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Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens

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Abstract

Context Functional connectivity—the facilitation of individual movements among habitat patches—is essential for species’ persistence in fragmented landscapes. Evaluating functional connectivity is critical for predicting range shifts, developing conservation plans, and anticipating effects of disturbance, especially for species affected by climate change.

Objectives We examined whether simplifying forest structure influenced animal movements and whether an experimental approach to quantifying functional connectivity reflects normal behavior, which is often assumed but remains untested.

Methods We evaluated functional connectivity for Pacific marten (*Martes caurina*) across a gradient in

forest structural complexity using two novel methods for this species: incentivized food-titration experiments and non-incentivized locations collected via GPS telemetry (24 individuals).

Results Food titration experiments revealed martens selected complex stands, and martens entered and crossed areas with reduced forest cover when motivated by bait, particularly in the winter. However, our telemetry data showed that without such incentive, martens avoided openings and simple stands and selected complex forest stands equally during summer and winter.

Conclusions Detections at baited stations may not represent typical habitat preferences during winter, and incentivized experiments reflect the capacity of martens to enter non-preferred stand types under high motivation (e.g., hunger, curiosity, dispersal). We hypothesize snow cover facilitates connectivity across

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openings when such motivation is present; thus, snow cover may benefit dispersing animals and increase population connectivity. Landscapes with joined networks of complex stands are crucial for maintaining functional connectivity for marten, particularly during summer.

Keywords Connectivity · Forest management · Fuel reduction · Functional connectivity · Landscape fragmentation · *Martes americana* · *Martes caurina* · Marten · Movement · Titration experiment

Introduction

Populations may decline rapidly, potentially to extinction, if habitat loss and fragmentation exceed critical thresholds (Andren 1994; Swift and Hannon 2010). Disruption in functional connectivity, or the degree to which the landscape facilitates movement between patches of habitat (Taylor et al. 1993), may result in populations falling below a critical habitat threshold due to reduced access to important resources (Fahrig 2003; Buchmann et al. 2012). However, factors that affect and determine functional connectivity are difficult to measure and interpret. Connectivity could be diminished because it may be physically difficult for individuals to cross patches (e.g., forest birds crossing water bodies, Moore et al. 2008) or behaviorally avoided due to increased risk of predation.

Measuring functional connectivity is difficult because it requires replication of experiments at landscape scales (Belisle 2005; Betts et al. 2015). However, without such experiments, establishing ecological mechanisms for movement is challenging (McGarigal and Cushman 2002). Both experimental and observational approaches have been used to quantify animal movement behavior. One promising experimental method, titration experiments (Kotler and Blaustein 1995), uses incentives at predetermined distances to identify whether and how far an animal is willing to travel into adjacent stands of contrasting types. By experimentally standardizing food abundance, titration experiments bring rigor to functional connectivity tests and quantify the risk an animal is willing to take when motivated (Belisle 2005; Kotler and Blaustein 1995). Foraging theory suggests that an individual will forage in a patch only if the benefit

exceeds the marginal costs of predation risk (Stephens et al. 2007). These advantages of titration can also be weaknesses as it is unclear whether the subject would have traveled into a non-preferred patch in the absence of incentives. Further, such experiments typically evaluate behavior over short time periods (McGarigal and Cushman 2002). A functionally connected landscape must allow individual movement during all times of the year, without incentives such as bait. Observational approaches, such as surveillance of radio-marked individuals, therefore offer an important contrast. Non-experimental locations from telemetry data provide longer-term assessment of animal movement decisions, resting and denning structures, and stand preferences. To our knowledge, no study has yet tested how experimental titration techniques compare with routine movement behavior.

Mature forest is declining in most regions globally (Hansen et al. 2013), generally causing increased fragmentation of remaining mature forest habitats (Fahrig 2003). It is therefore essential to evaluate functional connectivity in patchy landscapes—particularly for forest specialists which are often reluctant to enter gaps, or openings (Hadley and Betts 2009). North American martens (*Martes americana*, *M. caurina*) are strongly associated with structurally complex mature forests (Spencer et al. 1983; Buskirk and Powell 1994). Marten populations consistently decline, or become locally extirpated, in areas below a threshold of 65–75 % forest cover (Hargis et al. 1999; Potvin et al. 2000; Moriarty et al. 2011). One hypothesis is that such a threshold exists due to disrupted functional connectivity among patches at reduced habitat amounts, but this ‘movement hypothesis’ has not been well tested. Though initial evidence suggests that martens are reluctant to venture into openings (Cushman et al. 2011; Heinemeyer 2002), it is unknown how martens perceive stands that are managed to retain forest cover but reduce structure. Current forest management practices in many dry forests include both tree removal (openings) at small scales (<5 ha) and thinning and fuels reductions, creating stands with 30–40 % canopy cover and reduced vertical and horizontal complexity (Stephens et al. 2012, 2013) intended to mitigate the risk of large and severe fires (Stephens et al. 2013). These treatments, depending on the residual tree configuration, may affect stand use by wildlife (Kalies et al. 2010; Fontaine and Kennedy 2012). Management

practices that remove forest complexity may negatively influence marten movement within home ranges and dispersal. If movement was significantly disrupted, this result could increase incentive to reconfigure future management and facilitate connectivity for martens and other forest dependent species (Stephens et al. 2014a).

