevada by comparing 3 pairs of ski and control areas. Over 3 spring-summer and 1 winter season we systematically surveyed for martens using live traps (spring-summer) and hair snares (winter) and captured a total of 96 (63M:33F) individuals. Adult male survival was lower at ski areas compared to control areas but female survival was not affected. Male survival results were consistent with the observed age structure that was skewed towards males aged 1-2

years old (88%) in ski operations areas compared to 64% in controls. Estimates of seniority, the recruitment probability of being previously in the population, for sub-adults of both sexes were lower at ski areas, suggesting recruitment of this age class to the adult age class may be reduced. We also used genetic data to identify if the parents of yearling martens occurred in each study population. Fifty-three of the 96 yearlings were born from 2008-2010. Parentage assignments showed 42% of these yearlings had one or more parent identified as occurring in our study population. Although ski areas had a few more breeding age females, 14 at ski areas versus 10 at controls, more female denning attempts occurred at ski areas, 25 at ski versus 10 at controls. Despite ski areas supporting more breeding age females and 1.5 times the breeding attempts, more immigrant offspring were captured at ski areas, 24 versus 17 at controls. Despite the higher number of breeding attempts at ski areas versus controls, there were only small differences between the number of local recruits (6 at ski versus 10 at controls) or emigrants (3 at ski versus 5 at controls) to other study areas. Overall, the per capita female recruitment rate of offspring to the larger population was >4 times higher at controls (1.5) than ski areas (0.36). Martens persist at ski areas, but they do so with reduced male survival and reduced recruitment rates of offspring. Adult and juvenile survival are the most influential demographic rates on population growth. Ski areas may represent ecological traps by continuing to support habitat cues that attract martens, but reduce individual fitness that can result in reduced population growth.

Key words: Pacific marten, *Martes caurina*, recreation, ski area, fragmentation, survival, parentage, recruitment.

INTRODUCTION

Wildlife population persistence requires that individuals survive and new individuals are produced and recruited at rates meeting or exceeding the rate of mortality and emigration. In many wildlife species, habitat resources and stressors influencing these vital rates are not uniformly distributed in space or time. This creates variation in vital rates that vary depending on how habitat quality or stressor intensity affects survival and reproduction of individual populations (e.g., Aldredge and Boyce 2007). Source-sink dynamics can arise when local populations exhibit mortality rates that exceed birth rates (sinks) and are only able to remain occupied because of immigration from elsewhere in the population where births exceed mortalities (sources) (Pulliam 1988).

Assessing the overall contribution of individuals or local populations to the overall species remains challenging to demonstrate empirically because of the challenges in accurately estimating local survival and recruitment rates as well as dispersal rates of young of the year (Runge et al. 2006). Survival estimation is typically done using capture-recapture, however this method is unable to disentangle true survival from emigration, yielding estimates of apparent survival (White and Burnham 1999). Recent advancements in methods to separate the processes of survival and emigration (Schaub et al. 2014) can be used to avoid this problem. Estimating recruitment rates requires quantification of immigration and emigration, which can be accomplished by estimating the number of young produced in an area of interest and the number of these young recruited into the larger population. Marking of young prior to dispersal is one alternative for quantifying emigration to the broader population however this is impractical for many species. Genetic parentage assignment provides a means to identify or rule out individuals as parents of offspring, and therefore provides an alternative for quantifying rates of emigration and immigration.

To determine where offspring originated, the identity, and spatial locations of the parents of each offspring must be identified. Parent-offspring dyads can be identified with a high degree of certainty by evaluating a sufficient number of variable genetic loci such as microsatellites (e.g., Blouin et al. 1996). Palsbøll (1999) proposed that recruitment rates could be quantified by using genetic parentage assignments to compare the number of parent-offspring dyads present in a population with overlapping generations. The number of parent-offspring dyads present are a function of the degree of immigration from other populations versus the level of within population recruitment. A high number of parent-offspring dyads should be present in a self-sustaining (source) population compared to few in a population with high proportions of recruitment from immigration (sinks). Peery et al. (2008) used the distribution of close relatives to quantify the impact of migration and identify sink populations in the marbled murrelet (*Brachyramphos marmoratus*). However, to completely evaluate the contribution of areas within a population to recruitment, the contribution of emigrants from that area to the broader population must also be quantified (Runge et al. 2006).

The combination of habitat fragmentation from development and winter recreation activity has been shown to affect the movement and seasonal habitat use of Pacific martens (*Martes caurina*; Slauson et al. 2017), but it is unclear if these impacts also influence vital rates. We evaluated the effects of ski area development on survival, reproduction, and recruitment rates of offspring for Pacific martens by comparing 3 pairs of ski and control study areas in the Lake Tahoe region of California and Nevada. Ski area development results in the fragmentation of forest habitat from the creation of networks of ski runs and roads, leaving residual forest patches typically only accessible by crossing open ski runs and roads. Martens have been found to use residual forest patches in ski areas, but do so by moving between forest patches with the shortest

available crossing distances (<15 m for females and <18 m for males; Slauson et al. 2017).
During winter, when ski recreations activities were present, martens reduced their use of habitat
in ski operations areas and female density was <50% of that in control areas (Slauson et al. in
2017). However, once ski recreation activities ceased martens, including denning females,
resumed their use of habitat in ski areas.

Adult and juvenile survival are the most influential vital rates on marten population growth
(Buskirk et al. 2012). The most important factor influencing survival is predation (McCann et al.
2010), with prey availability (Thompson 1987), disease, and trapping (Hodgeman et al. 1994)
playing lesser roles. Large-bodied predators most often kill martens in areas where escape cover,
vertical tree boles and overhead cover, have been reduced by forest management (e.g., Ellis
1997). The creation of ski runs results in the removal of most or all escape cover. If martens are
more susceptible to predation when crossing runs, their overall survival rates at ski areas can be
diminished.

In martens, the production and recruitment of young into the population is typically
completed over a single year. Martens are polygamous, with females solely responsible for
raising of kits. Females are able to give birth to their first litters at 2 years of age. Parturition
occurs in early spring, mid-March to early April (Mead 1994), and juvenile martens disperse
from their natal territory in late summer and early fall when they are 4–6 months of age (Johnson
2008). Dispersal can take > 4 months to complete (Johnson 2008), therefore the majority of
juvenile recruitment from dispersal should be completed by the following spring. While
dispersal distances of 70-214 km have been reported for martens (Fecske and Jenks 2002,
Johnson et al. 2009), most studies have found that the majority of juvenile martens in both
managed and unmanaged forest landscapes dispersed short distances (≤5 km, Broquet et al.

2006; <15 km, Phillips 1994; $\bar{x} = 15.5$ km, Pauli et al. 2012). In addition, Johnson et al. (2009)

found that mortality risk increased with natal dispersal distance and that the majority of juveniles

surviving to adulthood dispersed <15km in both managed and unmanaged forest landscapes.

The overall objective of this study is to determine if developed ski areas affect the survival,

reproduction, and recruitment rates of Pacific martens. To evaluate the effects of ski areas we

systematically sampled marten populations and collected DNA from all individuals at 3 pairs of

ski and control study areas over 3.5 years. We used a genetic capture-mark-recapture analysis to

estimate survival. Subsequently we used the genotypes to evaluate paternity, natal dispersal, and

recruitment of dispersers into each population. Our hypotheses were that survival and

recruitment would be lower in ski areas due to increased predation risk.

METHODS

Study Design

The study was conducted in the Sierra Nevada mountains of California and Nevada, on the Lake

Tahoe Basin Management Unit and El Dorado National Forest, both administered by the U.S.

Forest Service. Elevations ranged from about 2000 – 3000 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*).

Our study design compared 3 pairs of treatment (Heavenly, Sierra-At-Tahoe, and Homewood

ski resorts) and control study areas (Figure 4-1). Controls were nearby areas that best matched

the topographic (elevation and 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

using digital elevation models and remotely sensed existing vegetation data (USDA, Pacific Southwest Region, Remote Sensing Lab, Updated Feb 2010) based on California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) habitat types in a geographic information system (GIS). 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 (Figure 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) and used historical (1940-1969) aerial photography to identify the type of vegetation (e.g., forest, wet meadow) that occurred in each developed area prior to development. Lastly, we used current habitat conditions in adjacent undeveloped areas (with the same pre-development habitat type) to identify the structural characteristics, tree size class, that would be present if development had not occurred.

Field Methods

From 2009-2011 we sampled the 6 study areas using a combination of live capture during each of the three spring-summer (May-July) seasons and non-invasive hair snares for a single season during the winter of 2009. We sampled martens using systematic survey grids that covered the ski operations areas and included areas outside the ski operations areas to include individual martens that may either use habitat in ski operations areas seasonally or only overlap the edges of ski operations areas (Figure 4-1). 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 established 500 m apart in the center of each

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grid cell where live traps (spring-summer) and hair snares (winter) were used to detect or capture

martens, respectively. The number of stations sampled at each ski and control pair was

proportional to the size of 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 (Figure 4-1).

Capture, Aging, and Reproductive Status

In the spring-summer seasons, we trapped martens at each station using a single wire

mesh live trap (Tomahawk Co, Tomahawk, WI, USA, Model #105), modified with plywood

cubby boxes on the ends to provide security for captured animals. Traps were baited with

chicken and a sponge soaked with olfactory lure (Gusto, Minnesota Trapline Products, Pennock,

MN) was tied to the nearest tree branch. Once established, traps were checked at least once daily

for 13-15 consecutive days. Martens were chemically immobilized and examined to determine

their sex and to be marked with a uniquely numbered passive integrated transponder (PIT) tags

for individual identification (12.5mm; Biomark, Boise, ID). Use of PIT tags facilitated scanning

and individual identification of martens in traps, allowing for immediate release of recaptured

martens. Martens were captured and processed using methods approved by the California

Department of Fish (SC-4683) and Wildlife and Nevada Department of Wildlife (S-31799)

Scientific Collecting Permit Programs.

To age most individuals, one upper first premolar was removed for cementum annuli

analysis to determine age (Poole et al. 1994). Teeth were sent to Matson's Laboratory

(Milltown, MT) to be aged. For individuals missing all pre-molars, or when tooth samples were

too poor to enable accurate age estimation, the combined tooth wear of incisors, canines, and

molars was used to estimate an age class based on its similarity to known age individuals of the

same sex. We identified 53 yearling offspring (36M:17F) born in 2008 (n = 17), 2009 (n = 19), and 2010 (n = 17). We collected DNA samples from blood for captured individuals during tooth extractions by dabbing Whatman^{TM} 903 Sample Collection Cards on the tooth extraction site on the gums. During the winter, we collected hair samples from individuals detected at baited hair snares. Reproductive status could only be determined for females during captures. Each year we determined the denning status for each female based on the presence or absence of enlarged teats, presence of suckling rings, and whether teats expressed milk.

Survival Estimation

To estimate survival, we used the robust-design mark-recapture analysis to estimate survival in program MARK (version 8.1, White and Burnham 1999). To estimate the age-specific recruitment rates for sub-adult martens to breeding age we selected the Pradel model for seniority that estimates the probability an individual is alive and in the population at time *i* that it was also alive and in the population at time *i*-1;. Pradel models do not allow for age effects, so we created 8 groups to represent all possible combination of age-at-first capture (sub-adult < 2 years or adult ≥2 years), sex, and treatment (ski and control) combinations. Robust design models are a combination of the Cormack-Jolly-Seber live recapture model and the closed capture model (Kendall et al. 1995, 1997). The robust-design models identify primary sampling periods where population gains, via births, immigration, and losses, via death and emigration, can occur and shorter secondary 'encounter' periods where the study population is effectively closed to gains and losses. Our primary sampling periods occurred over three 12 month (spring 2009-2011) and one 3 month (winter 2009) periods while our secondary encounter periods spanned three 15- (spring) and one 30-day period (winter 2009). The encounter histories for each individual consisted of 54 encounter occasions. Because we suspected both heterogeneity

in initial capture (c) and recapture probability (p) from season, sex, and possibly age we selected the full heterogeneity p_i, p, and c closed capture version of the Pradel survival and seniority model.

