

AN ABSTRACT OF THE DISSERTATION OF

Katie M. Moriarty for the degree of Doctor of Philosophy in Wildlife Science presented on November 21, 2014.

Title: Habitat Use and Movement Behavior of Pacific Marten (*Martes caurina*) in Response to Forest Management Practices in Lassen National Forest, California.

Abstract approved: _____

Clinton W. Epps

ABSTRACT

Some of the most pressing conservation concerns involve declining populations of species with low fecundity and highly specialized foraging and reproductive requirements. Yet, we often lack a functional understanding of how individuals of those species interact with their environment, specifically how their movement is affected by human-induced changes. In order to maintain connectivity and viable populations, public land managers require science to inform how changes in structure affect the individual movements and thus population connectivity of sensitive species. I collected detailed movement data on Pacific martens (*Martes caurina*) in Lassen National Forest, California, during 2010-2013. Martens are small carnivores that are closely associated with old forest elements (e.g., large snags and logs). Marten populations rapidly decline with loss and fragmentation of forest cover. As such, martens are a U.S. Forest Service Management Indicator Species and a Species of Special Concern in the state of California. My goal was to understand martens' behavior in forest patches that were altered by thinning to remove ladder fuels—small diameter trees, understory vegetation, and branches near the ground. Such fuels treatments are increasingly prevalent on public lands, especially in dry forests, to reduce risk of high-severity and high-intensity fire.

Although previous research suggested martens selection for dense forest and avoid gaps in forest cover, no information was available describing martens' use of simplified thinned patches. The objectives of my dissertation were to: (1) test whether marten movement and activity could accurately be measured using miniature GPS collars, and (2) evaluate marten use, selection, and behavior in patches that differed in structural complexity.

Global positioning system (GPS) telemetry provides opportunities to collect detailed information from free-ranging animals with a high degree of precision and accuracy. Miniature GPS collars (42-60g) have only been available since 2009 for mammals and have not been consistently effective. Furthermore, all GPS units suffer from non-random data loss and location error, which is often exacerbated by dense vegetation. Given these constraints, it was questionable whether GPS collars would be an effective tool for studying martens. In Chapter 1, I evaluated how satellite data and environmental conditions affected performance of GPS units. I used a paired experimental design and programmed the GPS unit to retain or remove satellite data before attempting a location (fix). I found that short intervals between fix attempts significantly increased the likelihood of fix success. Locations estimated using at least 4 satellites were, on average, within 28 m of the actual location regardless of vegetation cover. Thus, location estimates at short intervals with >4 satellites were not typically biased by dense vegetation.

Accurate fine-scale information on martens was necessary to quantify and interpret patch use and habitat selection. I evaluated martens' use and behavior in three forest patch types that differed in structural complexity (complex, simple, and open). In Chapter 2, I quantified use patch use in two seasons—summer and winter. I used food-

titration experiments to standardize motivation of martens to enter different patch types and compared these short-term incentivized experiments with year-round observational telemetry data (GPS and very high frequency telemetry). Martens selected complex patches and avoided both simple patches and openings, but not equivalently—openings were strongly avoided. With baited incentive, martens were more likely to enter simple patches and openings during winter, when deep snow was present. Because marten patch use differed during winter, I concluded that researchers should use caution when using seasonally collected data to create year-round habitat models. Overall, movement was most limited during summer when predation risk likely deterred martens from moving through simple patches and openings.

In Chapter 3, I quantified habitat selection and marten behavior using fine-scale movement data. I evaluated movement-based habitat selection at two scales: (1) selection of home ranges within landscapes and (2) selection of patches within the home ranges. I characterized marten movement patterns and tested whether variance, speed, and sinuosity of movements differed by patch, sex, and season. Martens selected home ranges with fewer openings than available in the landscape, and selected complex patches over simple patches and openings within their home range. On average, martens moved approximately 7 km per day and greater than 1 km per hour – which is notably high for a 600-1000g mammal. Martens moved more slowly, consistently, and sinuously in complex patches. In openings, martens traveled linearly with greater variance in their speed. In simple patches, movement generally was linear and rapid with some variation. I hypothesized that martens used complex patches for foraging and acquisition of resources, traveled through simple patches with the potential for infrequent foraging bouts, and very infrequently crossed openings. Although I found some differences in

movement behavior between sexes and seasons, behavior was generally consistent for both sexes in different patch types. I provide general conclusions in Chapter 4 and discuss considerations for future research and management.

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Habitat Use and Movement Behavior of Pacific Marten (*Martes caurina*)
in Response to Forest Management Practices in Lassen National Forest, California

by
Katie M. Moriarty

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APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Katie M. Moriarty, Author

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This work synthesizes ideas and efforts from a dynamic community. Although I have the honor of presenting this new body of knowledge, it would not have been possible without the support and assistance of this larger group.

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** With the exception of the field crew, people were listed in alphabetical order by first name.*

CONTRIBUTION OF AUTHORS

My committee, Clinton Epps, William Zielinski, Matt Betts, and John Bailey, all contributed to study design suggestions throughout the project and assisted with manuscript edits. Dalton Hance provided statistical suggestions for the functional connectivity chapter.

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CHAPTER 1 : RETAINED SATELLITE INFORMATION INFLUENCES GLOBAL
POSITIONING SYSTEM (GPS) PERFORMANCE IN A FORESTED ECOSYSTEM:
AN EXPERIMENT WITH MINIATURE GPS DEVICES (<60G)

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ABSTRACT

Miniaturization of GPS components allows studying movements of animals <1kg. However, GPS units suffer from non-random data loss and location error. GPS units efficiently estimate locations by utilizing stored satellite configuration information, including both almanac data reflecting satellite positions at weekly temporal scales and ephemeris data reflecting positions valid less than 4 hours. Using the smallest GPS collars (45-51g) available for mammals, we evaluated how satellite data and environmental conditions affected performance of GPS units in 27 mobile trials and field reliability during 56 deployments on Pacific marten (*Martes caurina*). We programmed a test GPS unit to retain or remove satellite data (continuous/cold start mode) before attempting a location (fix), thereby mimicking short and long fix intervals. We used generalized linear mixed-models to identify factors that predicted fix success in each mode. In continuous mode, fix success was 2.2 times higher, not strongly influenced by environmental obstructions, and improved after a location with ≥ 4 satellites (3-D). In cold start mode, fix success was negatively correlated with vegetation cover. Location

error was less for 3-D fixes. Censoring cold start fixes with 3 satellites (2-D) and 2-D locations prior to the first 3-D fix in continuous mode decreased location error by 91% and 55%, respectively, ensuring all locations were accurate within 50m. Although we could not isolate the influences of ephemeris versus almanac data, the significance of previous fix success and reduced battery expenditure underscores the benefits of ephemeris data and short fix intervals. Field deployments exceeded expectations and miniature GPS are a promising tool; however, only 66% of 56 units functioned upon delivery. Once tested and deployed, 28% failed. This study demonstrates the need for integrating standardized GPS testing protocols with the same fix schedule as field deployments for wildlife research, especially for miniature GPS units or animals inhabiting obstructed environments.

INTRODUCTION

Global positioning system (GPS) telemetry provides opportunities to collect detailed information from free ranging animals with a high degree of precision and accuracy (Frair et al. 2010). Recent miniaturization of GPS receivers and electronics has enabled researchers to use lightweight GPS collars (80-125g) to study mammals greater than 2.5 kg (Blackie 2010, Recio et al. 2011, Brown et al. 2012, Adams et al. 2013). Smaller “miniature” GPS collars (42-60g) for mammals have been available since 2009, but have not been tested or reported in peer-reviewed scientific literature (but see Cypher et al. 2011, Thompson et al. 2012). However, this technology is not without disadvantages. GPS failures and technical malfunctions can severely reduce performance, limiting sample size and data quality (Hebblewhite and Haydon 2010). Use of lightweight GPS collars has been cautioned because limited battery life may increase malfunctions and

reduce their functionality as a data collection tool (Blackie 2010, Cypher et al. 2011). This limitation is compounded by GPS error which affects all GPS units regardless of size, and includes both location error and failed location attempts resulting in missing data (Frair et al. 2010). GPS error can systematically bias resource selection studies (Frair et al. 2004, Visscher 2006), home range estimation (Horne et al. 2007b), and evaluation of movement patterns (Hurford 2009). As such, minimizing bias due to GPS error and maximizing battery life are upmost importance for research with free ranging animals, especially for miniature collars.

Although performance of any GPS device is affected by a range of environmental conditions and locations of available satellites (Grewal et al. 2007), during wildlife research, GPS error is most often attributed to satellite signal obstruction due to vegetation, topography, or animal behavior (Frair et al. 2010). Failed location attempts are most often associated with dense canopy cover (Frair et al. 2010, Recio et al. 2011), and a combination of factors (e.g., canopy cover, topography, satellite availability) can explain increased location error (Recio et al. 2011). Furthermore, GPS error may be compounded by multiple obstructions (Augustine et al. 2011). For instance, the bottom of a ravine may have both topographical and vegetation obstruction. Such interactions may differ between study areas and collar brands, potentially explaining the wide range in percent fix success (successful GPS locations divided by the total attempts) and location error reported in studies in mountainous terrain (Lewis et al. 2007, Sager-Fradkin et al. 2007). GPS error also may be influenced by animal behavior through individual habitat preferences or when an animal rests or dens in areas obstructed from satellites (e.g., burrows, cavities, buildings) (D'Eon and Delparte 2005).

A largely unrecognized factor that may influence GPS error is the fix schedule, or user-parameterized duration between fix attempts. Fix schedule has been assumed to have little (Cain et al. 2005) or no influence on GPS error, but this has not been verified. GPS error may be reduced, and battery life increased, if the time between fix attempts is short enough to allow the GPS receiver to retain two types of satellite information: almanac and ephemeris data. Almanac data include coarse orbital parameters of satellites and are valid for several weeks (2008, Tomkiewicz et al. 2010). Ephemeris data are precise satellite locations and are valid for one to four hours depending on the GPS receiver (1996, Grewal et al. 2007, Tomkiewicz et al. 2010). Retaining satellite information reduces the time and power necessary to obtain a fix (Singh 2006), and as such may allow the GPS time to average its position and decrease location error. For instance, Augustine et al. (2011) simulated the influence of time on fix success when the GPS receiver was 60% obstructed by vegetation; they predicted ~90% fix success at a 15 minute fix interval but only ~50% fix success at a 2 hour fix interval, presumably because of the declining relevance of the ephemeris data over that longer time interval. Although these simulations were not intended to be extrapolated to different GPS receivers and study areas, they suggest that fix success is proximally affected by fix interval and ultimately by satellite information, particularly ephemeris data. Simulations or tests to evaluate the influence of fix schedule on location error have not been performed.