We evaluated functional connectivity for Pacific marten (*M. caurina*), a sensitive species designated by the U.S. Forest Service, using two novel methods for this species: incentivized food-titration experiments and non-incentivized locations (no bait) collected via telemetry, including the smallest global positioning system (GPS) collars available and very high frequency (VHF) transmitters. We sought to quantify the movement behavior of martens across a gradient in forest complexity: (1) structurally “complex” stands characterized by multistory, dense conifer vegetation with little or no history of management in the last 50 years; (2) structurally “simple” stands which were either naturally sparse or formerly complex but had been subjected to management activities to reduce fire hazard which reduced understory complexity (Stephens et al. 2013); and (3) “openings” which included natural or managed areas with little or no overstory canopy cover. We predicted marten would be more willing to use stands with increased structural complexity due to availability of escape and foraging cover. We also tested whether functional connectivity was mediated by season (summer, winter); movement behavior could vary seasonally since martens raise kits and breed during summer when there is an abundance of both prey and potential predators. Conversely, martens can experience thermal stress and food limitation during winter (Taylor and Buskirk 1994), potentially causing greater risk tolerance during movement. Snow also provides subnivean access (Pauli et al. 2013), a form of cover unavailable during summer.

Methods

Study area

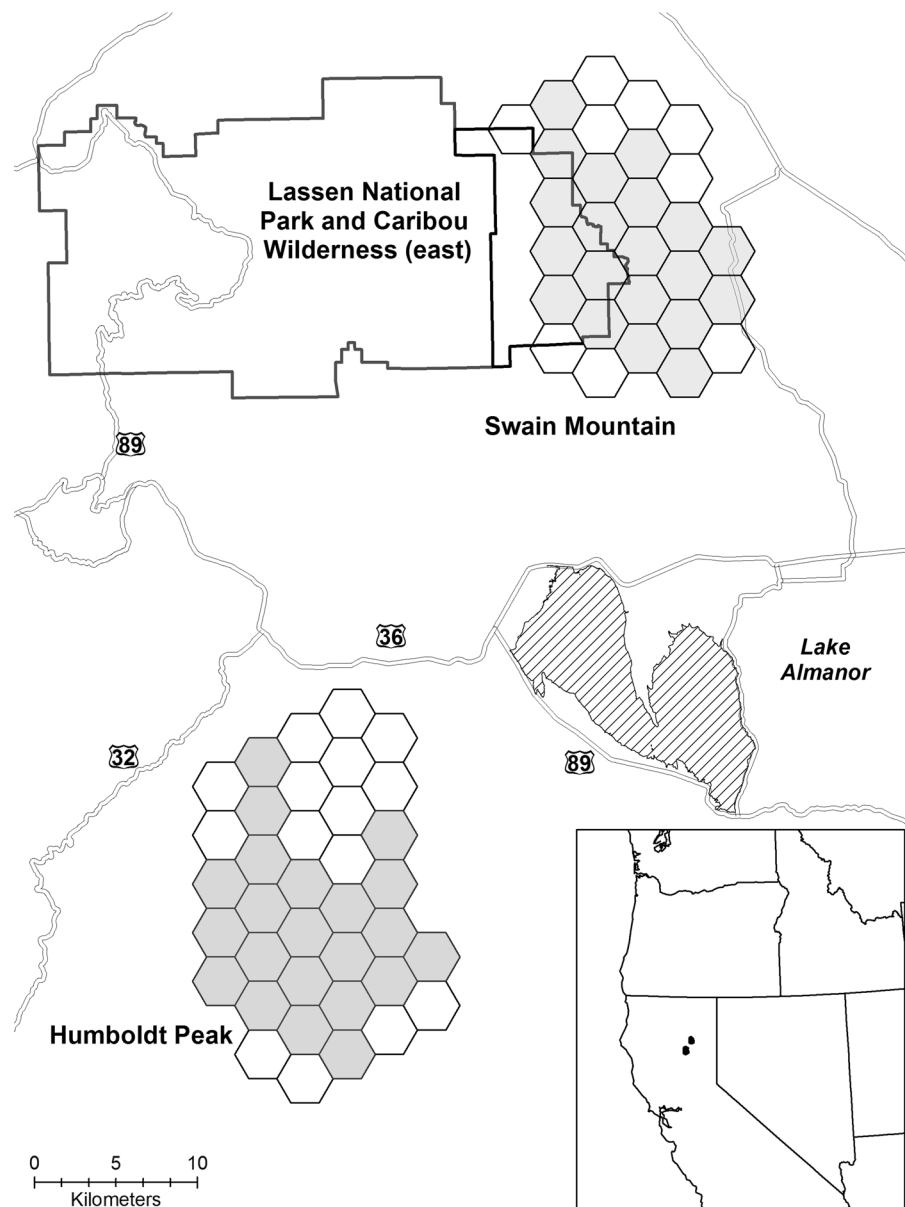
This research was conducted in Lassen National Forest (LNF), California, where marten populations were confirmed over 8 years of previous monitoring (Fig. 1, Zielinski et al. 2015). This area also was part of a 13-year