Candidate models were built and evaluated, hierarchically. First, candidate sub-models were developed to evaluate season, sex, age, treatment, and time influences on initial capture (p) and recapture (c) probability. Then, the top model from this first modeling step was used to evaluate our alternative hypotheses on the parameters of main interest, survival and seniority. We compared alternative models using each model's AICc score to calculate ΔAIC and their Akaike weights (w_i) (Burnham and Anderson 2002). Model fit for capture-recapture models is typically done by calculating $ĉ$, however this calculation is not currently possible for Pradel models (White and Garrott 1999).

Age Structure

We summarized the age structure for each sex by treatment, ski and control areas, by counting the total number of individuals captured in each age class during the spring-summer season of each year from 2009-2011. In addition, we also summarized the age structure for martens with the majority of their capture locations (>33%) in the ski operations area at each ski study area. Age structure can be a useful indicator of survival, but it can also be misleading when populations are not stable or do not exhibit stable age distributions. We used age structure both descriptively and as a secondary line of evidence for comparing with our survival analysis estimates. We compared age class proportions using a z-tests.

Genetic Analysis

We extracted DNA from blood and hair samples using the standard methods (e.g., Tucker et al. 2012, Juarez et al. 2015). We used primers for 16 microsatellite loci: 6 of which were previously developed for martens (Ma1, Ma2, Ma3, Ma8, Ma18, Ma19), 6 that were developed for wolverine (*Gulo gulo*; Gg3, Gg7, Gg42, Ggu234, Ggu216, Gg443), and single markers for fisher (*Pekania pennanti*; Mp197), North American river otter (*Lutra Canadensis*; Lut604), American mink (*Mustela vison*; Mvi1321), and ermine (*Mustela erminea*; Mer04). These primers were used with the polymerase chain reaction (PCR) to amplify regions of the genome similar to Tucker et al. (2014). The PCR reaction was conducted in a volume of 10 ul which contained 1.0 ml DNA, 1x reaction buffer (Applied Biosystems, Foster City, CA, USA), 2.0 mM $MgCl_2$, 200 mM of each dNTP, 1 mM reverse primer, 1 mM dye-labeled forward primer, 1.5 mg/ml BSA, and 1U Taq polymerase (Applied Biosystems). The PCR profile was 94° C/5 min, ([94° C/1 min, 55° C/1 min, 72°C/30 s] x 36 cycles). The resultant products were visualized on a LI-COR DNA analyzer (LI-COR Biotechnology).We used DROPOUT (McKelvey and Schwartz 2005) as implemented in Schwartz et al. (2006) and MICROCHECKER v2.2.3 (Van Oosterhout et al. 2004) to detect genotyping errors. If the genotype at a locus differed in one or more of these amplifications or an inconsistency was determined by using our computer screens, we conducted an additional round of three PCR amplifications for the samples under question. If a consistent genotype could not be determined after multiple amplifications then that locus was removed from the dataset. Samples that amplified at fewer than 12 loci were removed from further analysis.

Prior to using microsatellite data for parentage analysis, we conducted standard diagnostics on each loci to determine if they could reliably be used for this analysis. Each microsatellite locus was tested for deviation from Hardy–Weinberg proportions (HWP) and

linkage disequilibrium (LD) in GenAlEx 6.5 (Peakall and Smouse 2012) within each population, between pairs of loci, and at the global level. We measured the level of genetic diversity and variation within and among putative populations at neutral microsatellite loci by calculating the mean number of alleles per locus (A), allelic richness (AR) per population, and mean observed and expected heterozygosities (H_o and H_e), and the fixation index (F_{IS}) as implemented in GenAlEx 6.5 (Paekall and Smouse 2012).

Paternity and Maternity

We assessed parentage using a combination of genetic and demographic exclusion and likelihood-based inference methods. First, we excluding any potential parent by the absence of shared alleles at ≥ 2 loci. We then evaluated remaining candidate parents using the combination of their age and reproductive status. To be considered further as candidate mothers, female martens had to be ≥ 2 years of age the year an offspring was born because sexual maturity occurs at 1 year of age and with delayed implantation following mating, leading to females typically giving birth to their first litters at age 2. Although we identified 20% of yearlings with evidence of lactation, it is rare and yearling females are not often successful in weaning kits as older females. Furthermore, considering yearlings as candidate mothers would likely lead to higher mis-identification rates of siblings as mothers rather than true mothers. To be considered as candidate fathers, males also had to be ≥ 2 years of age when an offspring was born, ensuring that they too had reached sexual maturity (1 year of age) during the year of offspring inception. Finally, denning status, not lactating during year of offspring birth for any candidate mother, was used for exclusion.

Following the exclusion process, we used program COLONY (version 2.0.5.9, Wang 2008) for likelihood-based inference to identify parents when >1 candidate remained and as a

secondary means to confirm single parents identified from exclusion alone. In cases where either the identification of parents differed between exclusion and COLONY or multiple candidate parents remained, we also considered the spatial locations of: 1) candidate parents relative to offspring capture locations and used exclusion by distance when candidate parents that were >2 times the typical dispersal distance (>30 km) and 2) we considered the spatial location for one or both parents and excluded individual parents in candidate clusters by distance when potential parents would not have been spatially co-located ($<$ 5 km apart or within the same study area) during the year when mating would have occurred. This latter criterion is justified due to the observed low rate of adult dispersal (5% overall) during the course this study. In cases where parentage assignments differed between the exclusion process and COLONY, we used the assignment from the exclusion process.

Comparing Recruitment Rates Among Ski and Control Study Areas

To compare recruitment rates we needed to identify whether each offspring captured was the result of local recruitment or immigration from outside the focal study area. Furthermore, we needed to identify which immigrants represented emigrants from another one of our study areas. For each offspring, we identified if the parents occurred in the study area it was captured in (local recruit), is the parent occurred in another study area than where it was captured (emigrant/immigrant), or if the parents were not in the dataset (immigrant). A shortcoming of this type of analysis occurs when potential parents are not among the captured sample of individuals. However, our analysis of capture probability for individuals using our sampling protocol yielded very high individual capture probabilities for both sexes ($>$ 0.9). Thus our sampling design provided both a high density of trap locations and sufficient duration to likely capture all resident individuals in each study area at least once. Offspring were considered local

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recruits if both parents, or only the mother, was located in the study area of capture. We did not

consider the presence of only the father of offspring sufficient to consider them produced from

that study area because males have much larger home ranges than females and males can leave

their home ranges during the mating season, thus were likely to mate with females occurring

outside our study areas. Offspring were classified as emigrants from a focal study area if both

parents or only their mother was located in the focal study area and the offspring was captured in

another study area. Offspring were identified as immigrants to a focal study area if their parents

were in other study areas or the parents were not in the dataset. Offspring captured in >1 study

area were classified independently for each study area in which they were captured. We

compared the numbers of offspring identified as local recruits, immigrants, and emigrants

between ski and control study areas using paired t-tests, respectively. We also estimated the

female per capita recruitment rates of offspring to the overall population between ski areas and

controls using the following equation:

Total number of offspring recruited / total denning attempts

Where a denning attempt is defined as a single female with evidence of lactation in a single

denning season. For statistical comparison of these rates we used a z-test for two population

proportions and calculated the recruitment proportion for ski and control areas as:

Total number of offspring recruited / (total denning attempts * 2 offspring)

where the average number of offspring produced per denning attempt (n = 2) was derived from a

combination of published range-wide estimates (Bull and Heater 2001, Buskirk et al. 2012) and

unpublished estimates local to California (K. Slauson unpubl data). Finally, we estimated

dispersal distances for all emigrants by measuring the straight-line distance from the centroid of

their mother's capture locations and the centroid of the offspring's capture locations.

RESULTS

Captures

Over the 4 primary sampling periods, we captured 96 individual martens (63M:33F), 51 on ski

areas (33M:18F) and 49 on control areas (34M:15F), a total of 587 times. No marten mortalities

or injuries due to live trapping or processing occurred. During spring-summer live trapping we

captured males an average of 8.4 times (SE = 1.2) and females an average of 4.5 times (SE =

0.7). Initial captures (66% M:34%F) and recaptures (78%M:22%F) were male-biased. During

the spring-summer martens were captured at all 6 study areas, with between 19 – 25 individuals

captured at ski areas and 17- 21 individual captured at control areas annually.

   During the single winter season, we collected 256 marten hair samples, representing 38

unique individuals (26M, 12F), and 24 (63%; 16M:8F) of these individuals were recaptured in

one or more of the following spring-summer seasons. Overall, hair 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 1 brush per snare, unless DNA amplification failed.

Thirty-three of 38 individuals (87%) were represented by >1 hair sample and individuals were

captured an average of 7.5 times (SE = 1.1) for males and 4.2 times (SE = 0.9) for females.

During winter, martens were detected on all 6 study areas, 23 individuals (14M:9F) at control

areas and 17 individuals (13M:4F) at ski areas.

Survival Estimation

   We developed a total of 31 candidate models, 16 alternative sub-models for capture and

recapture probability were run first. Then the top capture and recapture probability sub-model

was used to develop 15 alternative models for survival and seniority (Table 4-1). The overall top ranked model had the majority of support of the model weights ($w_i = 0.80$) and all other candidate models had ΔAICc scores >7 (Table 4-1). The top ranked model for survival and seniority had a year and month interaction where capture probability was conditional on the month (declining from May, June, to July) in the spring and variable over time in the winter (Table 4-2). Capture probability was best modeled by season (winter and spring-summer), where during winter at hair snares probability of capture for both males and females varied from 0.04 to 0.74 during the secondary encounter period. During the spring-summer, capture probability in live traps for both sexes was most influenced by month (May to July) and daily capture probabilities varied from 0.06 (0.02) to 0.17(0.03).

Recapture probabilities differed by sex, with males having greater recapture probabilities in both winter (c = 0.51, SE = 0.04) and spring-summer (c = 0.36, SE = 0.02) compared to females (winter c = 0.35, SE = 0.06, spring-summer c= 0.19, SE = 0.02). Apparent survival was best modeled for males by age class and treatment, with adult male apparent survival rates significantly lower at ski areas than at controls (Table 4-2). Female survival rates differed little between ski areas and controls and were best estimated by age class by combining treatments (Table 4-2). Seniority estimates were best estimated by age class, with both sub-adult male and female martens showing lower seniority probabilities at ski areas, however due to large variances estimates the confidence intervals for these estimates between sub-adults at ski and control areas overlap (Table 4-2).

Age Structure

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For males, there were no differences between the proportion of any age class >8% between ski and controls areas (Figure 4-2). However, males with >33% of their capture locations in ski operations areas had significantly higher proportions of the 1-2-year old age class (64% controls versus 88% operations areas; z = 2.1, p = 0.03) than controls. Accordingly, there were also fewer males >2 years of age in ski operations areas (12%) compared to controls (36%; Figure 4-2). For females, there were no differences >8% in the proportion of any age class between ski areas, control areas, or ski operations areas (Figure 4-2).

Reproductive Status

We captured 29 females on a total of 43 occasions to assess denning status. Overall there was very little variation in the proportion of females showing evidence of lactation during each season, with 100% (28/28) of females >1-year old showing evidence of raising kits during the season they were captured. As expected, 1-year old females showed a very low rate of denning activity with only 3 of 15 (20%) of yearlings showing evidence of lactation. Therefore, we considered all adult females (>1-year old) as actively denning and sub-adults (1-year old) not likely to be denning. Of the 24 females captured that exhibited evidence of denning activity from 2008-2010, they collectively had 35 observed denning attempts from 2009-2011, 25 (71%) of which occurred in ski study areas versus only 10 (29%) in control study areas.

Genetic Analysis

We found deviations from HWP in 6 of 96 (16 loci x 3 ski areas x 2 treatments) tests. However, after Bonferroni correction, only 2 were significant and there was no pattern across loci (Table 3). We did not detect any LD among loci across or within populations. Given the

deviations from HWP were relatively small and loci were independent, all loci were retained in our analyses and we proceeded with our genetic analyses.

The number of alleles per locus ranged from 2 to 7 (mean = 4.6 SE = 0.42), and allelic richness was similar across populations, although lowest for the Homewood Ski (2.15) and highest for the Heavenly control (2.47) populations (Table 4-3). Averages for H_o and He for the global population were 0.51 and 0.51, respectively, and the observed heterozygosity (H_o did not significantly differ from the expected heterozygosity (H_e; Table 4-3).