Here, we evaluate effectiveness of the smallest GPS collar commercially available for mammals (42-52g) in conjunction with a study on the movement of a small carnivore, Pacific marten (*Martes caurina*; 0.5-1.2kg). Our study focuses on factors that affect fix success, with particular emphasis on the role of satellite information. Martens were an ideal species on which to test fix success because their habitat preferences and behavioral

characteristics are similar to mammals with the lowest reported GPS collar fix rates: fishers (*Pekania pennanti*) (25-38%, Thompson et al. 2012) and wolverines (*Gulo gulo*) (46%, Mattisson et al. 2010). Martens are often associated with rugged topography and dense forests with multi-layered canopies (Spencer et al. 1983), which are known to obstruct GPS signals and increase location error. In addition, martens rest in highly obstructed areas such as tree cavities for periods greater than 4 hours which surpasses the maximum duration for which ephemeris data are useful. To infer the accuracy of data collected using these collars on free-ranging marten, we conducted a controlled experiment with repeated mobile trials (GPS unit was actively moving) of a test GPS collar within known marten home ranges. Further, we discuss the benefits and shortcomings of miniature GPS collars for field research as this represents the first formal study using these devices on small, free-ranging and forest associated mammals.

First, we compare the degree to which retention of satellite information (ephemeris and almanac data) affects fix success in forested patches that differ in structural diversity and overhead cover. Second, we model how potential environmental obstruction, retained satellite information, or the combination of factors influences fix success. We use these predictions to evaluate how fix success differs across our study area during active movement by martens (when valid ephemeris data would be available, continuous mode) or after emerging from an obstructed rest site or den (when ephemeris data would no longer be valid, cold start mode). Third, we evaluated the performance and precision of the GPS units by testing whether time to estimate locations and location error differed in each mode. Lastly, we evaluated whether miniature GPS collars (cumulatively the GPS, very high and ultra-high frequency components) were an effective tool for studying forest associated mammals less than 1kg.

METHODS

Study area and stratification of patch types

We conducted trials of GPS telemetry devices in Lassen National Forest, California, during March 2011-January 2012. The study area was mountainous, with elevations ranging from 1500-2100 m. Forest stand types included red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole (*Pinus contorta*) or mixed conifer.

When designing our experiments, we stratified the landscape into three forest patch classifications that we predicted would influence marten occurrence. “Complex” stands had structurally diverse understories and overstory canopy cover (CC) ranging from 35-68% ($48.2 \pm 1.6\%$, $\bar{X} \pm \text{SE}$) as estimated with a moosehorn coverscope (Fiala et al. 2006). “Simple” stands had been subjected to a variety of forest management activities that reduced understory complexity and branches near to the ground; these activities typically reduced the density of flammable vegetation and resulted in overhead canopy cover between 15-48% ($26.3 \pm 2.1\%$). “Open” stands included natural or managed areas with little or no overstory canopy cover ($3.2 \pm 0.9\%$, 0-14%), including meadows, frozen lakes, and recently logged areas. We did not consider shrub cover in our stratification because patches of shrub and small trees were rare in these high elevation montane forests. Patch type was included in our analyses to represent potential influences of understory vegetation and stand density on GPS performance.

Experimental manipulation of satellite information memory

The receivers we evaluated were 48 track channel JP-18S4 GPS receivers (FMO Electronics, Langewiesen, Germany) in Quantum 4000 Enhanced Micro-Mini GPS collars (Telemetry Solutions, Concord, California, USA), hereafter "miniature GPS". We

tested these receivers in two forms: 1) a test device with a rechargeable battery and 2) marten-deployed collars. The test unit contained identical GPS components and software. At each fix attempt, we programmed the GPS to collect satellite information for a maximum of 120 seconds and then stay on for an additional 30 seconds in hopes of improving data quality.

We manually programmed the test unit to estimate locations in two modes: continuous and cold start. Continuous mode is comparable to standard GPS collar settings where almanac and ephemeris data are retained after downloading from satellites and can include three fix conditions: hot, warm, or cold start (Grewal et al. 2007, Tomkiewicz et al. 2010). A “hot start” fix can be acquired in less than 1-8 seconds depending on the unit if both almanac and ephemeris data are retained and there are ≥ 3 connected satellites. A “warm start” fix can be acquired within 25-35 seconds if only almanac data are retained with ≥ 3 connected satellites. A “cold start” fix could be acquired in 25-35 seconds if neither almanac nor ephemeris data are available with ≥ 3 connected satellites. Expected time to fix with a cold, warm, or hot start is similar among modern multi-channel GPS units (Tomkiewicz et al. 2010). We manually programmed test receivers to remain in “cold start” mode for selected trials. We used cold start mode to simulate a GPS on an animal that routinely uses obstructed areas for longer than 4 hours and predicted that mode would have the lowest fix success and highest location error. We were unable to program GPS units to collect data with only warm start conditions, which would be ideal for comparisons with animal-deployed collars as the GPS receiver could retain almanac data from previous downloads; however, we assumed that almanac data would be downloaded in the same amount of time as ephemeris data based on manufacturer specifications.

Mobile trials

We used mobile GPS testing to determine how satellite information influenced fix success in differing patch types. Our trials were conducted using a test device that was moved through the environment to simulate the movements of a marten. Although we considered traditional stationary GPS tests (D'Eon et al. 2002, Lewis et al. 2007, Frair et al. 2010), we concluded that mobile tests would better represent conditions for animal-deployed collars (Augustine et al. 2011). We conducted mobile trials with the test device attached to a saline-filled water bottle to simulate proximity to an animal's body (Frair et al. 2010). We attached 4 strings between the bottle and a cross made of plastic pipe, similar to the handle used for marionette puppets. The string length was such that the GPS receiver was at the height of a marten-sized mammal (~20cm from the ground) when held by the tester, who manipulated the cross to simulate the bounding movement expected from martens and moved the device from one side of their body to the other to minimize blocking satellites. Although this level of realism, specifically use of a saline-filled water bottle, may be more important for VHF telemetry testing (Millspaugh and Marzluff 2001), our goal was to replicate conditions experienced on martens. We considered alternative mobile testing methods (Cargnelli et al. 2007, Jiang et al. 2008, Recio et al. 2011), but these were inappropriate within marten home ranges and in patch types with dense amounts of woody material.

During mobile trials, we collected data in two GPS modes (continuous and cold start) using a paired design. We first created meandering transects approximately 2 km long with predetermined start and end points. Half the trials were completely within a single patch type (i.e., complex, simple, or open) and the other half transited a roughly equal amount of each patch type in a random order within each trial to discern differences

between GPS fix success within a single patch type and between patch types. We walked or skied along each transect with the GPS in a randomly chosen mode. At the end of that track, the GPS was reset to the alternative mode and we retraced our path. This ensured that data collected in both modes reflected similar conditions and time periods (within 2.5 hours). We assumed satellite availability and configuration would be similar within that period.

Along each transect we collected three types of data: 1) GPS fixes from the test device, 2) geo-referenced environmental data, and 3) a tracklog collected using a Bluetooth Garmin® 10x GPS positioned approximately 2 meters (m) above the ground at a scheduled fix rate of 15 seconds. We scheduled the test device to take fixes at the same 5-minute interval as the marten-deployed collars. We collected geo-referenced environmental data every 5 minutes, but offset the collection by 2.5 minutes from the test device to ensure the GPS receiver was moving when it attempted a fix. Observers collected site-specific environmental data, including patch complexity. Even though user-collected environmental data was offset by as much as 100 m within the 2.5 minute interval, the relative homogeneity of the patches chosen for our trials likely reduced the associated error. The tracklog was considered the reference position and location error was calculated as the Euclidean distance between the two corresponding spatial coordinates collected at the closest time (<31 seconds (s) passed between the paired GPS and tracklog locations due to tracklog inconsistencies). This approach was not ideal for estimating location error given that the Garmin 10X also had unknown associated error. However, that error was expected to be less than 10 m (Garmin 2006), whereas location error from low-quality fixes on GPS collars may exceed 500 m. Thus, while imperfect, we used this reference track to generate general description of location error in different

modes and habitats. Moreover, the paired design of our study allowed standardized comparison of relative error between modes.

Environmental covariates

Although the influence of environmental factors on GPS error is well known (Frair et al. 2010), we addressed the potential for interactions between environmental factors and satellite information (continuous, cold start) during mobile trials. After accounting for satellite information, we predicted that two environmental factors (vegetation and topography) would explain most variation in fix success. We did not directly replicate satellite obstruction due to animal behavior (e.g., resting in cavities) because our marten collars were set to take fixes only when the animal was moving using Telemetry Solution's SmartGPS technology (see manufacturer specifications and Brown et al. 2012), but our cold start mode simulated conditions encountered by a GPS receiver immediately after a marten emerged from a long rest in an obstructed location.

Topographic obstruction was represented by aspect, elevation, and satellite obstruction from topography. We calculated the number of available satellites at the mobile trial location and time using Trimble Planning software version 2.9 (Trimble Navigation Limited) (see Sager-Fradkin et al. 2007). Within our study area, there are few satellites between 315° and 45°, thus there were fewer satellites available for north-facing slopes than south-facing slopes. We calculated aspect and elevation in ArcGIS version 10.0 using a publically available 10-m resolution digital elevation model (Bowen et al. Accessed January 2010). We represented aspect by the variables northness ($\cos(\text{aspect} \cdot \pi / 180)$) and eastness ($\sin(\text{aspect} \cdot \pi / 180)$) (Zar 1999). Sky view factor (SVF) is a parameter corresponding to the amount of visible sky limited by topography. We used the program Sky-View Factor using the maximum number of calculated angles (64)

and a range of 30 pixels (Ošti et al. 2010, Zakšek et al. 2011). Complete satellite view (100%) indicated no obstruction due to topography. Our values for SVF ranged between 79-100% during our mobile trials; the study area had a SVF range between 57.2-100%, similar to other GPS tests (see Hansen and Riggs 2008).

GPS performance and modeling fix success

First, we compared fix success between patch types using a two-way factorial ANOVA adjusting with Tukey's Honestly Significant Difference to correct for multiple comparisons. We also calculated the risk ratio of a fix between all combinations of patch types (e.g., open vs. complex) in each GPS mode (Grimes and Schulz 2008).

We used generalized linear mixed-models with a logit-link to assess whether the probability of fix success was influenced by patch type or topographical obstruction (both cold start and continuous mode, paired trials), retained satellite information (continuous mode), or the combination of obstruction and satellite information (continuous mode). We represented topographical obstruction with SVF, elevation, and aspect. To describe whether satellite information was retained, we used binary variables indicating the presence/absence of previously acquired locations (previous fix) or previously acquired 3-D fix (≥ 4 satellites, previous 3-D fix). Track identity was retained as a random factor within each model using package lme4 (Bates et al. 2013) in program R (R Foundation for Statistical Computing, Vienna, Austria), because each track presumably experienced a unique combination of environmental effects. We used an information theoretic approach with Akaike's Information Criterion (AIC) to evaluate candidate models (Burnham and Anderson 2002), and used package MuMIn (Barton 2013) to average model coefficients from candidate models ($\Delta AIC < 4$) (Burnham and Anderson 2004) and calculated mixed-

model R^2 estimates (Nakagawa and Schielzeth 2013) to evaluate relative model fit. All figures were created in ggplot2 (Wickham 2009).