effort to manage forests intensively within 12,545 km² as mandated by the Herger-Feinstein Quincy Library Group Recovery Act (Owen 2003; Pinchot Institute 2013) with a primary focus on fuel reduction treatments that resulted in forest simplification. Thus, our study area provided a unique combination of intensive marten research and forest management. Elevations in this mountainous region ranged from 1500 to 2100 m. Forest vegetation types included red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*Pinus contorta*), mixed conifer, and riparian areas. Natural openings included perennial meadows, talus lava fields, and frozen lakes during winter. Data were collected January 2010–April 2013. We defined the summer season as snow-free months (July–November) and winter as periods with snow cover (December–June). Average minimum and maximum temperatures in July are 6.9 and 29.5 °C respectively, and −6.9 and 5.3 °C in January (Western Regional Climate Center, 1948–2005). Winter mean annual snow depth was 134 cm (California Department Water Resources, 1981–2014). We experienced 118, 15, and 68 % of the average snowfall during winter 2011, 2012, and 2013 respectively (Supplemental Figure A1).

Study design

We classified each forest stand as complex forest, simple forest, or an opening (Supplemental Table A1, referred to as “complex”, “simple”, and “opening” hereafter). Stand classifications were created in ArcMap v10.1 by combining the most recently available U.S. Forest Service vegetation map (Northern California Interior, CalVeg Existing Vegetation (EVEG) 2009) with a Forest Service Activity Tracking (FACTS) geodatabase (2012) that represented all management activities (i.e., human-caused alterations in stand composition). Using management history (FACTS) to define simple stands was essential because thinning practices increase the stand’s average tree diameter (Stephens and Moghaddas 2005), and thus will change the GIS stand designation from predicted low to high quality marten habitat (CWHR 2006) despite loss of both forest cover and understory structure. A change detection analysis was conducted and inaccurate polygons (<5 %) were manually updated and modified (R. Martinez, LNF, GIS coordinator, personal communication). Our final product was a map at 30 × 30 m resolution that classified each

Fig. 1 Our study occurred in two independent sites (Humboldt Peak, Swain Mountain) within Lassen National Forest, California. We detected and/or radio collared Pacific martens in the hexagon sample units highlighted in grey



stand into one of our three categories (Supplemental Table A1). Vegetation characteristics differed between stand types, most prominently between complex and open (Supplemental Table A2). Canopy cover, basal area, shrub cover, sapling cover, and number of sound logs differed between stand types, confirming a structural difference between our GIS classifications.

To ensure that we were studying martens exposed to gradient of stand types, we divided the landscape into 61 6.2 km² hexagons (Fig. 1) and stratified our live trapping effort. Using a 3-km grid, we evenly

distributing trapping effort among hexagons with either >60 %, 40–59 %, or <40 % complex stands. We used modified Tomahawk live traps (108 model, Hazelhurst, Wisconsin, USA) and chemically anesthetized martens (Mortenson and Moriarty 2015) to collect samples and fit adults with a VHF collar (MI-2, Holohil Systems LTD., Carp, Ontario, Canada). We also deployed GPS collars programmed to collect location data every 5 min (Quantum 4000 Micro-Mini, Telemetry Solutions, Concord, California, USA) on individuals that previously wore VHF

collars. We collected telemetry data (VHF triangulations and other point locations) weekly and, for GPS, during 1–8 days per season when the marten was moving (Moriarty and Epps 2015). We restricted our analysis to locations with predicted error less than 50 m (Moriarty and Epps 2015). We sampled only martens that were >2 years old.

Both experimental and observational approaches required that we estimate home ranges. Titration experiments required placing detection stations in locations used exclusively by individual martens, and the non-incentivized telemetry study required determining stand preferences within home ranges. Because the titration experiments were conducted before all the telemetry data were collected, we estimated use areas for these experiments by generating minimum convex polygons once 20 locations were collected. Later in the project we had more location data, and for the purpose of estimating stand use within home range, we used time-influenced Local Convex Hulls (50–583 locations/individual within a season; Lyons et al. 2013).

We captured and processed martens using methods approved by Oregon State University's Institute for Animal Care and Use Committee (Permit: 3944, 4367) and California Department of Fish and Wildlife Memorandum of Understanding with a Scientific Collecting permit (Permit: 803099-01). We used capture techniques that minimized spread of potential diseases (Gabriel et al. 2012) and followed recommendations by the American Society of Mammalogists (Sikes, Gannon and ACUC 2011) and the Association for the Study of Animal Behaviour (ABS 2012).