Parentage and Recruitment

The combination of the genetic and demographic exclusion steps resulted in an average of 0.94 to 2.5 candidate mothers and 1.6 to 3.8 candidate fathers per offspring with 0 or 1 loci differences, respectively (Table 4-4). Overall 80% (86 of 108) of all parentage assignments were made using the combination of the exclusion and COLONY analyses, either both methods agreed on assignments or COLONY results were used to select a final parent from a candidate set of >1 remaining from exclusion. From either exclusion alone or the combination of exclusion and likelihood methods, parents were identified as occurring in the dataset in 42% (36 of 86) of these cases and 92% (33 of 36) of these parent assignments included parents with 0-loci differences. In 19% (22 of 108) of cases, the parentage assignments differed between exclusion and likelihood assignments and in nearly all (86%, 19 of 22) of these cases exclusion identified a parent with 0-loci differences between offspring while COLONY did not identify a parent in the dataset (Table 4-4).

Breeding age females at ski areas (n = 14) were more numerous than at controls (n = 10), and had 2.5 more denning attempts at ski areas (n = 25) than controls (n = 10). However, the number of offspring captured had more mothers identified as occurring in controls (n = 11) and ski areas

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(n = 9) similarly. A total of 30 males were identified as fathers of offspring, 16 at ski areas and 14 at controls. The mean age of males siring young was 2.05 years (SE = 0.21, range = 1-4 years), with 2-3-year-old males siring proportionally more young compared to the availability of their age classes from 2009-2011 (Figure 4-3).

From 2009-2011 30 (18M:12F) marten offspring were captured at ski areas and 27 (22M:5F) were captured at controls (Table 4-5); 4 (13.2%) offspring moved between study areas from 2009-2011. Significantly more immigrant offspring were captured in ski areas (n = 24, 16M:8F) than controls (n = 17, 14M:3F; paired t-stat = -4.98, df = 2, p = 0.019). There was no significant difference between the number offspring recruited from within each study area for ski (n = 6, 2M:4F) and control (n =10, 8M:2F: paired t-stat = -0.22, df = 2, p = 0.42).   Overall, few of the offspring captured were emigrants to other study areas (14.8% of all offspring from 2008-2010 captured, n = 8, 6M:2F) and 5 of those were born in controls and 3 in ski study areas. Movement distances of the 7 emigrants averaged 10.8 km (SE = 2.1, range 3.6-20.9 km) and was shorter for males (mean = 8.9 km) than for females (mean = 16.5; Table 4-6). Total recruitment (local recruitment + emigrants) was higher for controls (n = 15) versus ski areas (n = 9) but was not significantly different (paired t-test = -1.15, df = 2, p = 0.18). However, the estimated female per capita recruitment rates from controls was 4.16 times higher (15 recruits / 10 denning attempts = 1.5 recruits per female denning attempt) for controls compared to ski areas (9 recruits / 25 reproductive attempts = 0.36 recruits per female denning attempt). When these rates are calculated for the expected number of offspring produced, controls (15 recruited / 20 produced = 0.75) have a significantly higher recruitment rate that ski areas (9 recruited / 50 produced = 0.18; z = 4.53, p < 0.001).

DISCUSSION

Apparent adult male survival at ski areas was lower compared to controls supporting our hypothesis that frequently crossing ski runs to utilize remnant habitat incurs fitness costs due to increased predation. However, female survival was no different between ski and control areas which is not consistent with this hypothesis. Females previously demonstrated selection for the largest remnant habitat patch sizes at ski areas (Slauson et al. in prep) and for moving between patches with the smallest ski run crossing widths (Slauson et al. 2017). These female behaviors may reduce the risk associated with crossing ski runs by minimizing the need for exposure. Although males moved between patches with shorter ski runs on average, use of small patches (e.g., < 10 ha) means they will have to leave them and cross ski runs more frequently. At ski areas, we have identified a tradeoff in sex-specific spatial organization of martens, where males can increase their fitness by overlapping one or more female home ranges at the cost of increased male mortality.

Apparent survival in capture-mark-recapture analysis cannot distinguish between the effects of survival and emigration. Our observed difference in male survival rates could also be due to an increased rate of adult emigration at ski areas compared to controls. However, if this were true we would expect to capture more adult males emigrating into other study areas, which we did not. Adult dispersal in martens is rarely reported in martens (e.g., Powell 1994). Only a single male ≥ 1 year old was identified emigrating from 2009-2011 and it was from a control to ski area. In addition, the age structure of males captured primarily in ski operations areas was skewed to predominantly younger males (1-2 years of age). Age structure can be an accurate indicator of underlying survival rates. In the case for adult males at ski areas, where we see more younger males, age structure is consistent with lower estimated rates of survival. Females did

not exhibit any difference in age structure between ski areas and controls, also consistent with the lack of difference in survival rates.

Denning activity, as indexed by the number of females showing evidence of lactation annually, was greater at ski study areas versus controls. This disparity between ski and control study areas may be due in part to differences in the amount and spatial arrangement of resource conditions (e.g., mesic forest types with >24" mean dbh trees) females select during the denning season (Chapter 3). While we attempted to control for both the amount and size classes of forest habitat types during selection of each ski area's matched control, it became clear that interactions amongst the patch sizes, size class, and locations of forest habitat in mesic versus xeric slope positons, as well as presence of large boulder substrate in subalpine conifer habitats were difficult to match between ski and controls areas. However, it is also possible that ski areas may have a positive effect on prey resources by the input of 2 subsidies: increased moisture and human food. Snow making activities at ski areas alter the annual precipitation regime by increasing both the duration and total amount of snow accumulation. The result is that ski areas have higher and more stable winter precipitation that controls. If this increase in moisture results in increased abundances of key prey populations, by increasing or stabilizing the production of food resources such as conifer mast and truffles, it can improve the resource conditions to support denning. Food scraps discarded by the high number of recreationists over the 3-4-month ski season can also potentially affect prey populations active during winter and similarly improve the prey resources to support denning. Regardless, resource conditions supporting denning by female martens appear to be limiting, occurring in <25% of the study landscape (Chapter 3). Maintaining these important resource conditions wherever they occur—on ski and control areas—will likely be important for overall persistence of marten populations.

Despite having more adult females and 2.5 times more denning attempts, the female per capita contribution of offspring from ski areas was >4 times lower (0.36 offspring per attempt) than at controls (1.5 offspring per attempt). In addition, the number of immigrants captured at ski areas was significantly higher at ski areas compared to controls. Collectively these patterns suggest that the recruitment of young is substantially reduced at ski areas and is consistent with our hypothesis that recruitment would be lower at ski areas due to the predation risks associated with crossing ski runs. Juvenile marten begin to disperse in late summer and early fall when they are 4-6 months old and have comparatively little experience with their environment and naturally have the lowest comparative survival rates compared to older age classes (reviewed in Buskirk et al. 2012).

Sub-adult martens also used smaller patch sizes and moved between patches with wider ski runs widths than adult martens during both winter and spring-summer (Slauson et al. 2017). These behaviors by sub-adults increase, both the frequency of crossing ski runs and the time they are away from escape cover, likely put them at greater risk of predation than adults. While we did not mark kits prior to dispersal to directly track their survival, the seniority estimates indicated that sub-adults were less likely to be recruited from the juvenile cohort at ski areas compared to controls, consistent with the recruitment rates calculated from the parentage analysis. We did not mark and follow juvenile martens to determine their dispersal paths and ultimate fates; thus, it is possible that juveniles may disperse at higher rates at ski areas compared to controls. This would be consistent with the avoidance response all age classes of martens exhibited to winter ski area recreation activities (Slauson et al. 2017). If this were true, we would also predict *more* emigrants to other populations, which we did not detect.

Prior research indicated that martens continue to occupy much of the habitat at ski areas, but move between remnant patches with the shortest ski run crossings (Slauson et al. 2017). Martens only show significant avoidance of using habitat when ski recreation activities are present (Slauson et al. 2017). In addition, martens breed at ski areas where suitable resource conditions are present (Slauson in prep). However, it appears that ski areas affect individual fitness by reducing juvenile recruitment rates and reducing adult male survival. Adult and juvenile survival are the most influential demographic rates on population growth for marten populations (Buskirk et al. 2012). Collectively these impacts have likely reduced the contribution martens occupying ski areas make to the overall population. Based on our estimates of the reduction in juvenile recruitment, the magnitude of reduction in the contribution metric may be a large enough to cause a negative population growth rate. For example, individual female martens with a life expectancy of 5 years may only have 4 reproductive attempts leading to a potential recruitment of less than two young ($4*0.36 = 1.44$). Individual males are not likely to reach age of 3 at ski areas thus are unlikely to contribute young to future generations unless they successfully breed with multiple females in a single season. Given these degrees of impact to influential vital rates, ski areas may represent ecological traps for martens, due to their continued attraction to using remnant habitat there but with impacts to survival and recruitment (Donovan and Thompson 2001).

Our results provide partial evidence, continued attraction to habitat at ski areas with the consequence of reduced fitness, that ski areas may represent ecological traps for marten. The majority of remnant habitat in the ski areas in our study was unaltered by development, with only ski runs, roads, and areas for infrastructure, collectively amounting to <20% of the operations area of each resort. However, ski runs and roads are high-contrast edge features where forest

habitat is completely removed. In addition, surface substrates (e.g., boulders, logs) are also cleared, further creating a high-contrast between the altered and unaltered habitat. It is in these high-contrast habitat fragmentation states that the most extreme species responses to fragmentation occur (Prugh et al. 2008). We hypothesize that marten encounters with larger-bodied generalist predators, attracted to foraging along the edges inherent in ski areas increases the risk of martens being killed by predators at ski areas. Identifying the causes of mortality for male and juvenile martens occupying ski areas will be an important next step for understanding these effects and for developing strategies to mediate these impacts.

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Table 4-1. Top models for modeling capture, recapture, survival, and seniority for Pacific martens in the Lake Tahoe region from 2009-2011.

			Model Parameters			Model Ranking		
Rank	Capture	Recapture	Survival	Seniority	fO	ΔAIC_c	*wi*	K
1	Spring (month)	Spring(sex)	Spring (sub-adult, adult)	Spring (age class x treatment)	Spring (constant)	0	0.8	32
	Winter (time)	Winter(sex)	Winter (sub-adult, adult)	Winter (sub-adult, adult)	Winter (constant)			
2	Spring (month)	Spring(sex)	Spring (sub-adult, adult)	Sub-adult x season	Spring (constant)	7.6	0.17	32
	Winter (time)	Winter(sex)	Winter (sub-adult, adult)	Adult constant	Winter (constant)			
3	Spring (month)	Spring(sex)	Spring (treatment x age class)	Spring (treatment x sex x age class)	Spring (constant)	14.9	0.02	14
	Winter (time)	Winter(sex)	Winter (age class)	Winter (treatment x age class)	Winter (constant)			
4	Spring (month)	Spring(sex)	Spring (constant)	Time	Spring (constant)	21	<0.01	25
	Winter (time)	Winter(sex)	Winter (constant)		Winter (constant)			
5	Spring (month)	Spring(sex)	Spring (sub-adult, adult)	Treatment x time	Spring (constant)	35.8	<0.01	23
	Winter (time)	Winter(sex)	Winter (sub-adult, adult)		Winter (constant)			

Table 4-2. Estimates for survival and seniority from the top ranked capture-recapture model using program MARK for Pacific martens (*Martes caurina*) in the Lake Tahoe region of California and Nevada from 2009-2011. NE is not estimated due to pooling of age classes for estimation.

Study Area	Sex	Age	Survival		Seniority	
			Mean (SE)	95% CI	Mean (SE)	95% CI
Ski	Male	Sub-adult	0.93 (0.01)	0.89 - 0.95	0.77 (0.08)	0.55 - 0.90
		Adult	**0.84 (0.04)**	**0.74 - 0.90**	NE	
	Female	Sub-adult	NE		0.65 (0.12)	0.57 - 0.97
		Adult	NE		NE	
Control	Male	Sub-adult	0.99 (0.01)	0.97 - 0.99	0.98 (0.10)	0.71-0.99
		Adult	**0.93 (0.01)**	**0.90 - 0.96**	NE	
	Female	Sub-adult	NE		0.91 (0.10)	0.45 - 0.99
		Adult	NE		NE	
Combined	Female	Sub-adult	0.97 (0.01)		NE	
		Adult	0.97 (0.01)	0.94 - 0.98	NE	
	Combined	Adult	NE		0.95 (0.02)	0.93 - 0.96

Table 4-3. Genetic variation at 16 microsatellite loci among the 6 study populations of Pacific martens (*Martes caurina*) from 2009-2011 in the Lake Tahoe region of California and Nevada. Standard errors are presented in parenthesis after each metric.