Location error was reported for each mode and patch type, and we used data permutation and a Wilcoxon-Mann Whitney test with a Bonferroni adjustment (following $\alpha=0.05$) for multiple comparisons to assess whether location error differed between patch types (Hothorn et al. 2008). The number of satellites acquired during a location can dramatically influence precision (Lewis et al. 2007), so for each mode we graphically depicted 2-dimensional (2-D) and 3-dimensional (3-D) locations, which require 3 and ≥ 4 satellites to obtain a fix, respectively. Battery life is a limiting factor for small collars, and we report time to fix (TTF) in each mode. We tested for differences in TTF between modes with data permutation and a Wilcoxon-Mann Whitney test.

Field data collection with miniature GPS collars – marten case study

As the first study using miniature GPS collars for mammals, we assessed functionality for field research. Marten GPS collars contained an identical GPS receiver as our test unit. In addition, GPS collars contained an ultra-high frequency (UHF) unit for remote downloading of GPS data and a very high frequency (VHF) transmitter to locate the collar. These features in concert with the GPS are essential for using the collars in the field. The GPS and UHF were powered with the equivalent of a 0.5 or 0.66-sized AA lithium battery. Expected battery life with continuous data collection was 11 or 14.3 hours depending on battery size (i.e., 0.5, 0.66), which equated to a minimum of 307 or 399 expected fix attempts, respectively. We chose the same schedule as the test units (5 minute fix interval) for evaluating movement paths, providing a minimum of 26 to 33 hours of data collection. To increase battery life when deployed on martens, we set GPS collars to attempt fixes only when activity sensors (accelerometers) recorded movement

(Brown et al. 2012), thereby largely avoiding fix attempts when the animal was resting in obstructed locations.

We tested marten deployed collars at two stages: as delivered from the manufacturing company and after marten deployment. Upon receipt from the manufacturer, we tested the GPS with our mobile trial methods (see above) in a large field with no topographical obstruction and at low elevation (1380 m) for a minimum of 25 minutes (4-6 fixes). We considered stationary tests, but on more than one occasion we observed that collars would function during stationary tests – but not when the collar was in motion. This may have occurred due to conflicts between the GPS and accelerometer attempting to record data simultaneously, but was often attributable to poor wiring, requiring refurbishment by the manufacturer. We considered the GPS acceptable if it obtained at least one fix with ≥ 4 satellites (3-D) that was accurate within 50 m. We tested the VHF with an R-1000 receiver (Communication Specialists, Orange, CA) and attempted to remotely download data. If all systems worked, we considered the GPS collar functional. If one or more systems failed, we considered the collar malfunctioning. We recaptured martens ≥ 10 days after GPS deployment, and considered the VHF functional if we received a signal within 30 kHz of the original frequency. We considered the GPS functional if the battery life (relative to expected battery life of 11 or 14.3 hours) and fix success were greater than 50%. We estimated battery life, the total amount of time the GPS was recording data, by adding the seconds for each GPS fix attempt (TTF). We report percent success during the first and last 9-month periods of our field work because we worked continuously with the company during the study to improve collar design and manufacturer tests before shipment.

Ethics statement

All necessary permits were obtained for the described study, which complied with all relevant regulations. 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). GPS deployments on martens were performed under anesthesia, and all efforts were made to minimize suffering and discomfort. We followed recommendations by the American Society of Mammalogists (Sikes et al. 2011) and used capture techniques that minimized spread of potential diseases (Gabriel et al. 2012).

RESULTS

We completed 27 mobile tracks with the test unit; 19 were paired with cold start and continuous modes and 8 were in continuous mode only. Track length was $\geq 1\text{km}$ ($\bar{x} \pm \text{SE} = 2317 \pm 145\text{ m}$) and the average duration was 55 minutes ($55 \pm 1.3\text{ minutes}$). We obtained an average of 14 fix attempts/track ($\text{SE} = 0.7$) and a total of 234 fix attempts in cold start and 366 in continuous modes.

Fix success

Fix success was higher in continuous (83.1%) than cold start (37.1%) mode (Figure 1). The GPS was 2.2 times more likely to obtain a fix in continuous mode than cold start mode ($\chi^2 = 128.78$, $P < 0.01$) and 1.2-6.6 times more likely to obtain a fix in continuous mode between patch types (Figure 1.1).

Fix success for trials remaining within a single patch type differed from trials that spanned all patch types, particularly in continuous mode and complex patch types ($\chi^2 =$

17.88, $P < 0.01$). We experienced an average $44 \pm 25\%$ fix success in complex patches ($n = 95$ attempts, 6 trials) in continuous mode if the unit initiated within the dense forest cover. In contrast, fix success in complex patches was greater than 93% if the GPS was initiated in either open or simple patches prior to entering the dense canopy (Table 1.1). The GPS was unable to obtain a fix in either cold start or continuous mode for the duration of 3 independent trials conducted entirely within complex patch types, suggesting a strong influence of satellite information on fix success.

Variables influencing fix success differed between continuous and cold start modes (Table 1.2). In continuous mode (previous 3-D fix), fix success increased with a previous fix in 3-D, but we observed inconsistent relationships with vegetation obstruction where fix success was positively correlated with complex and open patches and negatively correlated with simple. In contrast, fix success in cold start mode was negatively affected by increased vegetation cover and this was the only competitive model (Table 1.2).

Location error and time to fix

Location error did not differ between continuous and cold start mode when accounting for number of satellites and patch type (Table 1.3). Average location error was less for 3-D fixes ($\bar{x} \pm SE = 28.0 \pm 6.1$ m) than 2-D fixes (586.8 ± 64.0 m, $t=8.7$, $df = 82$, $P < 0.001$). Most (88%) of 3-D fixes were within 30 m and 97% were within 100 m of the true location (Figure 2a). Thus, 3-D fixes were accurate regardless of fix interval, previous 3-D fix, or mode. However, satellite information (mode) strongly influenced error of 2-D fixes. In cold start mode, location error for 2-D fixes ranged from 198.0 to 2097.7 m. In continuous mode, 2-D fixes ranged between 11.8 and 1772.4 m from the reference location (Table 1.3) and 2-D fixes with a previous 3-D fix in continuous mode had a median location error of only 30 m (Figure 2b). In cold start mode, censoring fixes

with 3 satellites (2-D) decreased average location error by 91%; in continuous mode, cold start censoring 2-D locations prior to the first 3-D fix decreased location error by 55% and ensured that all locations were accurate to within 50m.

Time to fix (TTF) was significantly less in continuous than cold start mode (39.6 ± 1.9 and 91.2 ± 3.2 seconds, respectively; $Z = 11.9$, $df = 86$, $P < 0.01$). Within continuous mode, TTF was significantly less when there was a previous fix: 38.4 ± 1.3 and 83.6 ± 4.2 seconds with and without previous fixes, respectively ($Z = 10.3$, $df = 119$, $P < 0.01$). There was no difference in TTF between cold start mode and fixes in continuous mode that lacked a previous fix ($Z = -1.4$, $df = 202$, $P = 0.15$), which emphasizes increased efficiency of the GPS with previous satellite information.

Field data collection with miniature GPS collars

GPS collars in the first test phase (direct from the company) functioned 66% of the time (56 new or refurbished collars). Malfunctions occurred with the GPS (27%), VHF (7%), and/or UHF (18%) systems. Following collar deployment on martens, we experienced 72.5% functionality ($n = 42$ deployments). Malfunctions were attributed to either GPS (20%) or VHF (12.5%) failure (the UHF could not be tested due to insufficient battery power).

We obtained between 6 and 681 fixes during marten collar deployments (285.1 ± 30.1 fixes). We collected GPS data on martens for 0 to 9.8 days with a 5-minute fix interval operating when martens were active. We had an average fix success of $66.4 \pm 2\%$. Of the fixes obtained, 50-92% per collar deployment were 3-D locations ($79 \pm 2\%$). Fix success improved during the course of our study: average fix success improved from 10% in the first 9 months to 60% in the last 9-months ($n = 4$ and 7 deployments, respectively). Average total battery life, summed across all periods when the collar was attempting a

fix, was 9.87 ± 1.3 and 11.0 ± 0.9 hours for the 0.5 and 0.66 AA battery size. We had premature battery failure in 40% of marten collars.

DISCUSSION

This is the first published study to experimentally evaluate the influence of satellite information retention (ephemeris and almanac data) on GPS error. Although field-deployed collars would not be set in cold start mode, manually reprogramming the GPS to erase all satellite information allowed us to gauge expectations for GPS data collected with long fix intervals or for conditions expected on free-ranging animals that, like martens, rest and den in chambers within trees, snags, logs, or below ground, rocks, or snow (Martin and Barrett 1991). While resting in an obstructed area, the GPS would be unlikely to connect with satellites for a prolonged period (greater than 4 hours), after which satellite information (ephemeris data) would need to be collected anew.

In our study, retained satellite information (almanac and ephemeris data) affected the probability of fix success. GPS collars were 2.2 times more likely to obtain a fix with satellite data (continuous mode) than without (cold start mode). Our paired mobile trials strengthen these results because data were collected under similar conditions expected for free-ranging animals and data were collected along the same transect within a similar time period (~2 hours), maintaining similar satellite availability and orbital position.

Obstruction from vegetation predicted fix success most strongly when satellite information was not available (cold start mode), which may explain why vegetation cover has little to no effect on fix success when the duration between fixes is short (e.g., this study, Lewis et al. 2007, Recio et al. 2011, Quaglietta et al. 2012, Adams et al. 2013). In complex patches with dense forest cover and a multi-story canopy, the GPS devices we

used were 6.6 times less likely (11% versus 69% fix success) to obtain a fix when in cold start mode than when in continuous mode. Fix success rates less than 50% may be typical in areas with vegetative obstructions and a fix interval greater than the interval for which ephemeris data are valid, i.e. 1-4 hours (Sager-Fradkin et al. 2007, Blackie 2010, Ott and van Aarde 2010). Our controlled experiment suggests that the combination of vegetation obstruction and lack of satellite information imposes a substantial amount of GPS bias within many data sets.

Although fix success was not strongly influenced by vegetation or topographical obstruction in continuous mode, these factors influence GPS performance and should be considered in wildlife research. Overall fix success in continuous mode was 83%, which was less than (Cargnelutti et al. 2007) or comparable to (Jiang et al. 2008, Recio et al. 2011, Thompson et al. 2012) estimates from other mobile trials in forested environments. In continuous mode, fix success was most affected by retained satellite information and weak relationships with vegetation obstruction (patch complexity). Although our study suggested that fix success decreased with vegetation obstruction – especially in cold start mode – that decrease was less than reported by Augustine (2010), where the influence of topographical obstruction and vegetation obstruction accounted for 79% of the variation in fix success during stationary tests. With our mobile trials we did not collect precise vegetation data during the exact time or location when the GPS was attempting a fix. Future studies should consider stationary tests stratified across the range of topographical and vegetation within a study area in concert with mobile trials to fully investigate all factors. The effect of vegetation and topography on fix success would differ for each study area (Frair et al. 2010, Wells et al. 2011), implying that our specific predictions of odds of obtaining fixes should not be blindly applied to other systems. Further, short-term

satellite information (ephemeris data) is expected to improve fix success when a GPS receiver is partly obstructed by vegetation or affected by animal behavior, but not when the GPS receiver is completely obstructed by topography (Augustine et al. 2011). Thus, decreasing the fix interval may not greatly improve fix success in study areas with deep ravines, cliffs, and areas of diverse topography.