Incentivized food-titration experiments

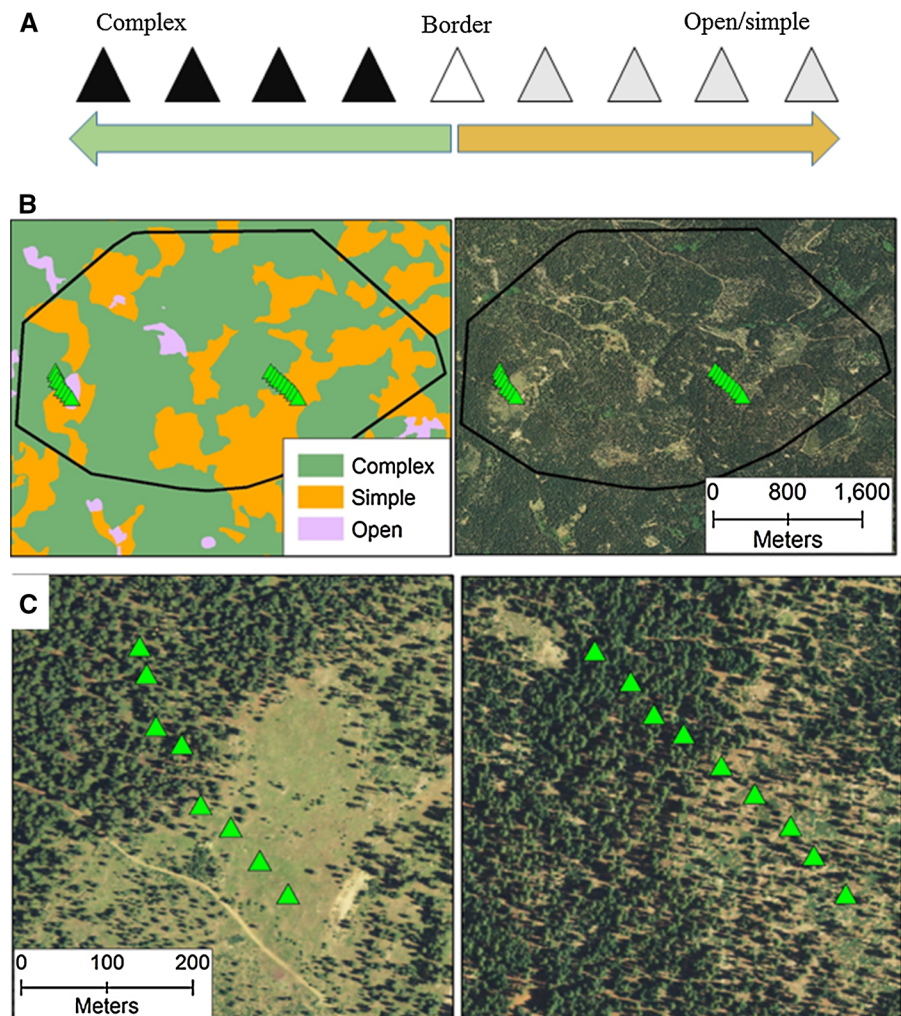
We conducted each titration experiment within an individual's home range where it had exclusive use (its territory) to minimize intraspecific interactions and to reduce the possibility that >1 marten of the same sex visited bait stations. Titration experiments used 400-m linear arrays of 9 detection devices (stations) spaced 50-m apart. We first used a stratified random design to identify potential locations with contrasting stand types, then examined each location to ensure an entire array could be placed within selected stand types. The center station was placed at the border between a complex stand and either a simple stand or opening, and the array was placed perpendicular to the edge boundary (Fig. 2).

We conducted two experimental treatments for each marten: (1) complex into open and (2) complex into simple (Fig. 2). Subjects received these treatments in random order within each season (winter and summer) and no individual marten had more than one titration experiment available at any one time.

We detected martens using track plate stations composed of Coroplast triangular enclosures and aluminum plates coated with printer toner, a piece of tacky white paper for track collection, and approximately 50 g beaver meat as bait (Ray and Zielinski 2008). We applied a commercial scent lure (Gusto, Minnesota Trapline Products, Pennock, Minnesota, USA) to each station at the beginning of each experiment. We monitored stations for a minimum of 16 days, replacing bait and track paper every 4–5 days, for a total of 4 survey visits. We monitored stations within the titration experiment using digital remote cameras and verified that the individually marked radio collared marten visited the stations.

We first evaluated if there was a difference in each marten's willingness to move into stand types between season (summer, winter), comparing data from martens that had been exposed to the same array during both seasons. If we detected a seasonal difference, we evaluated stand use for each season in separate models. Otherwise we combined data for both seasons. We used a generalized linear mixed model (GLMM) with logit-link to identify differences in the relative odds of a marten using different stand types (Grueber et al. 2011). We included random effects for 'individual' home range and for the experimental 'array' nested within home range to account for lack of independence caused by potential differences in marten behavior and repeated experiments within each home range. We also included random effects for titration 'stations' within arrays to account for possible spatial correlation of nearby stations, and for 'visit' nested within array to account for temporal correlation of visits. We report the contrast between seasons within stand types (e.g., odds of detection in complex stands during winter versus summer) using the `glht` function in package `multcomp` and report Wald Z statistics and adjusted p-values for multiple comparisons (Hothorn et al. 2014). The final mixed model allowed us to estimate the willingness of martens to travel into a simple or open stand while accounting for the paired comparison of adjacent complex stands.