Population			Microsatellite DNA				
	ID	*n*	*A*	*AR*	H_o	H_e	F_{IS}
Heavenly Control	HEC	10	3.50 (0.38)	2.47 (0.31)	0.51 (0.06)	0.53 (0.06)	-0.027
Heavenly Ski	HES	17	3.81 (0.37)	2.37 (0.33)	0.50 (0.05)	0.50 (0.05)	-0.44
Homewood Control	HOC	16	3.68 (0.37)	2.44 (0.30)	0.55 (0.06)	0.53 (0.05)	-0.09
Homewood Ski	HOS	9	3.38 (0.30)	2.15 (0.23)	0.48 (0.05)	0.49 (0.05)	-0.05
Sierra Control	SC	18	3.75 (0.36)	2.29 (0.23)	0.52 (0.06)	0.52 (0.05)	-0.02
Sierra Ski	SS	26	4.06 (0.40)	2.22 (0.28)	0.47 (0.05)	0.48 (0.05)	-0.003
Global Population		96	3.70 (0.15)	2.32 (0.11)	0.51 (0.02)	0.51 (0.02)	-0.04

Table 4-4. Parentage assignments for 53 Pacific marten offspring captured from 2009-2011 in the Lake Tahoe region of California and Nevada. Parent assignments in bold indicate differences between exclusion and likelihood assignments. Where > 1 candidate parent was identified from exclusion alone, the selection criterion used to identify the single parent was indicated by: E-exclusion using 0-loci differences, EBD-exclusion by distances > 30 km from offspring capture locations, EBA-exclusion by parent age, EBPD-exclusion by distance between candidate parents. NID indicates that a parent was not identified as not occurring in the dataset.

Off-spring	Capture Location	Candidate Parents by Exclusion				Parentage by Likelihood Program COLONY		Final Parentage Assignment		Recruitment Class	
		0-Loci Diff.		1-Loci Diff.						IMMIGRANT /LOCAL	Emigrant
		Mom	Dad	Mom	Dad	Mom (Prob.)	Dad (Prob.)	MOM	DAD		
F01	HOS	3	1	1	4	**NID**	M03 100%)	**F04 (HOS) EBD**	M03 (HOS)	LOCAL	NO
F02	HOC	1	1	0	0	F03 (100%)	M04 (100%)	F03 (HOC)	M04 (HOC)	LOCAL	NO
F07	HOC	0	1	3	3	NID	M56 (100%)	NID	M56 (SC)	IMMIGRANT	NO
F08	SS	2	7	3	3	F10 (69%)	M13 (100%)	F10 (SS)	M13 (SS)	LOCAL	NO
F09	SS	0	0	1	2	NID	NID	NID	NID	IMMIGRANT	NO
F12	SC	2	2	3	6	F18 (34%)	M60 (100%)	F18 (SC)	M60 (HES)	LOCAL	NO
F13	HES	1	2	0	1	F10 (100%)	NID	F10 (SS)	NID	IMMIGRANT	YES
F15	SS	2	4	3	5	F10 (100%)	M13 (100%)	F10 (SS)	M13 (SS)	LOCAL	NO
F16	SS	1	1	2	1	**NID**	M49 (92%)	**F27 (SS) E**	M49 (SS)	LOCAL	NO
F17	SS	0	4	3	8	NID	M22 (100%)	NID	M22 (HES)	IMMIGRANT	NO
F19	HES	1	5	2	5	**NID**	**M22 (100%)**	**F12 (SC) E**	**M19 (SC) EBD**	IMMIGRANT	YES
F20	HES	1	1	0	2	NID	**NID**	NID	**M19 (SC) E**	IMMIGRANT	NO
F25	HOS	0	0	5	0	NID	NID	NID	NID	IMMIGRANT	NO
F27	SS	1	1	2	1	NID	M49 (92%)	NID	M49 (SS)	IMMIGRANT	NO
F28	SC	0	0	4	7	NID	NID	NID	NID	IMMIGRANT	NO
F29	SC	2	6	10	8	NID	M17 (100%)	NID	M17 (SC)	IMMIGRANT	NO
F30	SS	0	0	6	3	NID	NID	NID	NID	IMMIGRANT	NO
M01	HOC	0	0	0	2	NID	NID	NID	NID	IMMIGRANT	NO
M01	HOS									IMMIGRANT	NO
M07	HOC	1	2	2	2	F03 (100%)	**NID**	F06 (HOC) EBA	**M12 (HOC) E**	LOCAL	NO
M07	HOS									IMMIGRANT	YES
M09	HOS	0	0	4	2	NID	NID	NID	NID	IMMIGRANT	NO
M10	HOC	1	0	2	6	**NID**	NID	**F26 (HOC) E**	NID	LOCAL	NO
M11	HOC	2	4	3	3	F05 (100%)	M05 (100%)	F05 (HOC)	MO5 (HOC)	LOCAL	NO
M15	SS	0	0	0	2	NID	NID	NID	NID	IMMIGRANT	NO
M16	SS	0	3	5	4	NID	**NID**	NID	**M14 (SS) EBD**	IMMIGRANT	NO
M18	SC	2	3	0	3	**NID**	M57 (100%)	**F33 (SC) E**	M57 (SC)	LOCAL	NO

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M24	HEC	0	0	0	3	NID	NID	NID	NID	IMMIGRANT	NO
M25	SS	0	1	1	2	NID	**NID**	NID	**M49 (SS) E**	IMMIGRANT	NO
M26	SS	2	3	2	3	**NID**	M49 (100%)	**F32 (SC) E**	M49 (SS)	IMMIGRANT	NO
M27	SS	0	1	2	5	NID	M14 (4%)	NID	M14 (SS)	IMMIGRANT	NO
M28	SC	0	0	1	0	NID	NID	NID	NID	IMMIGRANT	NO
M29	SC	0	0	1	0	NID	NID	NID	NID	IMMIGRANT	NO
M30	SS	0	2	5	6	NID	M13 (100%)	NID	M13 (SS)	IMMIGRANT	NO
M31	SS	2	1	2	0	NID	M03 (98%)	NID	M03 (HOC/HOS)	IMMIGRANT	NO
M32	SC	1	2	0	1	F18 (92%)	M17 (100%)	F18 (SC)	M17 (SC)	LOCAL	NO
M33	SC	1	1	0	3	F23 (100%)	NID	F23 (HEC)	NID	IMMIGRANT	YES
M34	HES	1	2	1	3	F21 (100%)	M22 (100%)	F21 (HES)	M22 (HES)	LOCAL	NO
M35	HEC	0	0	0	0	NID	NID	NID	NID	IMMIGRANT	NO
M36	HOC	7	3	6	7	F04 (100%)	M03 (100%)	FO4 (HOS)	M03 (HOC/HOS)	IMMIGRANT	YES
M37	HOC	0	1	0	0	NID	M12 (100%)	NID	M12 (HOC)	IMMIGRANT	NO
M38	HES	1	2	4	6	**NID**	**M22 (100%)**	F12 (SC) E	**M22(HES)/M12(HOC) E**	IMMIGRANT	YES
M40	HES	0	2	7	9	NID	**NID**	NID	**M13(SS)/M64(HEC) E**	IMMIGRANT	NO
M41	HES	0	0	3	12	NID	NID	NID	NID	IMMIGRANT	NO
M42	HES	4	6	11	14	**NID**	**M12 (99%)**	**F33 (SC) EBD, EPL**	**M19(SC)**	IMMIGRANT	YES
M43	HEC	0	1	4	2	NID	**NID**	NID	M16 (SS) E	IMMIGRANT	NO
M43	SC									IMMIGRANT	NO
M44	HEC	2	0	2	0	F23 (100%)	NID	F23 (HEC)	NID	LOCAL	NO
M45	HEC	0	0	4	5	NID	NID	NID	NID	IMMIGRANT	NO
M46	HOS	0	0	1	0	NID	NID	NID	NID	IMMIGRANT	NO
M47	HOS	0	1	2	6	NID	**NID**	NID	**M01 (HOC/HOS)**	IMMIGRANT	NO
M48	HOC	3	0	0	13	**F18 (14%)**	NID	**F26 (HOC) EBD**	NID	LOCAL	NO
M50	SS	1	4	5	10	**NID**	**NID**	**F08 (SS) E**	**M16(SS) EBD**	LOCAL	NO
M51	SC	0	1	3	4	NID	NID	NID	NID	IMMIGRANT	NO
M52	SC	1	2	5	6	F10 (100%)	**NID**	F10 (SS)	**M64(HEC) EBD**	IMMIGRANT	YES
M53	SC	0	1	2	1	NID	**NID**	NID	**M64(HEC) E**	IMMIGRANT	NO
M54	SC	2	4	1	3	**NID**	M20 (100%)	**F33 (SC) EBPD**	M20 (SC)	LOCAL	NO

Table 4-5. Number of Pacific marten offspring produced in or outside of each study area, based on parentage analysis using 16 microsatellite loci and using a combination of exclusion and likelihood methods from 2009-2011 in the Lake Tahoe region, USA.

Study Area	Offspring Captured (N)	Local Recruitment		Immigrants		Emigrants		Total Recruitment	
		N	% Offspring	N	% Offspring	N	% Emigrants	N	% Recruits
Heavenly Control	5	1	20%	4	80%	1	14%	2	9%
Heavenly Ski	8	1	13%	7	88%	0	0%	1	4%
Homewood Control	9	5	56%	4	44%	1	14%	6	26%
Homewood Ski	7	1	14%	6	86%	1	14%	2	9%
Sierra Control	13	4	31%	9	69%	2	29%	7	30%
Sierra Ski	15	4	27%	11	73%	2	29%	6	26%
Total Control	**27**	**10**	**37%**	**17**	**63%**	**5**	**63%**	**15**	**63%**
Total Ski	**30**	**6**	**20%**	**24**	**80%**	**3**	**38%**	**9**	**38%**

Table 4-6. Genetic-based dispersal distances of juvenile Pacific martens from natal home ranges to other study areas from 2009-2011 in the Lake Tahoe region of California and Nevada.

Emigrant	Capture Location	Mother	Study Area	Dispersal Distance (km)
F13	HES	F10	SS	20.84
F19	HES	F12	SC	12.08
M07	HOS	F06	HOC	5.94
M33	SC	F23	HEC	8.50
M36	HOC	F04	HOS	3.56
M38	HES	F12	SC	12.08
M42	HES	F33	SC	16.17
M52	SC	F10	SS	7.44

Figure 4-1. Location of the 6 paired ski and control Pacific marten study areas 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 classification and remotely sensed data available from EVEG (updated 2010).