The likelihood of fix success in continuous mode was strongly influenced by whether the GPS obtained a previous 3-D fix. The GPS was 50 times more likely to successfully obtain a fix if it had previously obtained a 3-D location. Furthermore, fix success differed if the trial was conducted entirely within a particular patch type compared to trials that crossed several patch types. This difference was more dramatic than error reported previously (DeCesare et al. 2005), and has implications for future GPS research. First, it implies that inferences from GPS tests should only be applied to free-ranging deployments with the same fix interval as the test (Cain et al. 2005, Augustine et al. 2011). Most importantly, collars with fix intervals greater than 4 hours will likely have reduced fix success compared to both stationary and mobile trials with shorter fix intervals (Sager-Fradkin et al. 2007, Thompson et al. 2012). Second, as observed in our trials, fix success in a particular patch type may depend on the unit's initial location. During 3 trials in complex stands with dense forested cover, we observed 0% fix success if the unit was activated within the stand. Conversely, we observed an average of 96% fix success if a location and thus accurate ephemeris data were obtained before entering the complex patch. Future mobile and stationary tests should activate the unit at the specific location of interest. Activating the unit along a road and transporting the GPS to a pre-determined testing location may significantly bias results.

Another consideration for future studies was that retained satellite information decreased time to fix, thus saving battery power for additional data collection. The average time to fix in continuous mode was 56 seconds less than cold start mode, which is an important consideration if the GPS is programmed to estimate its location for a maximum of 60 or 90 seconds. Short fix schedules improve median time to fix (Ryan et al. 2004), and decreasing fix time will inevitably increase battery life. However, very short fix schedules may not be appropriate for many studies, especially considering that the fix interval should allow enough time for an animal to move a distance further than expected location error to avoid spurious results (Frair et al. 2010).

We identified the conditions with large expected location error. Average location error in our study was strongly reduced by 1) eliminating 2-D fixes from data sets with long fix intervals or periods without satellite information, and/or 2) eliminating the all 2-D fixes after a series of failed fixes until a 3-D fix was obtained. As demonstrated in previous studies (Lewis et al. 2007, Ott and van Aarde 2010), removing all 2D fixes results in data loss and further biases data (Cargnelutti et al. 2007). However, in cold start mode mimicking fix intervals greater than 4 hours, every 2-D fix was inaccurate (>198 m). High location error compounds bias caused by less than 60% fix success (Frair et al. 2004, Nielson et al. 2009) and errors greater than 800 m were observed in $>15\%$ of 2-D data in cold start mode. In continuous mode, following a successful location in 3-D (suggesting that accurate satellite information was obtained), 95% of locations, including 2-D fixes, were accurate within 50 m.

Field data collection with miniature GPS collars

Malfunctions are expected from small collars (Blackie 2010, Cypher et al. 2011), an expectation supported by our observation that 34% of these collars malfunctioned upon

receipt. As such, we recommend testing all components thoroughly before field deployment to ensure that malfunctions are noticed before deploying on free-ranging animals. Following initial testing, our percent fix success in deployments on free-ranging martens was fairly high (66%), considering that martens are associated with dense forest cover and high amounts of topographical obstruction. This success seems largely attributable to the short fix interval. However, the accelerometer-based fix schedule that we used to reduce fix attempts when animals were resting (Brown et al. 2012) also likely contributed to our high fix success. Despite the observed malfunctions, the miniature GPS collars provided large amounts of reliable data and are a promising tool for small mammal research, especially considering this was one of the first studies using GPS technology for mammals around 1 kg (Reid and Harrison 2010).

Study limitations

We considered both stationary and mobile trials to assess fix success and location error, but collected data using only mobile trials. Stationary GPS trials provide opportunities to test GPS units in a controlled setting and multiple fix attempts at the same location provides the opportunity to calculate fix success rates and standardized metrics of location error (e.g., root mean square error, circular probability error) (Grewal et al. 2007). Further, stationary tests can elucidate whether location error was influenced by the number of satellites, satellite configuration, and conditions associated throughout a 24-hour period. Instead of continuous data collection, our mobile tests were conducted opportunistically during the day and we did not account for position or number of available satellites when designing the experiment. However, Augustine et al. (2011) suggest that stationary tests do not represent conditions GPS units experience while deployed on free-ranging wildlife and should not be used to determine probability of fix

success, location error, or GPS response to obstructions for wildlife research. Mobile tests are less consistent than stationary tests (Frair et al. 2010, Recio et al. 2011), but in our opinion better represent conditions experienced by animal-deployed collars and thus were more applicable for our study goals. We recommend both forms of GPS testing in concert in future studies, using mobile trial methods that allow the test GPS unit to be further from the observer (Cargnelutti et al. 2007, Recio et al. 2011).

Differences in GPS performance that we observed between cold and continuous mode were more dramatic than comparisons between studies with short (Recio et al. 2011) and long (Cain et al. 2005, Thompson et al. 2012) fix intervals, presumably because cold start mode eliminated both almanac and ephemeris data. We were unable to manually change the GPS software to attempt fixes in warm start mode (i.e., with almanac but not ephemeris data). Although differences in fix times between cold and warm start are not expected with multi-channel (48) GPS receivers (Tomkiewicz et al. 2010) due to their ability to efficiently download satellite data, we suspect that GPS error in cold start mode was exacerbated by the lack of almanac data. However, in continuous mode, the substantial decrease in error after the first 3-D fix highlights the greater importance of ephemeris data.

SYNTHESIS AND APPLICATIONS

These and other miniature GPS units (Reid and Harrison 2010) have limited battery life with fewer than 400 expected location attempts. We empirically demonstrate that retaining satellite information through short fix intervals (<1 hour) strongly increased average fix success and reduced average location error when compared to GPS units operating without retained satellite information (as expected with fix intervals greater

than 4 hours). Retained satellite information also decreased time to fix, thus improving battery life and efficiency. Likewise, we found that the negative effect of vegetation obstruction on fix success could largely be eliminated with a short fix interval because satellite information was retained. Researchers with different goals will need to establish the appropriate trade-off between fix schedules and length of collar deployment, but this study suggests short fix intervals can reduce GPS error by retaining satellite information and can increase the amount of expected data collected on mobile, free-ranging, small mammals. Maximizing satellite information to increase fix success also may be achieved by pulsing multiple fix attempts in sequence (e.g., 1 fix attempt every 10 minutes for 30 minutes or 1 fix attempt every hour for 3 hours). We utilized an activity-sensor fix schedule (Brown et al. 2012) which prevented the GPS from activating when the animal was resting, which may also be considered during pulsing >1 fix attempt with less than 30 minutes between attempts. However, shorter fix intervals is unlikely to help GPS error caused by substantial topographic obstruction.

Bias from large location errors may erroneously suggest that an animal utilized an area outside its preferred habitat, and negatively affects interpretation for habitat specialists (Visscher 2006), like the Pacific marten. Therefore, if attempting fine-scale analyses of habitat use, we recommend removing all 2-D locations when fix intervals exceed the period where ephemeris data are useful (greater than 4 hours). In conditions where fix intervals are short (less than 4 hours) but animals use dens or cavities for longer periods, we suggest censoring initial 2-D locations obtained after a 1-4 hour gap until the first 3-D fix.

Most importantly, because of the rapidly-changing nature of ephemeris data, researchers should not extrapolate findings from GPS tests that use a different fix interval from their

proposed study. Further, the trade-off between collar life and accuracy of locations resulting from a particular fix interval must be carefully balanced depending on the scale of the analysis in question.

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TABLES AND FIGURES

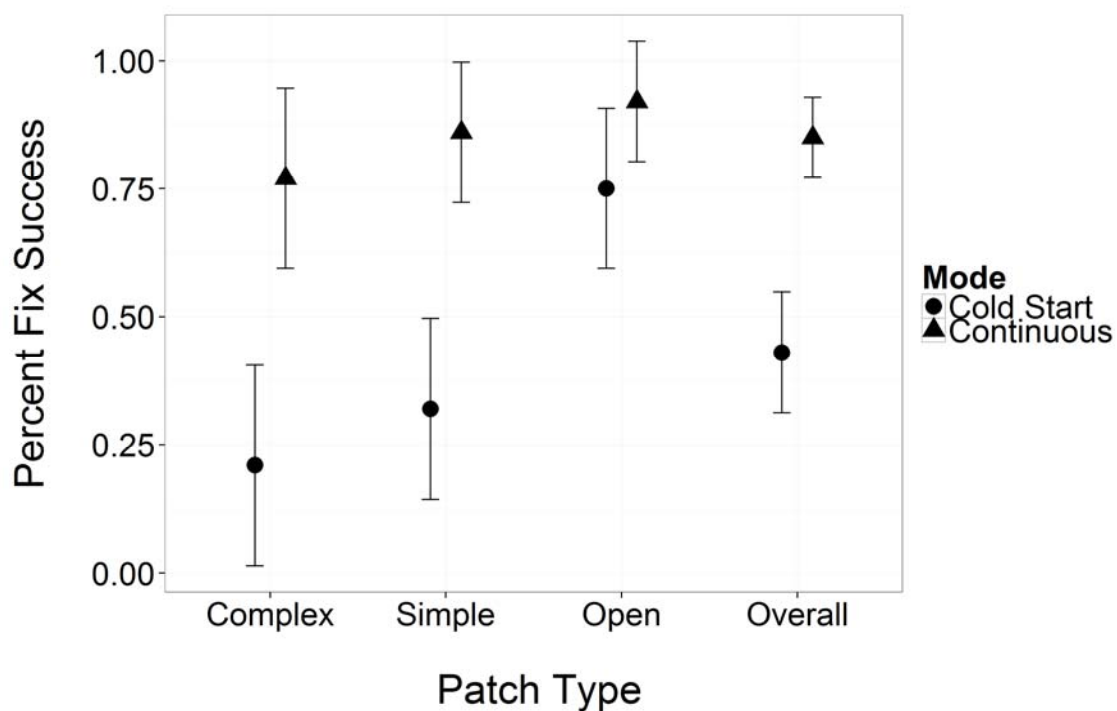


Figure 1.1. Fix success for miniature GPS collars differed with (continuous mode, triangles) and without (cold start mode, circles) satellite information (ephemeris and almanac data). Fix success was measured in 27 mobile GPS trials in Lassen National Forest, California, including 19 paired trials in both modes. Average fix success and 95% confidence intervals (bars) differed significantly between modes in all patch types but those without canopy cover (open).