Fig. 2 **a** A conceptual diagram of 9 detection devices within a food-titration experiment. The border station was placed between stand types that differed in structural complexity, contrasting between complex and simple or open. **b** Male home range M01 (*black outline*) with GIS designated patch map and aerial photograph to depict examples of titration experiment locations in this forested landscape. **c** Zoomed in titration lines within M01's home range and aerial photographs as featured in B, *left* complex into open, *right* complex into simple



Second, we evaluated if the distances martens were willing to travel into each stand type differed during each season. Using a GLMM, we evaluated support for an effect of distance within stand type. Distance from the edge of complex stands was included in the model for simple and open stands as an interaction between stand type and distance. Distance for stations in complex habitat was set to zero. We used Wald Z statistics to determine if the interaction between distance and simple stand or if the interaction between distance and openings were supported by the data. Our models included random effects for 'individual', 'array', 'station' and 'visit' as above. We used R version 2.15 (R Core Team 2013), fit GLMMs using the `glmer` function and bound optimization by quadratic approximation within the `lme4` package (Bates et al. 2013).

Telemetry (no food incentive)

We conducted analyses to (1) assess habitat selection within home ranges, and (2) quantify whether distance from the edge of complex forest influenced stand selection. To evaluate stand preference we used a Manley–Chesson selection index (α) (Manly 1974; Chesson 1978). We defined individual GPS locations as stand 'use' and assumed all stands within the home range were 'available' (Jones 2001). Martens regularly moved greater than 7 km within their range during a 24 h period, so we feel the assumption of availability is reasonable. We calculated the index (α) for each individual's summer and winter home range as the proportion of used versus available, where used was the number of locations in a stand type divided by the sum of

individual locations, and available was the area in a stand type divided by the area of an animal's home range.

For our second analysis, we assessed whether there was a preference zone within stands (Hussey 2010), or a distance from the edge of an adjacent stand that martens used disproportionately. Using the Euclidean distance Spatial Analyst tool in ArcMap 10.1 (ESRI, Redlands, California, USA) we calculated the distance of each location from the edge of each stand. Distance data were divided into 50-m classes, below our expected location accuracy of 28 m (Moriarty and Epps 2015). For each individual winter and summer home range, we calculated a distance selection index within each stand type where used was the number of locations within a distance class divided by the sum of locations in a stand type. We defined 'available' areas as those within the distance class divided by the total area of each stand type. We interpreted indices and 95 % confidence intervals greater than 1 as 'selection' and less than 1 as 'avoidance'. Finally, we used a GLMM with an identity link to assess whether there was a difference in stand or distance selection between season or by sex, with 'individual' as a random effect. Our data included locations collected over short time periods, but our response (α) was unaffected by temporal autocorrelation (Manly et al. 2002) because we stratified our observational unit, a marten, over a gradient of stand compositions with our initial trapping efforts.

Our final dataset included 54 captured martens (37 male, 17 female), of which 38 (26 male and 12 female adults) were radio collared. We conducted 37 titration experiments within 21 marten territories (12 male, 9 female) during 2010–2011 (summer) and 2010–2013 (winter). We calculated seasonal home ranges for 24 individuals with greater than 50 locations: 16 males (12 summer, 13 winter) and 8 females (5 summer, 5 winter). Each home range was a mosaic of the three stand types (Supplemental Table A3). Mortalities of radio-collared animals created unequal sample sizes in our paired experiments (summer mortalities = 10 male, 0 female; winter mortalities = 0 male, 4 female).

Results

Incentivized food-titration experiments

Marten detections did not differ between seasons in complex stands ($z = -1.13$; $P = 0.59$), but did differ

by season within open ($z = 7.12$; $P < 0.001$) and simple ($z = 3.32$; $P < 0.01$) stands ($n = 12$ experiments, 8 martens). Therefore, we estimated the odds of detecting martens in each stand type separately in the summer and winter seasons.

Summer

In summer, the odds of detecting a marten in complex habitat were 97 times higher than in simple stands and 1282 times higher than in openings (Table 1, $n = 24$ experiments, 11 martens). The odds of detecting martens were 28 times less if the station was on the border between openings and complex stands than within a complex stand (Table 1), suggesting the negative influence of the opening extends into the adjacent complex stand. This was not observed when simple stands were adjacent to complex stands (Table 1, 1.1 times less). Variances (SD) for the random effects were high: 7.6 (2.7) for individual marten, 3.6 (3.7) for array, 4.1 (2.0) for each station, and 2.7 (1.6) for survey visit, suggesting martens differed in their willingness to visit baited stations in simple stands and openings. Distance from the border had no effect on the odds of detecting a marten in openings and simple stands (Table 1). In simple stands, martens either moved along the entire array or did not enter the stand. Martens did not enter openings and avoided stations 50 m within complex stands adjacent to openings (Supplemental Figure A2).