A. Study Area Locations

B. Study Area Habitat (top) and Tree Size Compositions (bottom)

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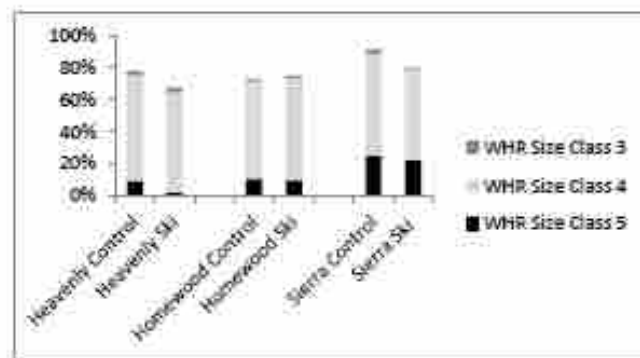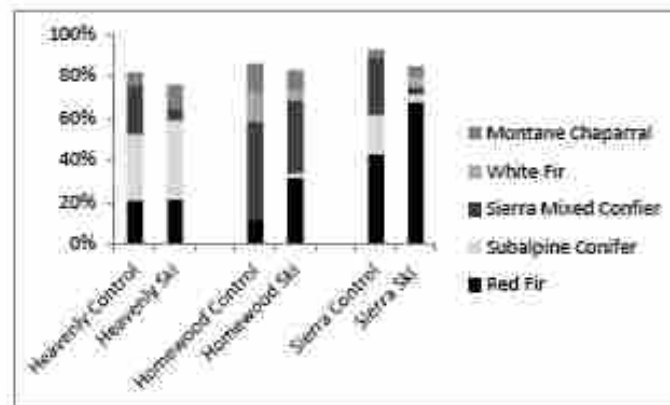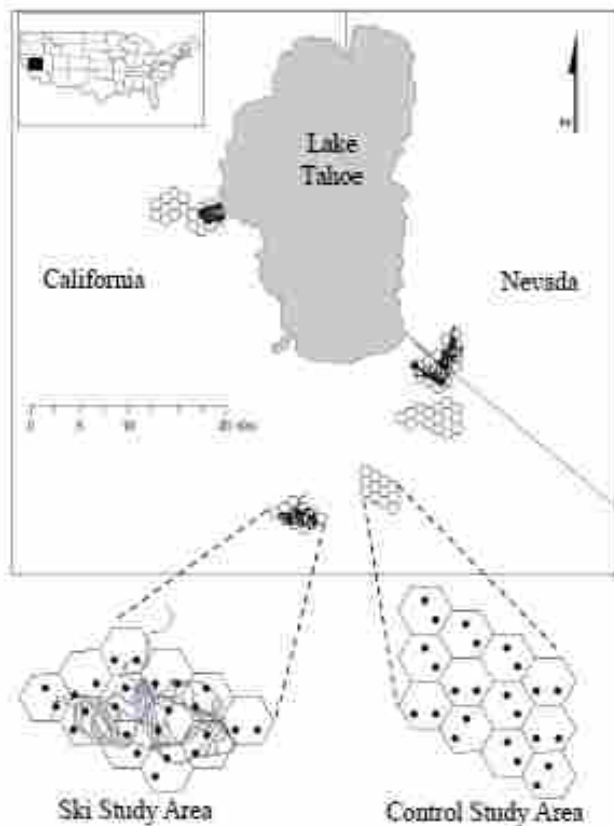
Figure 4-2. Age structure for Pacific martens captured annually from 2009-2011 in the Lake Tahoe region of California and Nevada.

A. Males
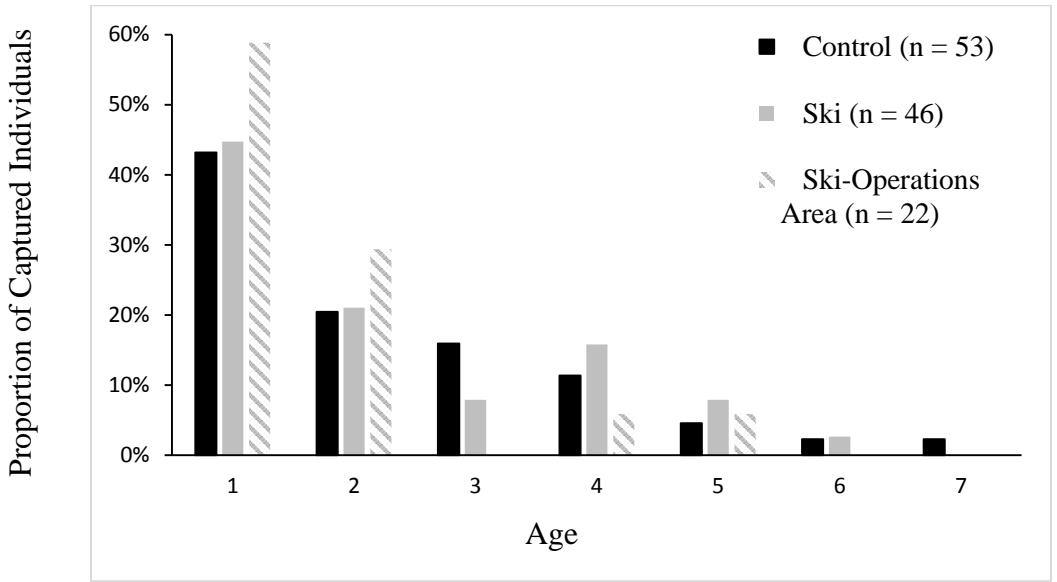
B. Females
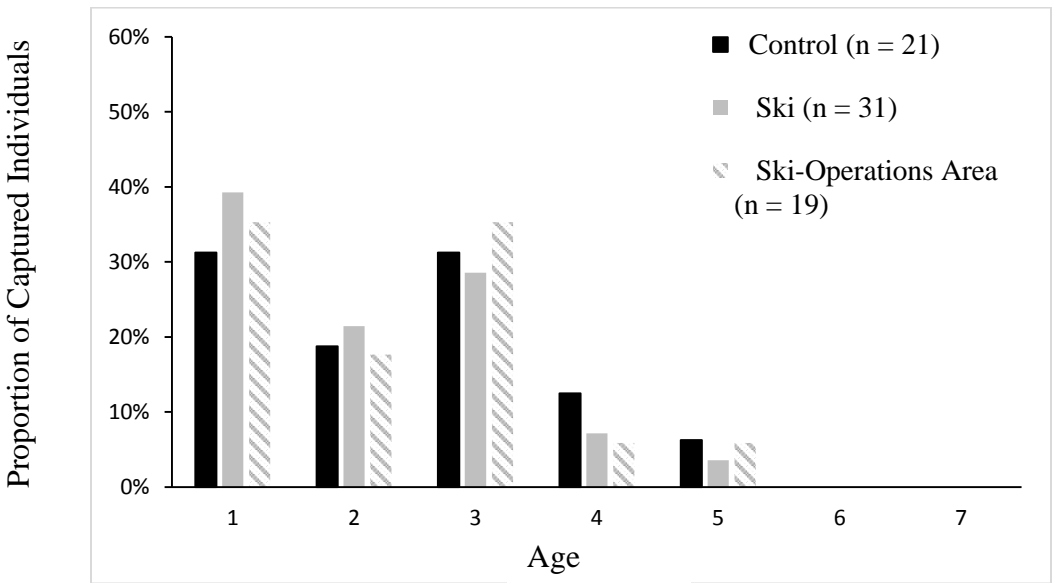
Figure 4-3. Cumulative age structure of male Pacific martens compared to the proportion of males siring young from 2009-2011 in the Lake Tahoe region of California and Nevada.
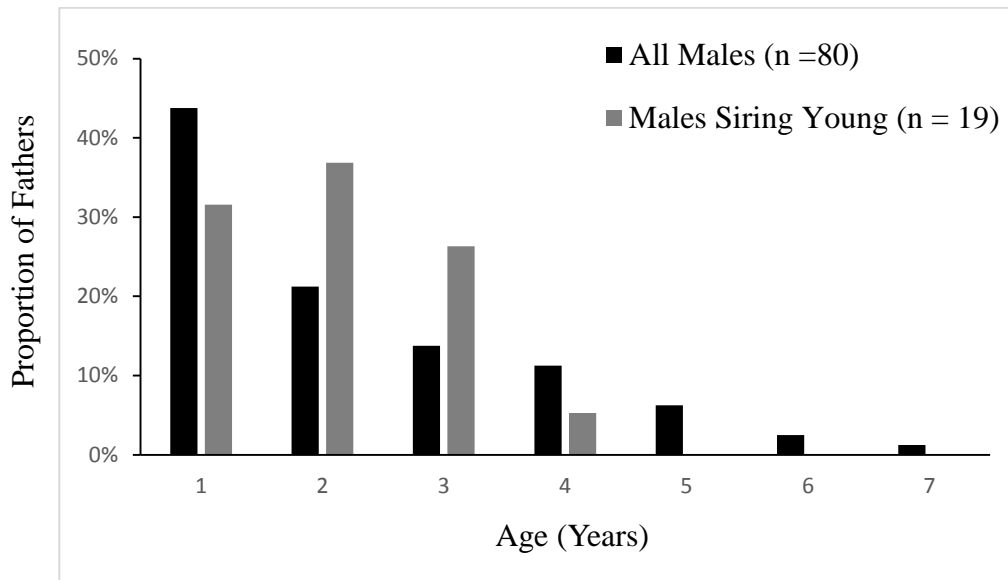
CHAPTER 5

Developed Ski Areas Represent Ecological Traps for Pacific Martens

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ABSTRACT

To understand the ultimate outcomes for relationships between species and resources and stressors, detailed empirical models linking resources and stressors to influential vital rates are needed. These habitat-performance relationships can provide the necessary foundation for strategic habitat management. We evaluated the demographic effects of ski areas on Pacific martens by comparing population performance at 3 pairs of ski and control areas in the Lake Tahoe region of California and Nevada from 2009—2011. We calculated the per capita contribution of individuals both collectively by treatment, ski or control, and for each focal population using the combination of apparent survival, emigration, and recruitment estimates from capturing 96 individuals (63M:33F) a total of 547 times across all 6 study areas over 3 reproductive cycles. Per capita contribution rates for martens at ski areas were 24% lower at ski areas compared to control areas. Population growth ratios suggest ski areas will require ≥ 3.8 breeding cycles to equal the contributions of martens at controls. Overall contribution rates at ski areas were nearly 1, meaning they can maintain local abundance but contribute little to the larger population. In contrast, control area annually contribute ~3 to 5 individuals to the larger population and represent population sources. Individual fitness components, survival and recruitment, was depressed for martens at ski areas; females may not contribute one or more offspring to the population and adult survival is reduced. Ski areas appear to fit the criteria for representing 'equal-preference' ecological traps by maintaining their attractiveness to martens. Martens at ski areas occur in equal densities and show similar habitat selection patterns compared to controls, but lower habitat quality produces significant fitness consequences— reduced recruitment of offspring for all individuals and reduced survival for males. Habitat conditions suitable for supporting actively denning females are the most limited resource

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condition, occurring in <25% of the study landscape. At ski areas, maintenance of large contiguous patch sizes and connecting these patches with short ski run widths are important for persistence of martens.

KEY WORDS marten, *Martes caurina*, ski area, recreation, source, sink, fitness.

INTRODUCTION

Detailed empirical models linking resources and stressors to both animal occurrence and fitness components, survival, reproduction and recruitment (McGraw and Caswell 1996), measures are necessary for understanding the underlying processes that determine population persistence. Quantitative models distinguishing the influence that variation in resource quality and stressor intensity can have on fitness outcomes within populations are needed to identify how these factors influence population dynamics and overall persistence. Accurate spatial representations of the resource and stressor conditions producing fitness outcomes affecting the most important life history stages are needed to guide effective management and conservation of many of the species of greatest conservation concern.

Despite the importance and need for these types of models, few examples exist linking population dynamics to landscape-level resource and stressor conditions. One example is the Northern spotted owl (*Strix occidentalis caurina*; Franklin et al. 2000) where fitness was maximized for owls occupying territories with a mosaic of young and old forest patches. Owl survival was linked to the amount of old forest, and reproductive success linked to the amount of young forest with higher quality prey resources. Another example is the Greater sage grouse (*Centrocercus urophasianus*), where nest success and chick survival were the two factors most limiting to persistence (Aldredge et al. 2001). These two factors were related to the combined probability of their occurrence (resource quality) and the risk for survival (stressor intensity).

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Only by viewing the combination of conditions influencing these factors can the proper habitat components be identified (Aldredge et al. 2007). Linking vital rates to the most sensitive life history stages to landscape-scale resource and stressor conditions can guide the effective mitigation of the resource and stressor conditions.

Ecological traps occur when sudden environmental changes act to uncouple the cues individual animals use to assess habitat quality from the true quality of that habitat (Robertson and Hutto (2006). The animal's preference remains unchanged, but the positive outcome normally associated with a given cur is now a negative outcome (Misenhelter and Rotenberry 2000). Human-altered landscapes represent can create ecological traps by introducing novel conditions that can impact individual fitness but still support the habitat cues that attract individuals (Battin 2004). For example, for the endangered sage grouse in Alberta, nearly 50% of suitable nesting and 66% of suitable brood rearing habitat was considered sink habitat for these life history stages due to the increased risks of predation in close proximity to human-created edge habitat and riparian areas (Aldredge and Boyce 2007). Another example is the Pacific marten in California and Nevada; populations which occupy and reproduce in forests with ski areas incur lower survival and recruitment than populations which are in adjacent and similar forest habitats (Chapter 4).