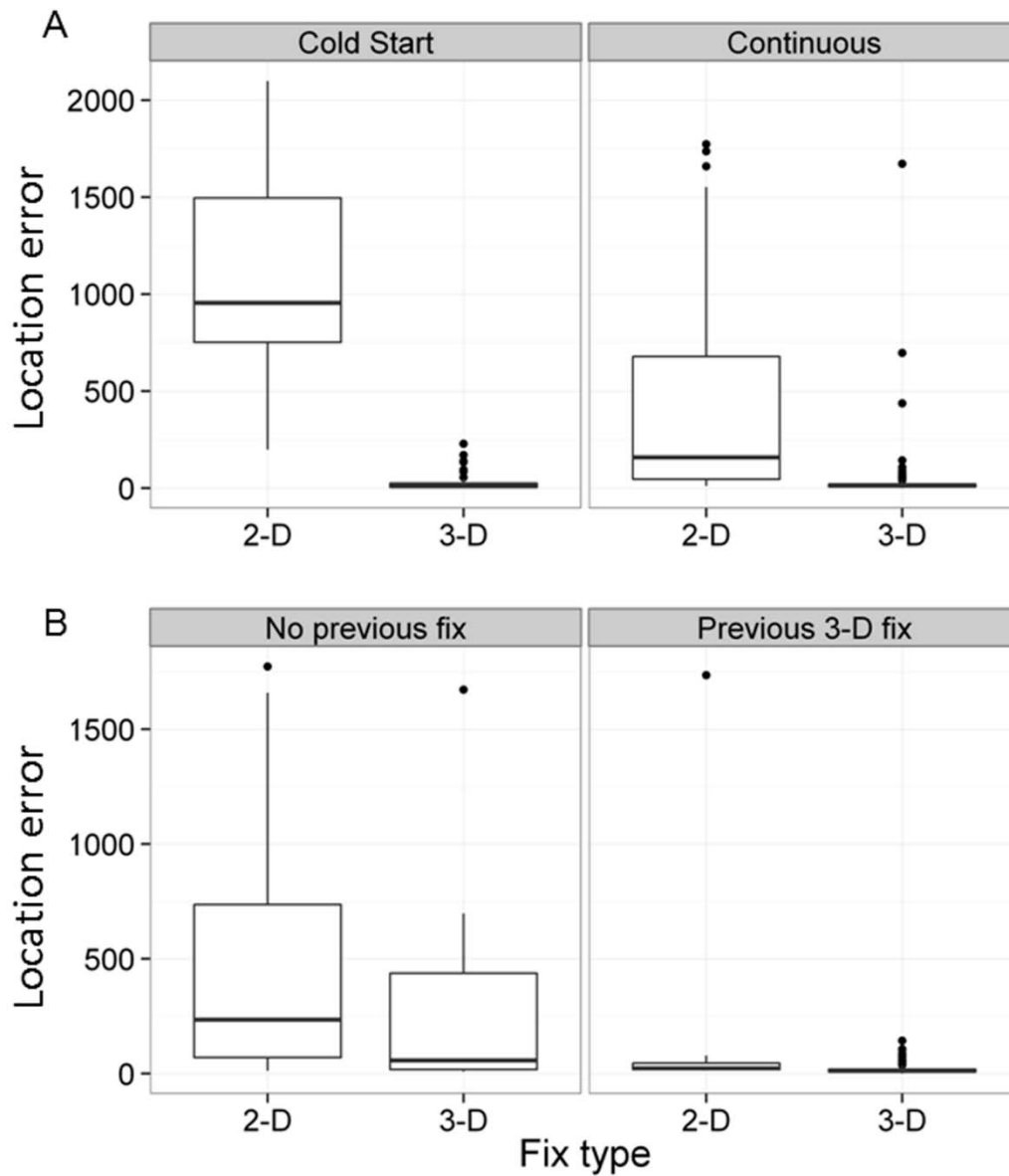


Figure 1.2. Location error of miniature GPS collars for 2 and 3-dimensional fixes between modes and with previous 3-D fixes. Median GPS location error (meters) for (a) 2 and 3-dimensional fixes differed in both cold start (ephemeris and almanac data not available) and continuous (ephemeris and almanac data available) mode, and (b) median location error in continuous mode differed with and without a previous 3-D fix during 27 mobile GPS trials.

Table 1.1. Fix success in each patch type was dependent on the trial type and patch of the GPS. We completed trials completely within a single patch type ("only", 10-14 fix attempts) as well as from one patch type into another (3-5 fix attempts), to mimic an animal moving among patches. We report the number of mobile trials and fix attempts, the average fix success and standard error.

		Continuous		Cold Start	
GPS direction		Trials, fix attempts	Fix success	Trials, fix attempts	Fix success
Complex	Complex Only	6, 62	44.3±24.5	3, 32	0±0
	Simple to Complex	4, 16	93.5±12.0	4, 16	17.5±11.8
	Open to Complex	4, 35	100±0	3, 20	13.3±14.4
Simple	Simple Only	5, 46	86.9±13.3	5, 54	3.7 ±3.3
	Open to Simple	2, 16	61.5±15.4	3, 19	42.1±12.7
	Complex to Simple	0, N/A	N/A	0, N/A	N/A
Open	Open Only	4, 43	95.7±2.9	4, 45	82.2±9.1
	Simple to Open	0, N/A	N/A	2, 6	100.0±0
	Complex to Open	1, 12	100.0±0	0, N/A	N/A

Table 1.2. Mean fix success rates (\bar{x}) and standard error (SE) from trials of miniature GPS units in complex, simple and open patch types were dependent on the trial type. We completed trials completely within a single patch type ("only", 10-14 fix attempts) and from one patch type into another (3-5 fix attempts) to mimic an animal moving among patches.

		Continuous				Cold start			
GPS direction		Trials	Fix attempts	Fix success (\bar{x})	Fix success (SE)	Trials	Fix attempts	Fix success (\bar{x})	Fix success (SE)
Complex	Complex Only	62	62	44.3	24.5	3	32	0	0
	Simple to Complex	16	16	93.5	12	4	16	17.5	11.8
	Open to Complex	35	35	100.0	0	3	20	13.3	14.4
Simple	Simple Only	46	46	86.0	13.3	5	54	3.7	3.3
	Open to Simple	16	16	61.5	15.4	3	19	42.1	12.7
	Complex to Simple	0				0			
Open	Open Only	43	43	95.7	2.9	4	45	82.2	9.1
	Simple to Open	0				2	6	100.0	0.0
	Complex to Open	12	12	100.0	0.0	0			

Table 1.3. Model selection results for linear mixed models of fix success for mobile miniature GPS units operating with (continuous mode) and without (cold start mode) satellite information, including differences in Akaike Information Criterion (ΔAIC), degrees of freedom (df), and model weight (w_i). Predictor variables included a previous successful location or 3D location (previous fix, previous 3D fix, continuous mode only), satellite view factor (SVF), aspect as represented by northness and eastness (Zar 1999), elevation, patch type (i.e., open, simple, complex), and the “track” or mobile path taken as a random effect.

Mode	Model name	df	ΔAIC	w_i
Continuous	Previous 3D fix	3	0.00	0.63
	Previous 3D fix + patch type	5	1.04	0.37
	Previous fix	3	24.36	0.0
	Patch type	4	37.73	0.0
	Intercept	2	44.39	0.0
	Patch type + SVF + northness + eastness + elevation	8	45.33	0.0
	SVF + northness + eastness + elevation	6	55.58	0.0
	Previous 3D fix + SVF + northness + eastness + elevation	7	56.08	0.0
Cold start	Patch type	4	0.00	1.00
	Patch type + SVF + northness + eastness + elevation	8	18.6	0.0
	Intercept	2	23.7	0.0
	SVF + northness + eastness + elevation	6	63.0	0.0

CHAPTER 2 : EXPERIMENTAL EVIDENCE THAT SIMPLIFIED FOREST STRUCTURE INTERACTS WITH SNOW COVER TO INFLUENCE FUNCTIONAL CONNECTIVITY FOR PACIFIC MARTENS

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ABSTRACT

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 negatively affected by climate change. We evaluated whether simplifying forest structure influenced animal movements and whether an experimental approach to quantifying functional connectivity reflects normal behavior, which is often assumed but, to date, remains untested. We evaluated functional connectivity for Pacific marten (*Martes caurina*) across a gradient in forest structural complexity (complex/dense, simple/thinned, and open) using two novel methods for this species: incentivized food-titration

experiments and non-incentivized locations collected via GPS telemetry (24 individuals). We predicted that (1) martens would use stands with greater structural complexity because these presumably provide prey, escape cover, and resting/denning locations, and (2) martens would be more willing to use simple or open stands during winter because of increased thermal stress, reduced prey availability, and fewer predators. Food titration experiments revealed martens selected complex stands, but 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. Thus, 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 that snow cover facilitates connectivity across openings and simple stands 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.

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, functional connectivity is difficult to measure empirically. It is often unclear whether

individuals encounter barriers and are physically unable to cross patches (e.g., Moore et al. 2008), or whether individuals lack incentive to cross patches due to insufficient or inaccessible prey or increased risk of predation.

Measuring functional connectivity is difficult because it requires replication of experiments at landscape scales. 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 (Kotler and Blaustein 1995, Belisle 2005). 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. 2007a). 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 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 (Heinemeyer 2002, Cushman et al. 2011), 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, Stephens et al. 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 recon 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 (see Appendix S1 in Supporting Information). 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, food limitation, and reduced predation risk during winter, 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 (Figure 2.1, Zielinski et al. *in review*). 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 1500-2100 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. 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 (Figure 2.2).

Study Design

To ensure that we were studying martens exposed to gradient of stand types, we divided the landscape into 61 6.2 km² hexagons (Figure 2.1) 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 *In press*) 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 minutes (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 *In press*). We restricted our analysis to locations with predicted error less than 50m (Moriarty & Epps *in review*). 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, Turner & Getz 2013).

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 (Figure 2.3). We conducted two experimental treatments for each marten: (1) complex into open and (2) complex into simple (Figure 2.3). 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 triangular enclosures and aluminum plates coated with printer toner, a piece of tacky white paper for track collection, and bait (Ray and Zielinski 2008). We applied a commercial scent lure 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 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.

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 habitat or if the interaction between distance and open habitat 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, Maechler & Bolker 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 locations within a home range as stand ‘use’ and assumed all stands within the home range were accessible and ‘available’ (Jones 2001). Martens regularly moved greater than 10 km within their range during a 24 hour 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, our expected location accuracy. 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 intervals, 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 (Table 2.1). 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 2.2, $n=24$ 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 2.2), 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 2.2, 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 2.2). In simple stands, martens either moved along the entire array or did not enter the stand. Martens did not enter openings and avoided stations 50m within complex stands adjacent to openings (Figure 2.4).

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 2.2). 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 2.2). 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 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 2.2, Figure 2.4).

Telemetry (no food incentive)

Unlike incentivized experiments, we did not detect differences in stand use between seasons (Figure 2.5; $F = 2.2$, $P = 0.53$). 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 (Figure 2.5). Males and females did not appear to use stands differently within each season (Figure 2.6), but our sample of females was small within season ($n=5$) and we did not model those data.