Winter

Overall, selection of stand types by martens was less dramatic during winter, when the odds of detecting a marten in complex stands were only 3 times higher than in simple stands and 10 times higher than in openings ($n = 19$ experiments, 11 martens; Table 1). Thus, martens were more readily detected in simple stands and openings during winter than during summer. Martens were equally likely to be detected at border stations of open or simple stands as at any station in a complex stand (Table 1). Variances (SD) for the random effects were low: 0.0 (0.0) for individual marten, 4.5 (2.1) for array, 1.3 (1.5) for station, and 4.3 (2.1) for survey visit; suggesting individual variation between martens' willingness to visit baited stations in open and simple stands was less important than variation across repeat visits and

Table 1 Fixed effects coefficients for the final generalized linear mixed model describing Pacific marten (*Martes caurina*) food-titration experiments (n = 37 titrations, 21 individuals)

Contrasting variables	Summer				Winter			
	Odds ratios	95 % CI	Wald's Z	P	Odds ratios	95 % CI	Wald's Z	P
Complex versus simple	96.7	17.3–980.7	−4.62	<0.0001	3	0.5–12.3	−1.91	0.06
Border—simple/complex	1.1	0.1–15.7	−0.05	0.96	1.4	0.2–8.5	−0.37	0.71
Distance into simple			−1.08	0.28			−0.46	0.64
Complex versus open	1281.5	189.6–20,424.8	−6.18	<0.0001	9.8	3.6–34.1	−4.07	<0.0001
Border—open/complex	28.2	3.8–365.8	−3.02	0.002	2.3	0.5–12.3	−1.08	0.28
Distance into open			−1.47	0.14			−0.85	0.40

We report the odds ratios of marten detection between stand types and within a season (summer/winter). Data were collected in Lassen National Forest 2011–2013

arrays. Distance from the border had no effect on the odds of detecting a marten in either simple or open stands because martens frequently were detected along all stations in the array regardless of stand type (Table 1, Supplemental Figure A2).

Telemetry (no food incentive)

Unlike incentivized experiments, we did not detect differences in stand use between seasons (Fig. 3; $F = 2.2$, $P = 0.53$). Marten, the random effect, did not explain as much variance (marten = 3.05, $SD = 0.12$) as in summer titration experiments. Instead, during both seasons, martens preferred complex stands, avoided simple stands, and strongly avoided openings (Fig. 3). Males and females did not appear to use stands differently within each season (Supplemental Figure A3), but our sample of females was small within season ($n = 5$) and we did not model those data.

After accounting for stand preferences (Fig. 3), effects of distance class within any stand type and season varied (Fig. 4). Martens preferred interiors and avoided edges while in complex stands, but when in simple stands and openings preferred edges adjoining complex habitat (Fig. 4). Preferences for other distance classes were not statistically significant. However, within each distance class, use of openings and simple stands varied significantly between seasons (Levene's test, $P < 0.01$), suggesting important potential differences in how martens perceive stands during summer and winter. In complex stands, martens used distance classes >125-m slightly more than they were available, especially in winter, reflecting weak

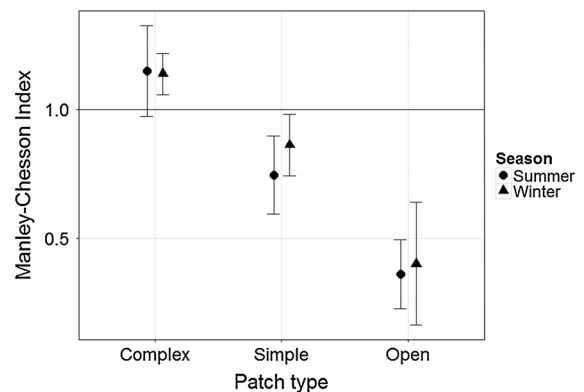


Fig. 3 Selection indices (mean and 95 % confidence intervals) for different patch types by season, estimated from non-incentivized methods [telemetry locations from 24 adult martens (8 female, 16 male)]. We observed significant differences between marten use of patch types ($F = 17.5$, $P < 0.01$), but no difference by season ($F = 2.2$, $P = 0.16$)

selection for interior portions of complex stands during winter (Fig. 4a). Martens used simple and open stand interiors more often during summer than winter (Fig. 4b, c).

Discussion

Structurally simple stands and openings, often created for fuel reduction treatments, substantially reduced the functional connectivity of landscapes for martens. Both food-titration experiments and telemetry showed that martens were less likely to use simple stands and much less likely to use openings compared to complex