North American martens (*Martes americana and M. caurina*) are of management and conservation concern due to their harvest for fur throughout their northern ranges and their sensitivity to habitat loss and modification from timber harvest. Both species are closely associated with mature and late-successional forest habitats and exhibit the strongest patterns of habitat selection at the landscape scale, suggesting a strong connection between home range composition and individual fitness (Thompson et al. 2012). Life-cycle analysis suggests that

adult and juvenile survival are much more influential for population growth rates than reproduction related vital rates (Buskirk et al. 2012). However, the distribution of suitable denning habitat can affect the overall number and density of females in a population. In a population of martens in the Sierra Nevada mountains, in chapter 2 I found that although martens occupied as much as 80% of the landscape, the sex ratio was highly male biased (~2:1) and female density was related to the distribution of suitable denning habitat that only occurred in ~25% of the landscape.

The factors influencing survival for martens in un-trapped populations are primarily related to the risk of predation. The majority of reported mortalities of martens have been from predation from larger-bodied habitat-generalist mammalian and avian predators (Bull and Heater 2001, McCann et al. 2010). The most frequently reported species include bobcat (Bull and Heater 2001, K. Slauson *unpubl data*), coyote (Bull and Heater 2001), fisher (Hodgeman et al. 1997), and great horned owl (Thompson 1994). The majority of sites where marten are killed are associated with habitats where escape cover has been reduced by humans, such as by timber harvest (Ellis 1997, Bull and Heater 2001). Modifications to suitable marten habitat in many of the study landscapes where predation has been reported appears to have influenced these events by increasing the abundance of larger-bodied predators and/or creating conditions that reduce escape cover, such as vertical tree boles.

The development of ski areas involves the loss and fragmentation of forest habitat to create networks of ski runs, roads, and infrastructure necessary to support this recreation activity. In addition to the modifications to habitat, the presence of high density recreation activities has been shown to elicit a seasonal avoidance response by martens (Slauson et al. 2017) similar to other wide-ranging species of wildlife (Fergeson and Keith 1982, Hamr 1988, Thiel et al. 2000).

Despite this seasonal effect, in chapter 3 I found that female martens return to reproduce where suitable habitat exists in ski areas once ski recreation activities cease and select the largest remnant patches of suitable denning habitat. However, in chapter 4 I found that the recruitment of juveniles in ski areas compared to adjacent control areas is significantly reduced, suggesting juvenile mortality may be higher at ski areas. In chapter 4 I also found that male martens exhibit reduced survival in these areas, possibly due to the increased risk of predation from frequently crossing open ski runs in order to traverse and defend their territories.

Our overall objectives are to quantitatively evaluate the fitness components, survival and recruitment, of martens occurring on and off ski areas. First, we calculated the contributions of local populations to the larger population by integrating estimates of survival, reproduction, and recruitment from our prior work in the study areas (Chapter 3). Our goal was to evaluate whether the relative contributions for populations on and off ski areas represented population sources or sinks, and to identify what demographic factors most influenced a population's contribution. Second, we integrated our previously developed landscape scale models for sex-specific density and movement at ski areas to identify habitats where martens are likely to occur and reproduce. We also evaluated the evidence on whether ski areas represented ecological traps for martens, where the environmental changes (e.g., fragmentation, human disturbance) act to uncouple the cues that animals use to assess habitat quality that typically lead to positive outcomes, which are now negative outcomes (Robertson and Hutto 2006). We used this model to identify strategic areas to suggest management actions that can promote persistence of the overall marten population.

METHODS

Study Design and Demographic Data

From 2009-2011 we systematically sampled the distribution and demographic characteristics of Pacific martens that occurred on 3 pairs of ski areas and control study areas in the Lake Tahoe region of California and Nevada (Figure 1). Details of the study area selection process and sampling design have been previously published (Slauson et al. 2017). During this effort, a total of 96 individuals (63M:33F) were captured across all 6 study areas and demographic data was collected over 3 reproductive cycles.

Calculating the Contribution of Local Populations

To calculate the contribution of focal subpopulation r to the metapopulation we used the metric C^r, which is the per capita contribution of a member of the focal subpopulation to the metapopulation (Runge et al. 2006). C^r was calculated using the following equation:

$$C^r = \phi_A^{rr} + \sum_{s \neq r} \phi_A^{rs} + \beta^r \left(\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs} \right)$$

where ϕ_A^{rr} is the probability that adults survive, and remain in the subpopulation, $\sum_{s \neq r} \phi_A^{rs}$ is the probability that adults survive and emigrate to the larger metapopulation, β^r is the number of juveniles produced per adult, ϕ_J^{rr} is the probability that juveniles survive and remain in the subpopulation, and $\sum_{s \neq r} \phi_J^{rs}$ is the probability that juveniles survive and emigrate to the larger metapoplation. There will be C^r individuals in the subpopulation at time t +1 per member of the subpopulation r and time t. If $C^r > 1$, the focal subpopulation contributes more individuals than it loses via mortality and is a source (Runge et al. 2006). If $C^r < 1$, the focal subpopulation loses more individuals to mortality than it contributes and is a sink.

C^r calculates the per capita contribution over a single breeding cycle or year. However, martens exhibit two population characteristics that suggest contributions vary by sex and age.

Survival rates can vary by sex (Payer 1999, McCann et al. 2010, Chapter 4) and the due to having a polygamous mating system, males on average will contribute fewer offspring than females, especially when sex ratios are skewed towards males. Sexual maturity in martens is age-specific (Mead 1994), thus not all age classes will contribute equally. To account for these factors we modified the equation for C^r to incorporate sex and age structure. First we developed equations separately for each sex. For females we extended C^r to encompass a structured local marten population using two steps (Runge et al. 2006 [Appendix A]).

Then for females, we developed a sex-specific equation and conditioned that β^r be represent two age classes, 1-year sub-adult old females (β_{SA}^r) and $\geq$ 2-year old adult females (β_{AD}^r). First, we considered each age class within each local population to be its own "site" and constructed its own contribution metric as the column sum of the of the metapopulation transition matrix. Second, we weighted the contribution metrics for the ages within each local population by their current relative abundances. The two female age class equations are given by

$$\text{Sub-adult } \ C_{SA}^r \ = \phi_{SA}^{rr} + \sum_{s \neq r} \phi_{SA}^{rs} + \beta_{SA}^r \left(\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs} \right)$$

$$\text{Adult } \ C_A^r = \phi_A^{rr} + \sum_{s \neq r} \phi_A^{rs} + \beta_A^r \left(\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs} \right)$$

where the superscripts refer to sites, and transitions among sites, and the subscripts refer to the ages (SA = sub-adult, AD = adult; Table 1). To combine the contributions for the age classes into a single contribution for a particular local population, the age-specific contributions were weighted by their relative abundances using the following equation from Runge et al. (2006 [Appendix A])

$$C_.^1 = \frac{\sum_{k=1}^{a} C_k^1 N_k^1}{\sum_{k=1}^{a} N_k^1}$$

Weighting by the current relative abundances rather than the stable age distribution has the advantage of avoiding asymptotic assumptions while expressing the current contribution of the local population. Then the contribution of all age classes for this single local population is given by the column sum of the transition matrix

$$C' = [\ C_{SA}^1\ \ C_{AD}^1\ ] = 1'A$$

For males, we used the same two age class-structured model as for females. In addition we had to account for the effect the observed skewed sex ratio in the overall population (1.9M:F) may have on C^r. With nearly 2 males per female in the population, breeding opportunities for males are lower and therefore their per capita contribution of juveniles is reduced compared to females. To account for this in the equation we added a sex ratio term (M^r) to the male equation

$$C^r = \phi_A^{rr} + \sum_{s \neq r} \phi_A^{rs} + \beta^r \left(\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs} \right) / X^r$$

where X^r is sex ratio of males to females for subpopulation r. If X^r is >1 then the per capita contribution of juveniles will decrease and if it is < 1 it will increase.

Estimating Demographic Parameters for Calculating C^r

The equation for calculating C^r can be broken down into three components: survival for residents (ϕ_A^{rr}), successful adult emigration ($\sum_{s \neq r} \phi_A^{rs}$), and per capita juvenile recruitment ($\beta^r \left(\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs} \right)$).

Survival for Residents—The combined probabilities of survival and of not emigrating are equivalent to the estimates of apparent survival from capture-mark-recapture analysis. We used previous sex- and age-specific estimates of apparent survival for our study area (Slauson et al. in prep; Table 1) for this component of the models.

Successful Adult Emigration—Adult dispersal is uncommon in marten populations and was only observed in a single yearling male (5%, 1 of 22 males) successfully emigrate from a control to ski area and no males emigrating from ski areas to controls from 2009-2011. However, due to our study design this is likely an underestimate because we could only detect successful adult emigration if the individual emigrating was captured in another study area, leaving many areas un-sampled for emigrants. However, our apparent survival estimates were high for all but adult males at ski areas (Table 1), suggesting adults remained residents and most dispersal movements were done by juveniles in our study population.

Juvenile Recruitment—We used our prior estimates for female per capita yearling recruitment for the study area, based on parentage analysis of yearlings, for this component of the model (Slauson et al. in prep). These estimates include the successful survival of both juveniles that survive and remain resident and successfully emigrate. They are essentially the outcome of the birth and survival components of the C^r equation. For ski areas, the per capita female recruitment rate was 0.36 yearlings per female and for control areas it was 1.5 yearlings per female annually. To make these estimates sex-specific we divided them in half to account for the contribution from each parent. We used paired t-tests to compare estimates of C^r for treatment and control as well as study area-specific comparisons.

Modified Contribution Metric: Relative C^r—Use of the estimates of the demographic parameters above resulted the derivation of a modified version of the contribution metric given by

$$Relative\ C^r\ =\ \phi_A^{rr}\ \ +\ \sim E_A^{rs}\ \ +\ \ \sim R_{SA}^{rr}\ +\ \ \sim E_{SA}^{rs}$$

where ϕ_A^{rr} is the probability of apparent survival for adults, $\sim E_A^{rs}$ is the relative rate of successful adult emigration, $\sim R_{SA}^{rr}$ is the relative rate of yearling recruitment into the focal population, and $\sim E_{SA}^{rs}$ is the relative rate of yearling recruitment into the larger metapopulation. We used this equation to calculate two overall *relative* C^r estimates, one for martens at ski areas and one for martens at control areas. The first step in this overall calculation was to calculate *relative* C^r for each of the 4 sex-age classes: adult-male, subadult-male, adult-female, subadult-female. During this stage of calculation individual estimates for each demographic parameter were randomly selected from within each parameter's 95% confidence interval for each sex-age class. Then this process was repeated 100 times, enough replication for the mean estimates to stabilize, for each sex-age class. The final step in the overall calculation of *relative* C^r was to combine the 4 sex and age-specific contributions by weighting them by their relative abundances using the equation from Runge et al. (2006 [Appendix A]) described previously.

Components of the Multi-Dimensional Habitat Model

     Male and Female Denning Season Density Models—Due to the differences between male and female marten density responses to habitat and stressors (Chapter 3), we applied the sex-specific models of density. For the density-habitat relationships models we used the variables amenable to management and that had the strongest influence on marten density during the spring-summer seasons (Chapter 3). Models for this season were selected because they overlapped the denning period for females and because we found no significant influences of habitat on marten density for either sex in winter across our study areas. The most influential variable for the female density model was the amount RWHR5 forest habitat types measured at the 1-km scale (Chapter 3), that include the amount of mesic habitat types (lodgepole pine, red

fir, subalpine conifer, whiter fir, Sierra mixed conifer) in size class 5 (mean DBH >24"). The most influential variable for male density was the amount of RWHRmd (same habitat types as RWHR5 but in size class 4-5 and with canopy cover >40%) measured at the 750-m scale. We classified all RWHR5 habitat as primary habitat and all additional RWHRmd habitat as secondary habitat.