After accounting for stand preferences (Figure 2.5), effects of distance class within any stand type and season varied (Figure 2.7). Martens preferred interiors and avoided edges while in

complex stands, but when in simple stands and openings preferred edges adjoining complex habitat (Figure 2.7). 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 $>125\text{-m}$ slightly more than they were available, especially in winter, reflecting weak selection for interior portions of complex stands during winter (Figure 2.7a). Martens used simple and open stand interiors more often during summer than winter (Figure 2.7b,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 stand types. These conclusions are consistent with previous research showing that martens seldom enter openings without tree cover (Cushman et al. 2011), but 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, procurable prey, and sites for denning and resting. Our study provided evidence that each of these requisites affected marten stand use, and that functional connectivity may be influenced by the amount of snow cover, likely due to less predation risk.

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. *In press*), 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 50m 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. Thus, winter snows in the Cascade and Sierra Nevada Mountain ranges may trigger elevational migration of predators and decrease the risk that martens experience in summer in areas lacking escape cover.

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 (Figure 2.2). 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). 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 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.

Once prey is captured, martens need places to safely consume it and rest. Resting locations often insulate martens from heat loss and weather. We found 106 resting locations (n=24 martens); 89% were in complex stands. Although resting structures are often retained in simple stands, other important elements of resting habitat such as dense patches of residual trees are typically lacking. Enhancing features used by prey, including low hanging branches and dense clusters of small trees, will also provide escape cover for resting sites and may increase marten use of simple stands.

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. 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.

SYNTHESIS AND APPLICATIONS

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). Corridors of complex stands could be useful as a link between preferred stands and thus reduce negative impacts of openings and simple stands. Heinemeyer (2002) suggested that marten corridors needed a width to length ratio of 1:2.5 or less. 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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TABLES AND FIGURES

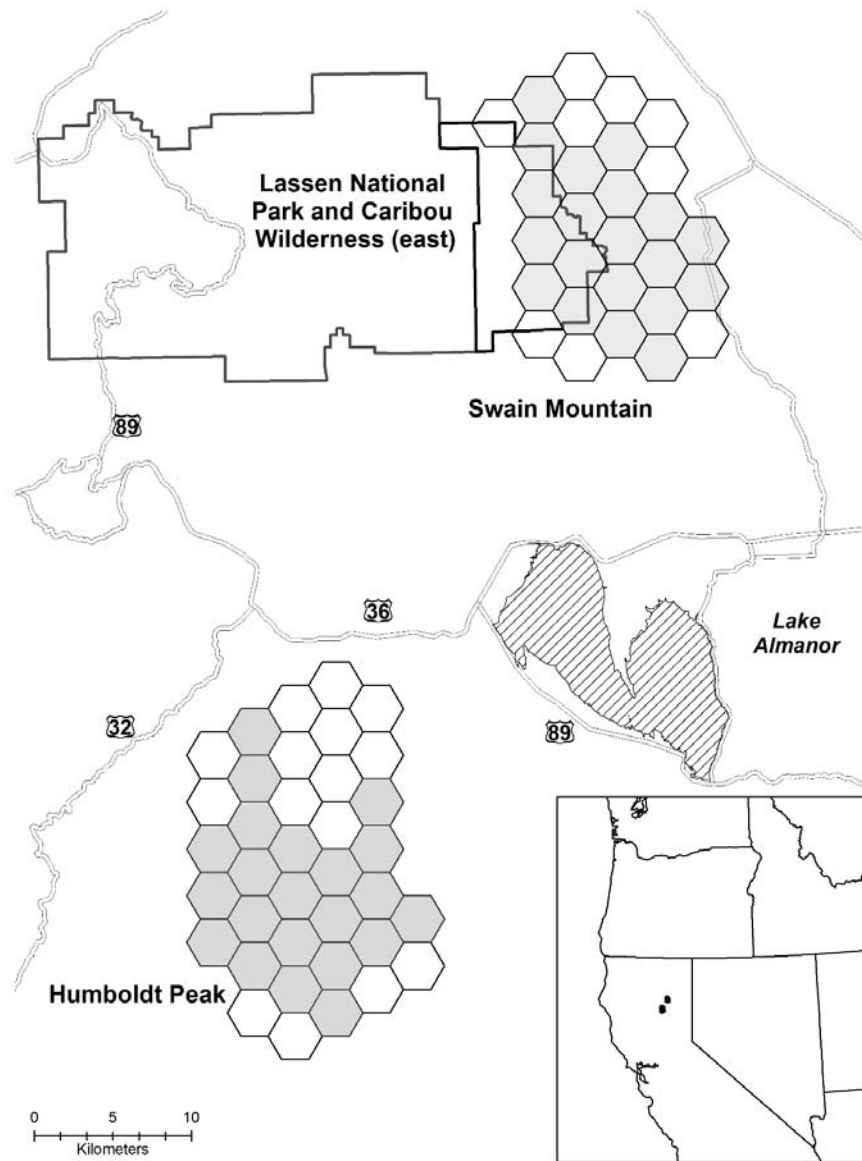


Figure 2.1. Our study occurred in two independent sites (Humboldt Peak, Swain Mountain) within Lassen National Forest, California. We detected and/or radio collared Pacific martens in the hexagon sample units highlighted in grey.

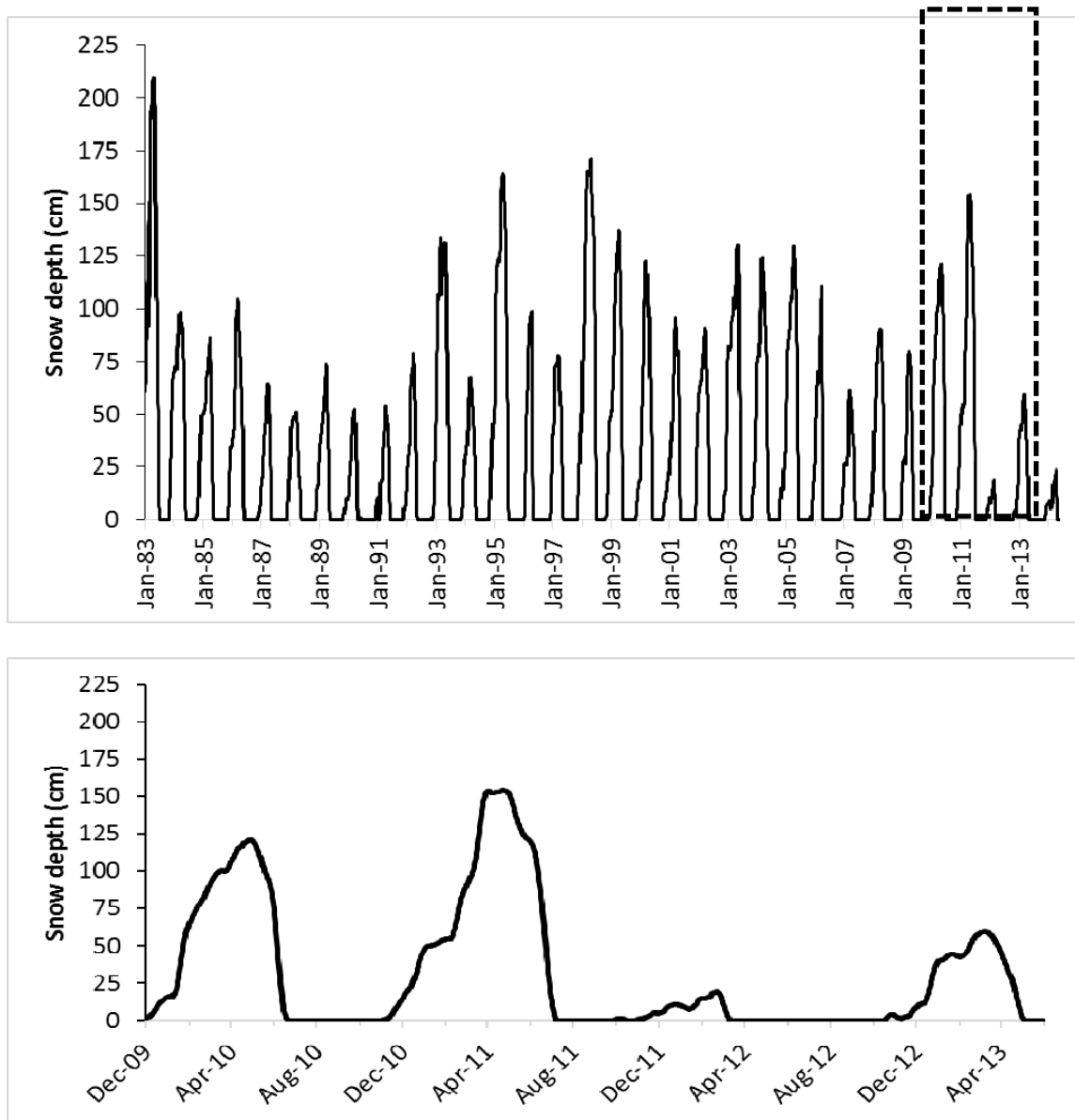


Figure 2.2. Snow depth in our study area and during data collection. Snow depth (cm) fluctuated between winter seasons at Humbug Summit Weather Station (HMB), Lassen National Forest, California. This station was located at 2010 meters elevation in a southeast-facing opening with $<5\%$ slope. It represents minimum snowfall depth within our study area. A) Smoothed 2-week average snow depth at HMB between January 1983 and May 2014 with our study period represented by the dashed box. B) Snow depth at HMB during our study (Dec 2009-May 2013).