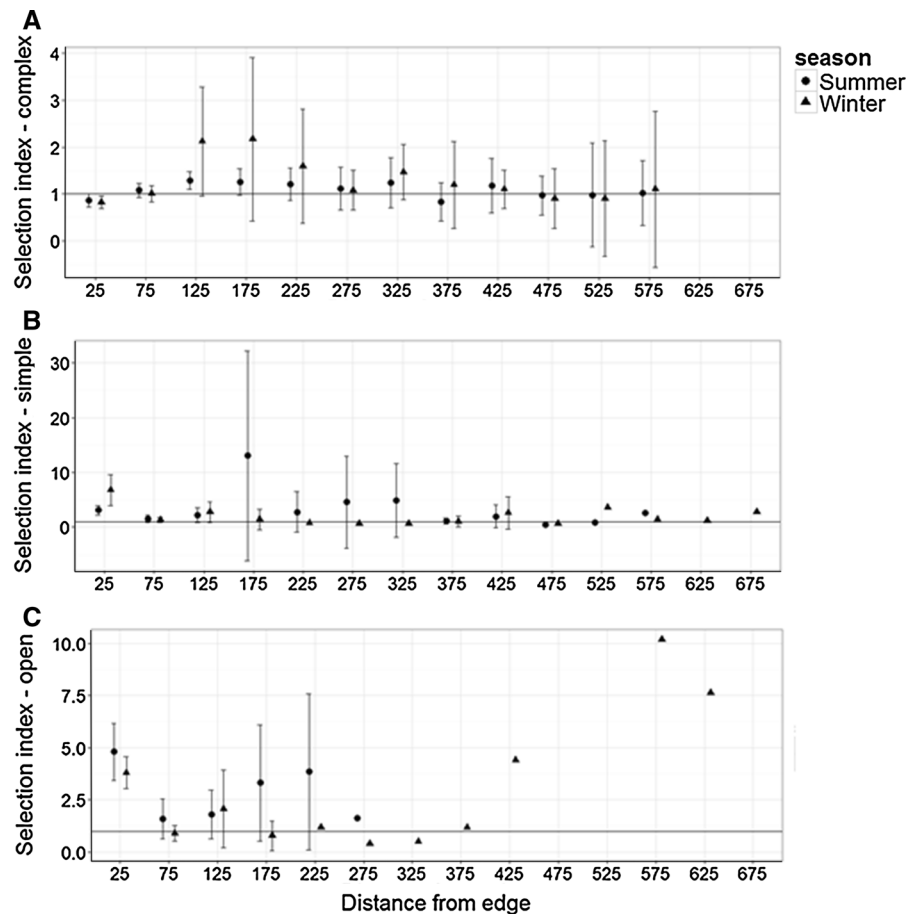


Fig. 4 Selection indices for martens (mean, with 95 % CI reported for $n > 1$) at distance classes *within* stand types, using non-incentivized methods (telemetry locations). **a** Marten in complex stands may have a weak preference for distances greater than 125-m, predominantly during winter ($n = 24$ martens, 6797 locations). **b** Marten use within simple stands reveals a high amount of variance within each distance class, especially during summer ($n = 24$ martens, 2190 locations).

c Not all martens traveled in openings and the number of locations was disproportionately low (<5 % of marten locations); however, our data reveal increased variation by distance class up to 225 m, especially during summer ($n = 19$ martens, 454 locations). The single points >175 m from edge resulted from one male individual using simple stands and openings created by a forest fire in 2001 (Storrie Fire)

stand types. These conclusions are consistent with previous research showing that martens seldom enter openings without tree cover (Cushman et al. 2011). However, our findings reveal that subtle changes to forest structure (e.g., thinning), typically assumed to be less harmful to the viability of forest-dependent populations than tree removal (Kalies et al. 2010), also negatively impacted functional connectivity. Increasing structural complexity within these managed stands could provide necessary requisites for marten persistence: decreased predation risk (Drew 1995), procurable prey (Andruskiw et al. 2008), and sites for denning and resting (Corn and Raphael 1992; Raphael

and Jones 1997). Our study provided evidence that these requisites affected marten stand use, and that functional connectivity may be influenced by the amount of snow cover.

Using both experimental and observational approaches provided important perspective for interpreting marten habitat use. Our food-incentive and telemetry results differed in respect to how martens used simple stands and openings. Telemetry revealed martens avoided simple stands and openings in each season equally. In contrast, martens were willing to use these stands during winter with food-incentive. Non-invasive survey methods for forest carnivores

often use bait and lure (Long et al. 2008) and many landscape habitat models have been built using detection data from baited stations (Kirk and Zielinski 2009). Marten habitat models built from summer and winter baited survey data can differ substantially (Zielinski et al. 2015), and our findings demonstrate that this difference may be important: detections at bait stations in simple stands and openings during winter may not reflect normal habitat preferences.

Seasonal differences in marten stand use can be explained by two alternate but not mutually exclusive hypotheses: predation risk and food availability. Forest simplification seemed to most reduce functional connectivity in summer, and our incentive-based experiments allow us to conclude avoidance was largely due to predation risk because martens commonly visited stations in adjacent complex stands. Even in the case of high food resource availability (i.e., bait), martens would not move through openings or simple stands in summer. In fact, martens avoided the border of openings 50 m within complex stands, as similarly observed elsewhere (Heinemeyer 2002). During winter martens were willing to enter simple stands and openings, possibly because deep snow may exclude predators (e.g., bobcat (*Lynx rufus*)) that cannot easily travel in snow (Krohn et al. 2004). In contrast, martens avoided openings during winter in areas where lynx (*Lynx canadensis*) would be an effective predator in deep snow, including the Rocky Mountains (e.g., Cushman et al. 2011) and eastern boreal forest (Hodgman et al. 1997; Payer and Harrison 2003). In our study area, raptors likely expand their home ranges or move to lower elevations during winter. Unlike McCann et al. (2010), we observed low mortality during winter and high mortality during summer (Moriarty, unpublished data). Thus, winter snows in the Cascade and Sierra Nevada Mountain ranges may trigger elevational migration of predators and decrease the risk experienced by martens during summer.