Ski Run Crossing and Patch Size Models—We used the ski run effects (Slauson et al. 2017) on marten movement to develop a movement permeability index for ski run crossings based on the upper thresholds of the 95% confidence intervals for each sex (Slauson et al. 2017). Ski runs were either: 1. Permeable to females (< 13m wide) 2. Permeable to just males (13-18m wide) or 3. Impermeable based on their crossing distances (>18m wide). Female martens exhibited selection for the largest patch sizes at ski areas (Slauson et al. (b)). We did not explicitly value patch size in the model.

RESULTS

Contributions of Populations at Ski and Control Areas

Estimates of the C^r for sex and age classes between ski and control areas were significantly lower at ski areas compared to controls (p = 0.03, df = 2; Table 5-1). Differences in treatment-level estimates of C^r were smallest for sub-adult females (0.12), but were >0.40 different for males and 0.52 different for adult females at controls versus ski areas (Table 5-1). Overall the individual contribution of martens at ski areas was 37% lower at ski areas (C^r = 1.03, SE = 0.02, 95% CI = 0.99-1.07) than controls (C^r = 1.41, SE = 0.10, 95% CI = 1.21-1.61). Considering the average reproductive lifespan for martens (<5 years), an average individual at a ski area will require it's entire lifespan to approximately equal the contribution of offspring that an average individual at a control does in a single year.

Mapping Primary and Secondary Source Habitat

Twenty-three percent of marten habitat across all areas was primary source habitat (RWHR5) (Figure 5-3), whereas 68.0% of marten habitat was secondary source habitat (RWHRmd). There was some overlap between primary and secondary, of all habitat across the 6 study areas (Figures 5-2). Primary source habitat correctly classified 87.5% (21/24) of the estimated home range centers for actively denning females from 2009-2011. The majority of these females had >29 ha of primary source habitat within 1-km of their home range centers and only 3 had small amounts (7-21 ha) of this habitat type combined with >100 ha of secondary source habitat (Figure 2). Four (12.5%) actively denning females had home range centers located outside habitat types we identified as primary and secondary source habitats. These four female home ranges centers were located in large patches (108-138 ha) of subalpine conifer habitat with spatially extensive surface rocks and boulder piles that are not easily identified using the CWHR vegetation classification system alone. The use of this unique habitat type for denning was limited to the most xeric study areas, Heavenly ski and control study areas (Figure 5-2). To identify these habitats as primary source habitats we had to rely on using their estimated home range centers and capture locations alone.

For males, primary source habitat correctly classified 37.7% (20/53) of their estimated home range centers and secondary source habitat correctly classified an additional 44.9% (25/53). Collectively primary and secondary source habitats correctly identified 84.9% (45/53) of male home range centers. The majority of male home range centers had >60 ha of either primary or secondary source habitat within a 750m radius.

Defining Ski Run Crossing Permeability

The permeability state suitable for females and males (crossings <13 m) represented 22.7% of all ski run crossings available at all 3 ski areas (Figure 5-2). The permeability state only suitable for some males (13-18m) represented 10.2% of all ski run crossings (Figure 5-2). And the permeability state unsuitable for supporting marten movement (>18m) represented 67.1% of all ski runs crossings (Figures 5-2).

DISCUSSION

Overall, ski areas significantly reduced the per capita contribution of martens to both their local sub-populations and the larger population. The magnitude of this reduction brings each sub-population at ski areas close to a $C^r = 1$, where these sub-populations are just able to maintain their numbers but contribute little to the larger population. In contrast, marten sub-populations at control areas collectively have a per capita contribution rate that is nearly 8 times that of martens at ski areas. Control populations can be classified as source populations as they are projected to maintain their own population sizes and contribute 3 to 5 individuals annually, primarily from juvenile recruitment, to the larger population. Ski area sub-populations are projected to require 2-16 years to contribute a single individual to the larger population.

The reduction in relative C^r is primarily driven by the reduced recruitment of juveniles, which affects the contributions for all sex and age classes. Adult male survival is the next factor affecting the lower C^r for ski areas and the sensitivity of C^r to changes in these two vital rates is consistent with their influence on marten population growth rates using life cycle analysis (Buskirk et al. 2012). Due to their polygamous mating system (Mead 1994), marten populations have the potential to sustain lower male survival which may have relatively little influence on C^r. To improve the conditions for martens at ski areas the most important factor is to increase the rate of successful juvenile recruitment into the population. Use of genetic methods to understand

juvenile recruitment rate (Chapter 3) precluded being able to directly track juvenile dispersal movements and if mortality occurs, to determine the causes for mortality. We caution that the estimates of juvenile recruitment for ski areas may be underestimated if juveniles are simply dispersing at higher rates, due to the onset of ski recreation activities that adults avoid, and at shorter distances that our sampling design would detect. Studying the movements and fates of juveniles born at ski areas will provide information to address these important next questions.

While marten sub-populations at ski areas may be able to maintain their abundances, individual fitness is reduced for all individuals via reduced recruitment of offspring and for reduced survival for adult males. The combination of these factors make ski areas sinks for adult male martens ($C^r < 1$). One form of an ecological trap is where the environment of an organism is altered in such a way that the ultimate factors have changed (e.g., reproductive success, survival) but the cues eliciting a settling response have not (Robertson and Hutto 2006). Ski areas are highly fragmented landscapes but appear to remain attractive to martens, with spring-summer densities equal to controls areas and both sexes exhibiting similar selection for resource conditions as they do in controls. However, at ski areas females make two distinct behavioral changes, they select large residual patch sizes of forest habitat and use the shortest available ski run crossings, likely as a means to reduce their risk of predation in these altered landscapes. Males appear to select habitat to overlap or be adjacent to females to secure opportunities for mating, but are less selective for both resource conditions in their home ranges and factors that can reduce the risk of predation, large patch sizes and the shortest ski run crossing distances, at ski areas. Thus the likely main settlement cues, suitable resource conditions for denning for females and presence of females for males remain at ski areas.

Martens at ski areas also occur in similar densities during the spring-summer seasons (Slauson et al. in 2017) suggesting that ski areas represent an 'equal preference' trap (Robertson and Hutto 2006). However, the ultimate factors have changed and individual fitness is reduced due to the significantly lower rates of juvenile recruitment and lower rates of survival for males. Therefore, ski areas mechanistically function as equal preference traps by reducing habitat quality without a loss in the attractiveness of the altered landscape to martens.

Our habitat models provide a means to strategically approach the management of marten habitat that can have the greatest benefit to population performance. Key to the use of the models is that marten habitat appears best viewed hierarchically, starting with the habitat conditions that support the production of kits. Habitat conditions capable of supporting denning female martens occurs in <25% of the study landscape (Chapter 3), therefore minimizing the degradation of suitable denning habitat in and out of ski areas is the most influential management action that can benefit marten population persistence. Martens appear to be spatially clustered around suitable patches of habitat capable of supporting denning, thus secondary habitat (i.e., RWHRmd; see Chapter 3) adjacent to primary (denning) habitat is the next most important for maintenance or improvement to support the clustering of males and females. At ski areas two additional considerations include: 1. The maintenance of large patch sizes of suitable denning habitat and 2. Maintenance or enhancement of short ski run crossings between these patches. Despite the differences in survival and recruitment between ski and control areas, our recommendations for management actions to promote marten population persistence at all areas emphasize the importance of maintaining suitable denning habitat.

ACKNOWLEGDGEMENTS

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Table 5-1. Demographic parameter estimates used to calculate the per capita contribution of a member of subpopulation r (C^r) for Pacific martens (*Martes caurina*) at ski and control study areas in the Lake Tahoe region of California and Nevada from 2009-2011.

Study Area	Sex	Age	Apparent Survival	Observed Adult Emigration	Juvenile Recruitment	Sex Ratio	Cr (SE)
Ski							1.03 (0.2)
	Male	Yearling	0.93 (0.01)	0	0.18	1.4	1.03 (<0.01)
		Adult	0.84 (0.04)	0	0.18	1.4	0.93 (0.01)
	Female	Yearling	0.97 (0.01)	0	0.018	NA	1.01 (<0.01)
		Adult	0.97 (0.01)	0	0.18	NA	1.15 (<0.01)
Control							1.46 (0.10)
	Male	Yearling	0.99 (0.01)	0.05	0.75	2.3	1.45 (0.02)
		Adult	0.93 (0.01)	0	0.75	2.3	1.40 (0.01)
	Female	Yearling	0.97 (0.01)	0	0.075	NA	1.13 (0.01)
		Adult	0.97 (0.01)	0	0.75	NA	1.67 (0.03)