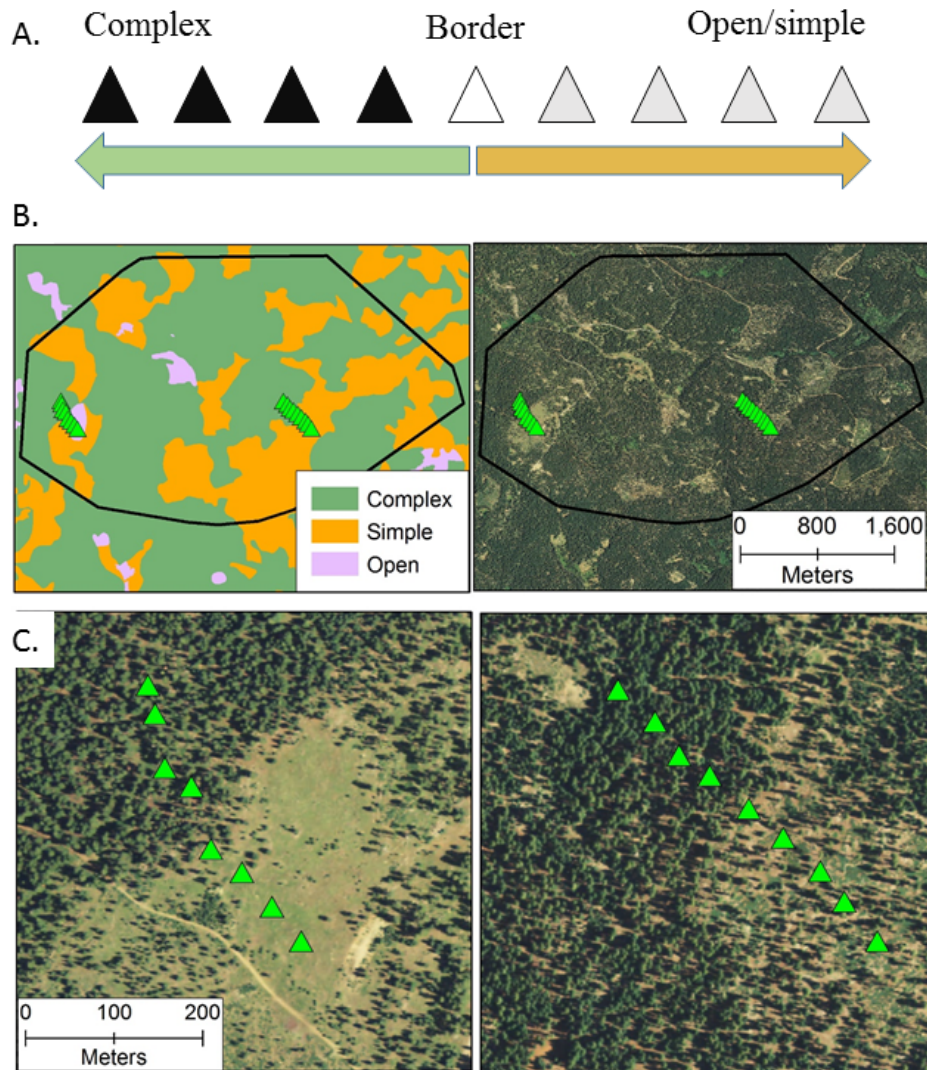
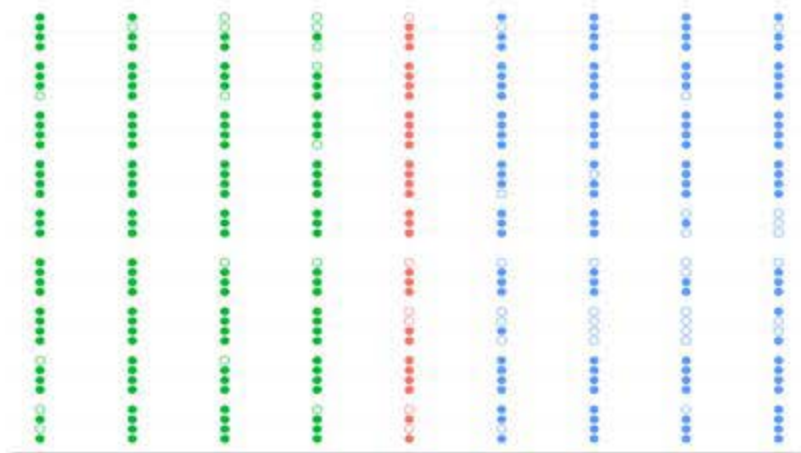


Figure 2.3. A) A conceptual diagram of 9 detection devices within a food-titration experiment. The border station was placed between stand types that differed in structural complexity, contrasting between complex and simple or open. B) Male home range M01 (black outline) with GIS designated patch map 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.

A. Summer – Complex (green) into Simple (blue)



C. Winter – Complex (green) into Simple (blue)



B. Summer – Complex (green) into Open (blue)



D. Winter – Complex (green) into Open (blue)



Figure 2.4. Raw data from titration experiments. Each row represents an individual titration array. Each column represents a station and a circle within a column represents a visit (4 visits total). Marten detections are indicated by filled circles. Summer detection data were represented as Complex into Simple stands (A, upper left) and Complex into Openings (B, lower left). Winter detection data were Complex into Simple stands (C, upper right) and Complex into Openings (D, lower right). Stand types were colored for complex (green), border of two stand types (red), and open or simple (blue).

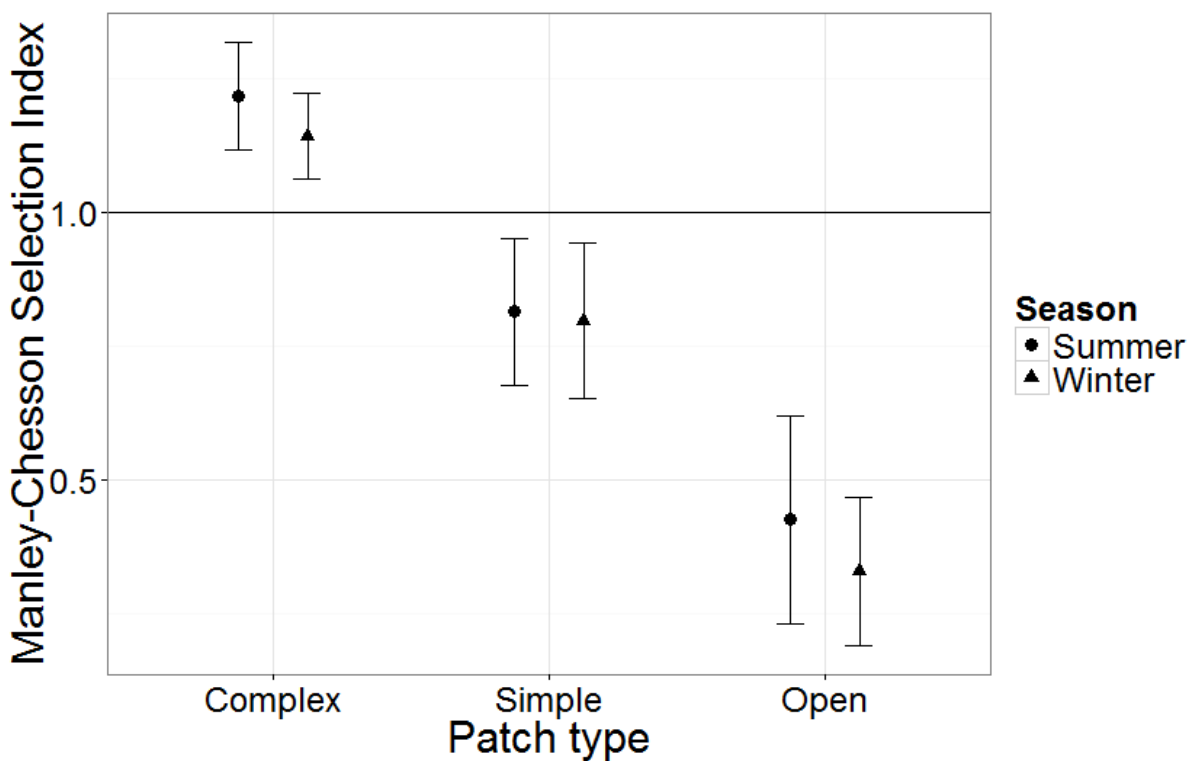


Figure 2.5. Selection indices (mean and 95% confidence intervals) for different patch types by season, estimated from non-incentivized methods (telemetry locations from 24 adult martens [8 female, 16 male]). We observed significant differences between marten use of patch types ($F = 17.5$, $P < 0.01$), but no difference by season ($F = 2.2$, $P = 0.16$).

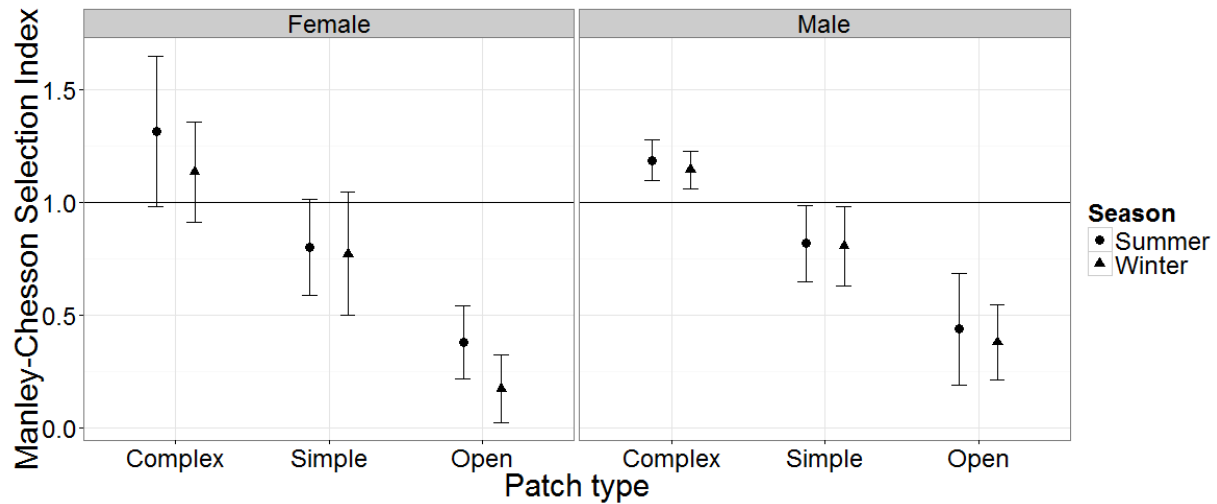
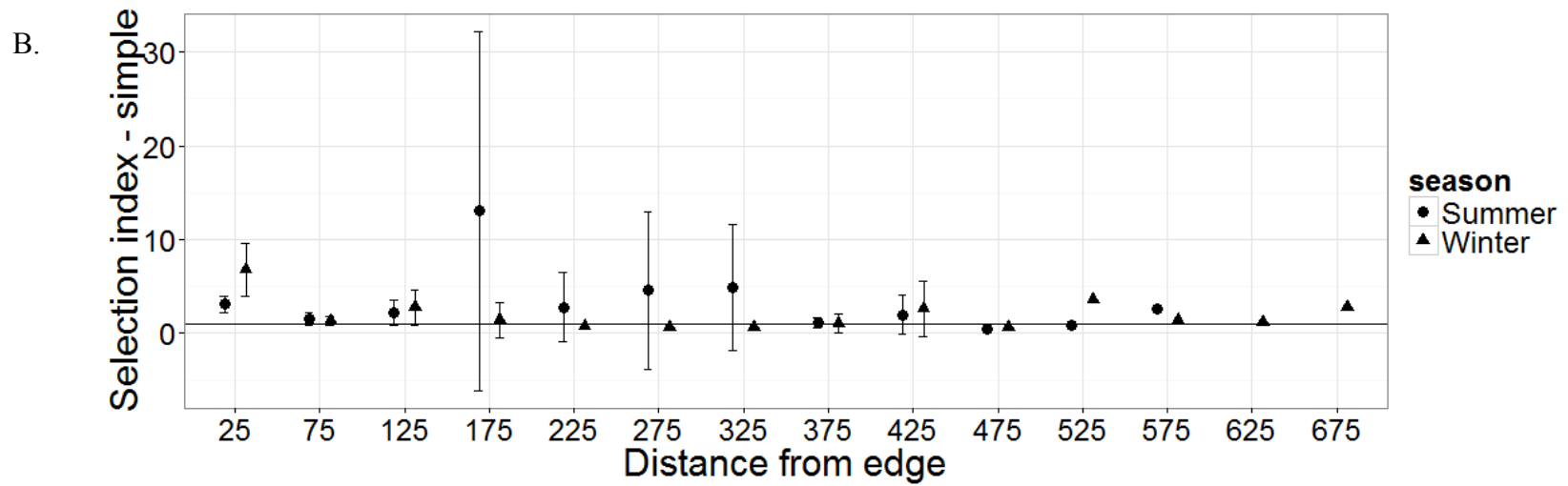
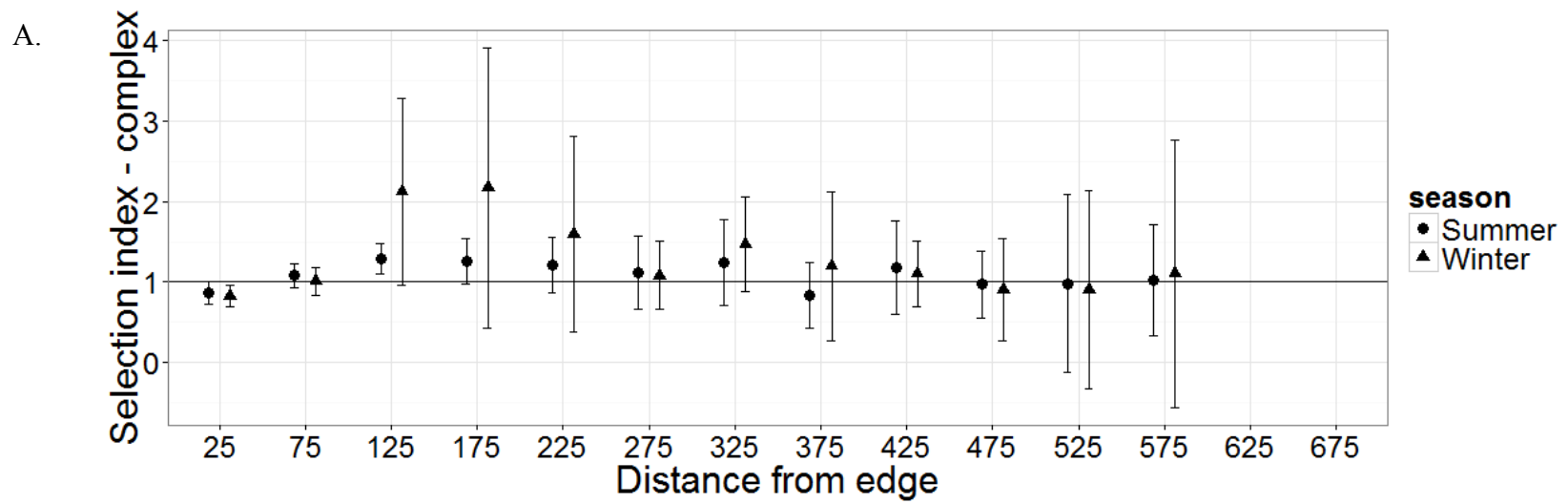