Unexpectedly low snow deposition during the winter of 2012 provided anecdotal evidence that snow depth can mediate marten use of different stand types. During that winter, but not the preceding or following winter when snow was deep, our titration data demonstrated that the odds of detecting martens in open and simple stands were indistinguishable from summer (Supplemental Figure A2). Therefore, functional connectivity may vary with snow depth and be greater in years with deep snow. Changing climates

are expected to reduce winter snowpack in our study area by more than 30 % (Klos et al. 2014), which we predict will decrease functional connectivity for martens.

Predation risk alone does not fully explain marten stand use. Differences in prey availability may also influence stand use, as martens' metabolic requirements require strategic and effective foraging. Declining food resources and increased activity make carnivore populations energetically vulnerable (Scantlebury et al. 2014). Martens consume 17–29 % of their body weight daily (Gilbert et al. 2009) and prey may significantly limit marten populations (Carlson et al. 2014). We suspect variation in marten use of openings and simple stands was related to uncharacterized differences in structural complexity that sometimes allowed for successful foraging and behavioral thermoregulation. In summer, martens may use simple stands to hunt chipmunks and ground squirrels (i.e., *Tamias spp.*, *Otospermophilus beecheyi*, *Callospermophilus lateralis*), the abundance of which increases or remains similar in response to some fuel treatments (Fontaine and Kennedy 2012; Stephens et al. 2014a). In winter, ground squirrels hibernate and most birds migrate, making food less available. Further, snowshoe hares (*Lepus americanus*) require low hanging branches and sapling cover for winter forage and resting (Ivan et al. 2014), which may explain low densities in simplified forests (Homyack et al. 2007). Therefore, with less predation risk in the winter, hunger may drive martens to exploit artificial baits in stand types they would not use during summer. Similarly, black-capped chickadees (*Poecile atricapilla*) were willing to move into gaps during food-titration experiments in winter only when they experienced energy stress caused by habitat fragmentation (Turcotte and Desrochers 2003). Without bait incentive, martens avoided openings and simple stands and instead used the interior of the complex stands where increased foraging opportunities were likely during this prey-restricted season.

Individual variation can have population-level impacts (Wolf and Weissing 2012), as personality may influence reproduction and dispersal (Cole and Quinn 2014). During summer, several martens were willing to travel within simple stands, as evidenced by the larger influence of individual as a random effect in our titration models. For telemetry data, variance of selection indices for different distance classes within

stand types also was higher in the summer in both simple stands and openings. Thus, despite overall avoidance of simple stands and openings, both study methods revealed significant variation in how adult individual martens used simple stands and openings—especially during summer when we hypothesize there was increased food abundance in these stands. Individual variation emphasizes need for robust sample sizes and replication (Johnson 2002), and we obtained consistent results across two sites.

Our study was conducted in an area intensively managed to reduce the threat of large-scale severe fires. We have demonstrated that martens do not perceive simplified forested stands as functionally connected. Complex stand structure may provide conditions suitable to prey and additional escape cover from predators. However, complex structure is also inherently prone to severe and high-intensity fire (Stephens et al. 2014b). Additional research is necessary to (1) balance additional structure within stands while achieving goals to reduce threat of large fires and (2) to understand spatial composition and configuration of habitat in relation to marten connectivity. Although thresholds have been detected in the amount of forest cover necessary for marten persistence (e.g., Hargis et al. 1999), it is unknown whether a similar threshold exists in the amount of simplified forest structure. Information on such thresholds and whether diversification of stand structure can make simple stands more favorable is urgently required.

Conclusion

Functional connectivity at landscape and regional scales is essential for gene flow, population supplementation, and metapopulation persistence (Crooks and Sanjayan 2006), particularly in the face of stochastic events such as large high-severity fires. At the individual level, functional connectivity among preferred habitats is also required to enable martens to acquire sufficient resources. Our study indicates that movement of resident adult martens is largely restricted to forested stands with dense, structurally complex cover, especially in summer when adult marten survival may be most at risk. Previous work shows that adult survival, rather than fecundity, is most important for marten population sustainability (Buskirk et al. 2012). Seasonal differences between incentivized and observational methods

suggest that detections at baited stations may not represent typical habitat preferences in the winter, but our incentivized experiments may reflect the ability of martens to enter non-preferred stand types during periods of increased motivation (e.g., hunger, intense curiosity, dispersal). We propose that deep snow cover reduces predation risk and facilitates increased movement among stand types. In high-elevation forests, future management strategies should increase structural diversity within stands to increase odds of marten use. Habitat connectivity improves population viability, which may be especially important in a changing climate that may result in decreased snow pack in marten ranges (Loss et al. 2011). Arranging stands to allow functional connectivity may therefore be essential. Directed research is needed to provide methods to increase structural diversity in managed stands while meeting the objective of reducing fire risk. The interaction of climate (mediated by snow depth), predator diversity and prey resources, and vegetation features that provide habitat combine to affect marten movements in montane forests.

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