Figure 1. Location and sampling design for Pacific martens at 3 pairs of ski and control study areas in the Lake Tahoe Region of California and Nevada, USA
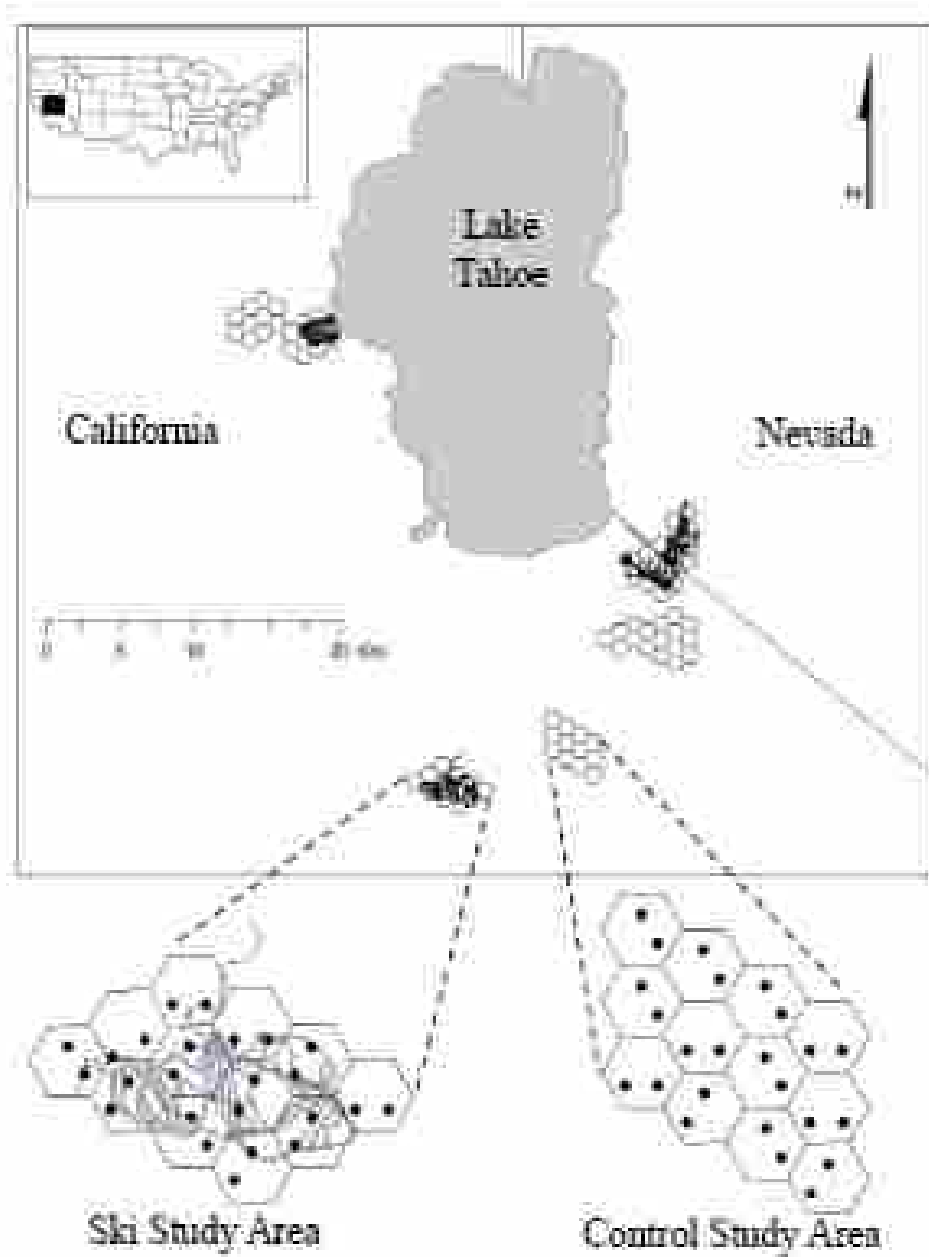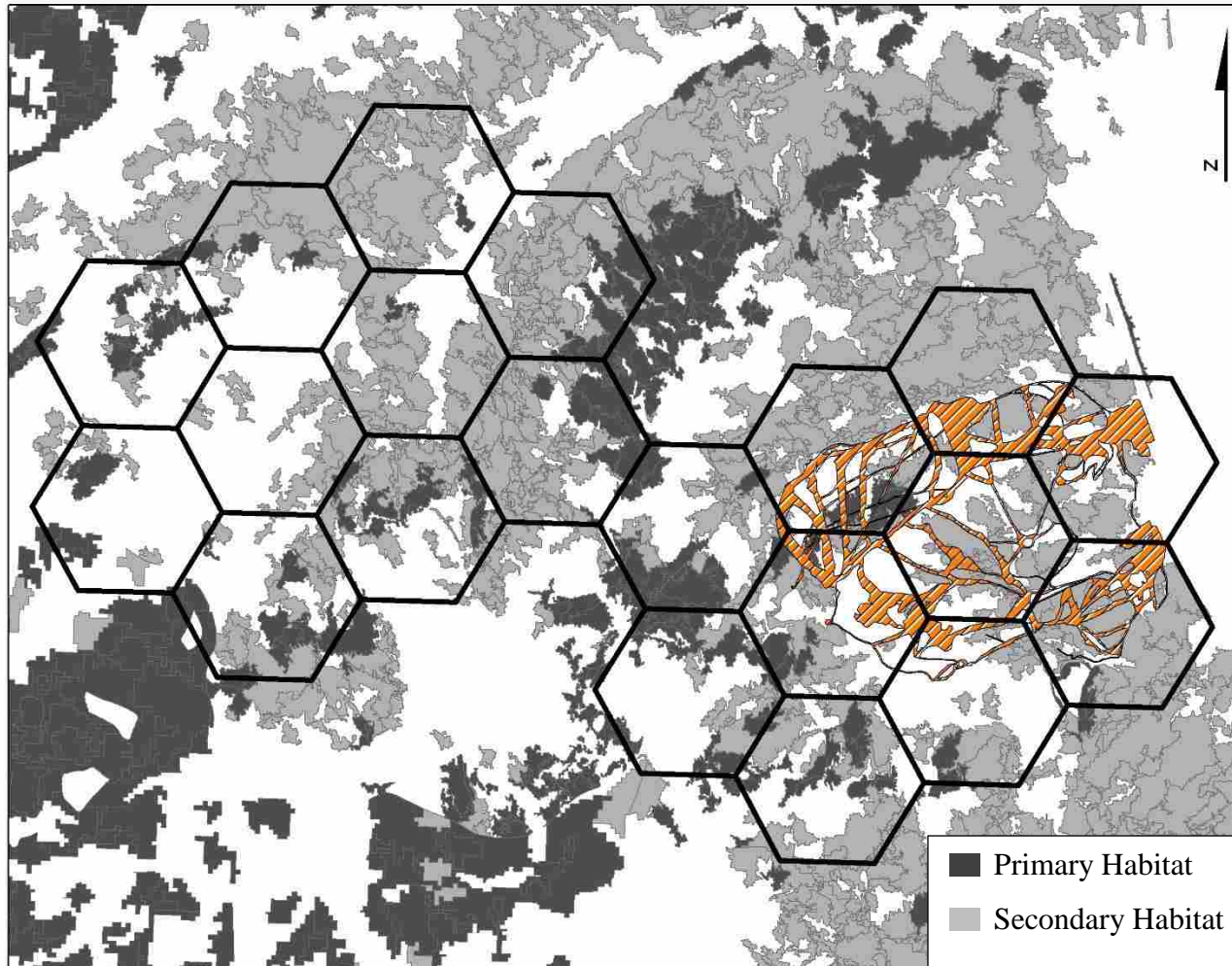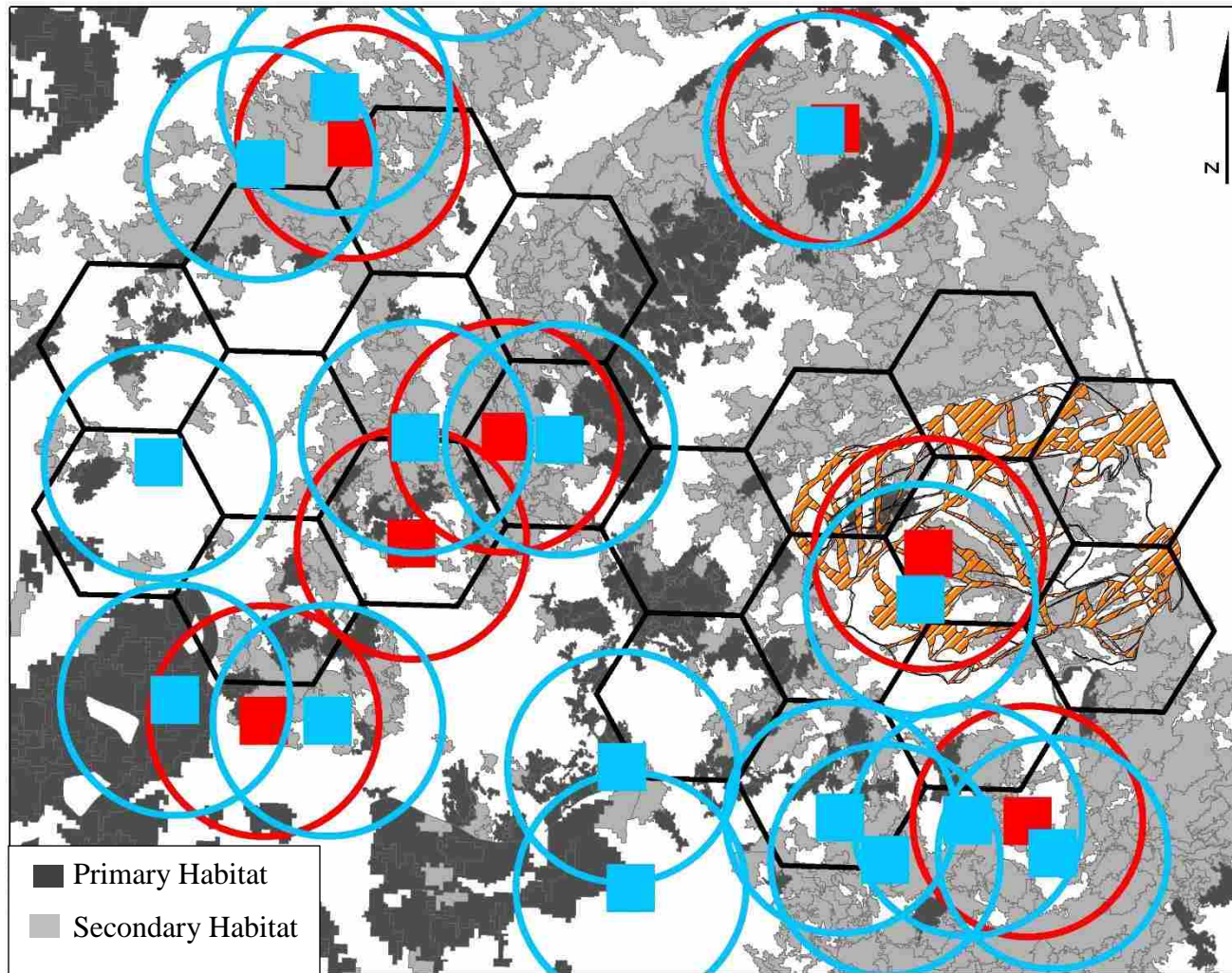
Figure 2. Multiple habitat states for Pacific martens (*Martes caurina*) at ski and control study areas in the Lake Tahoe region of California and Nevada from 2009-2011.
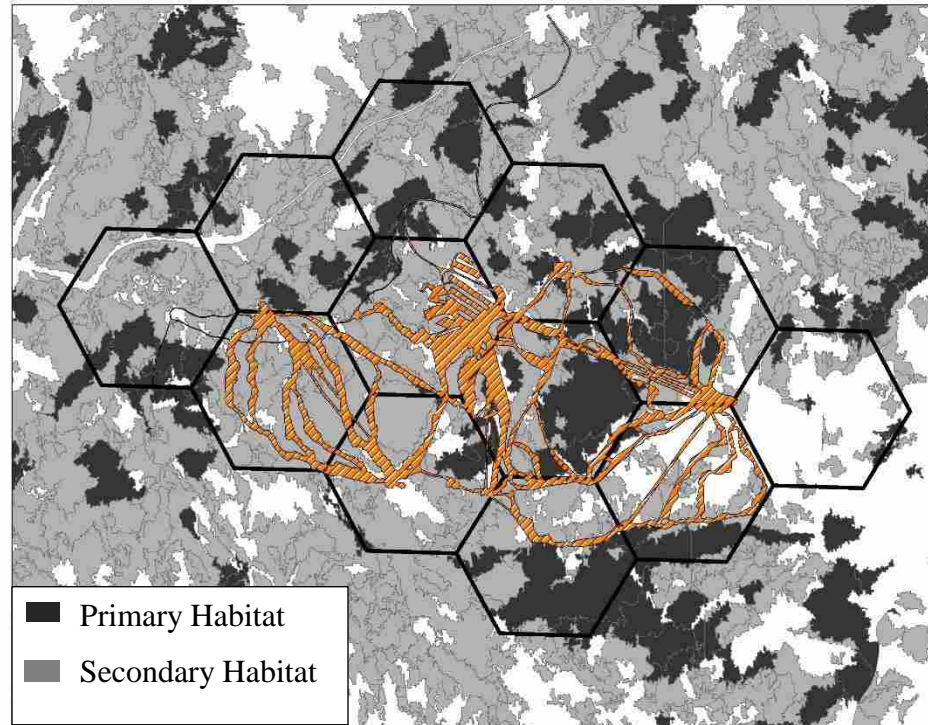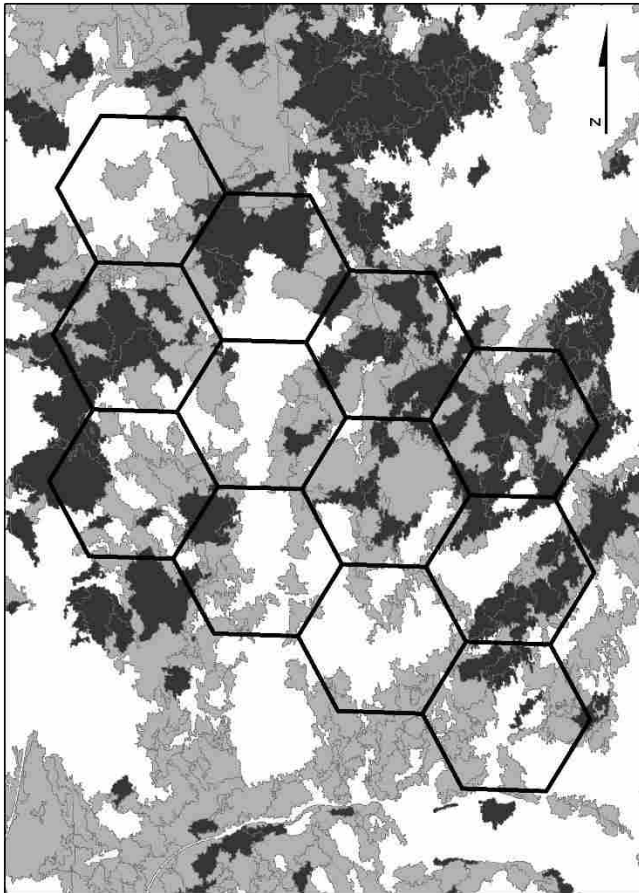
A. Homewood control (left) and ski areas (right).

B. Homewood control and ski areas with estimated home range centers for males (blue squares) and females (red squares) with approximate 1-km buffers around home range centers.

C. Sierra control and ski area.

Primary Habitat
Secondary Habitat

D. Heavenly control (left) and ski area (right).

Primary Habitat
Secondary Habitat