Figure 2.6. We did not observe differences between male and female patch use ($F = 0.50$, $P = 0.46$) within each season with non-incentivized methods (telemetry locations). We display mean (symbol) and 95% confidence intervals for winter and summer seasons (triangle, circle). Samples sizes differed between winter (5 female, 13 male) and summer (4 female, 12 male). During summer, one female (F05) contributed a high amount of variance in openings due to the number of locations in talus slopes, which may provide considerable cover. With female F05 included, the average selection value for open would change to 1.05 ± 0.67 (females), overlapping values for complex and simple stands (not displayed).



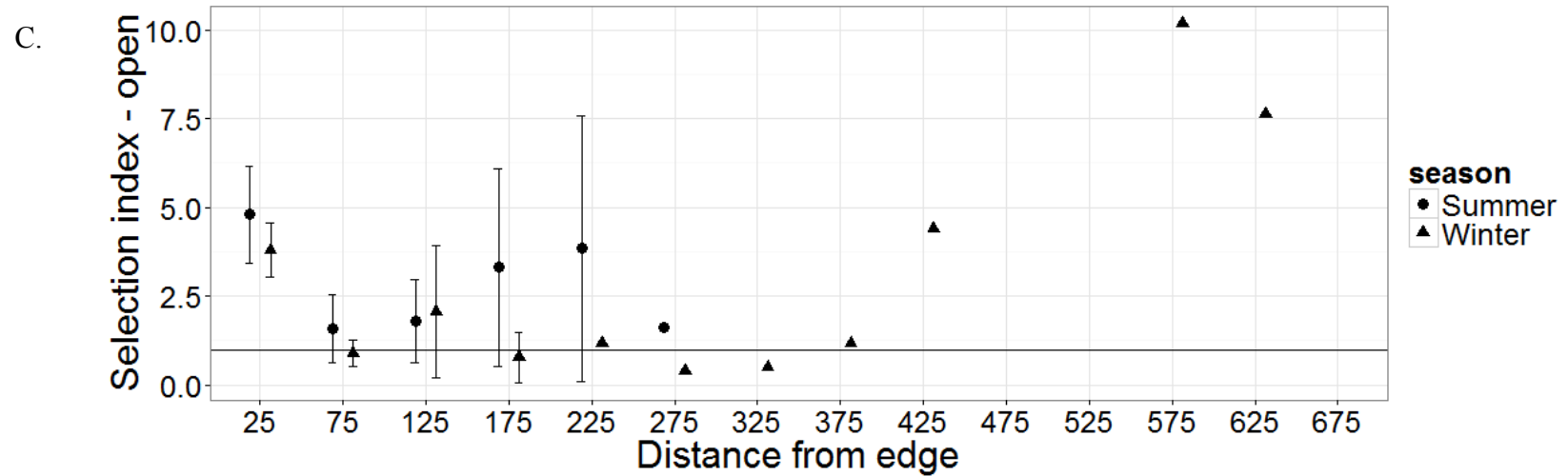


Figure 2.7. Selection indices for martens (mean, with 95% CI reported for $n > 1$) at distance classes *within* stand types, using non-incentivized methods (telemetry locations). A) Marten in complex stands may have a weak preference for distances greater than 125-m, predominantly during winter ($n = 24$ martens, 6,797 locations). B) Marten use within simple stands reveals a high amount of variance within each distance class, especially during summer ($n = 24$ martens, 2,190 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 225m, 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).

Table 2.1. Fixed effects coefficients for the final generalized linear mixed model describing Pacific marten (*Martes caurina*) food-titration experiments (n = 37 titrations, 21 individuals). 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.

Contrasting variables	Summer				Winter			
	Odds	95% CI	Wald's	P	Odds	95% CI	Wald's	P
	Ratios		Z		Ratios		Z	
Complex vs. 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 vs. 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

CHAPTER 3 : FOREST THINNING FOR FUEL REDUCTION CHANGES MOVEMENT PATTERNS AND HABITAT USE BY PACIFIC MARTEN

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ABSTRACT

Movement patterns reflect how animals maximize fitness while balancing foraging and breeding opportunities and minimizing predation risk. We evaluated whether simplified forest structure resulting from the thinning of forests to reduce fuels influenced movements of Pacific marten (*Martes caurina*), a small and highly mobile carnivore. We collected movement paths from 22 martens using GPS telemetry to both evaluate habitat selection and to describe movement patterns. We evaluated variance, speed and sinuosity, a measure of path complexity, in three stand types that differed in structural complexity (i.e., complex/dense, simple/thinned, and open). We hypothesized marten movement would differ between stand types and predicted that (1) martens would select stand types with increased structural complexity (complex > simple > open), (2) movements would increase in complexity (sinuosity, motion variance) and decrease in speed when martens travel through stands with increased structural complexity, (3) speeds would increase during summer indicating increased movement during the breeding season, and (4) males would move more rapidly due to their larger home ranges. Martens traveled 0.5-27.2 km per day and 0-4.5 km per hour. Martens selected home ranges with fewer openings compared

to the study area overall. Within home ranges, martens strongly selected complex stands over simple stands and openings. Speed and movement complexity were most consistent and movement was sinuous and slow in complex stand types compared with openings and simple stands. Movement was erratic and more linear in openings. In simple stands, movement patterns were intermediate between complex stands and openings. Females generally moved more slowly, sinuously, and less variably compared to males. Martens moved more quickly, less sinuously, and more variably during winter compared to summer. Simplifying stand structure is a high priority for forest managers to reduce risk of high severity and intensity fire; however, these stands were avoided and may negatively affect the ability of marten forage without increased predation. We recommend retaining structural complexity in montane forests, and to focus future research on how to strategically distribute the amount of thinning spatially and temporally.

INTRODUCTION

The analysis of movement patterns of individuals can provide a simple and direct way to determine how an animal perceives risk and balances acquisition of resources (Brown 1988, Turchin 1998). Movement can reflect foraging (Heinrich 1979), reproduction (Martin 1998), and predator avoidance behaviors (Kennedy et al. 1994, Frair et al. 2005). By testing predictions about how habitat influences individual movements, we can better understand how individuals perceive their environment and how future landscape changes may affect behavior. Movement patterns may provide important insights into resource selection at multiple spatial scales, especially if these patterns reveal information on energy expended or risks incurred (Buskirk and Millspaugh 2006). In a patchy landscape, animals are predicted to maximize resource use within the home range, or an area that provides an individual with resources for survival and

reproduction (Burt 1943), by selecting patches with the highest quality resources (Pimm et al. 1985).

Movement patterns within patch types should be indicative of an individual's ability to acquire and allocate resources (Van Noordwijk and de Jong 1986, Gaillard et al. 2010). For instance, an animal could maximize fitness by making short forays from a central location when food is localized and has small energetic returns (Giraldeau et al. 1994). If prey are localized but far from a centralized location, an animal would benefit from long distance foraging bouts punctuated by sinuous movement patterns in areas with expected "high quality" prey with increased energetic value. If prey are widely dispersed, the greatest energetic benefit may be accrued by searching with less sinuosity and searching a larger area (Barton and Hovestadt 2012). Thus, foraging patterns may be expressed through multiple behaviors. Direct and consistently fast movements could reflect traveling through areas with low prey density (Earl and Zollner 2014), and variable speeds combined with sinuous movements may relate to prey searching and pursuit (McIntyre and Wiens 1999, Jonsen et al. 2007). Another factor that influences animal movement is risk of predation. Animals may completely avoid risky locations or, while in risky areas, increase vigilance (Lima 1998). Increased vigilance and movement is thought to decrease likelihood of predation (Mitchell and Lima 2002). Movement may become slower or more cautious in periods with potential risk (Lima 1987), but most often animals tend to avoid or quickly move through non-preferred areas (Frair et al. 2005). As such, movement patterns can verify that individuals are selecting resources (Jones 2001, Buskirk and Millspaugh 2006, Morales et al. 2010), rather than simply occupying a non-preferred area, as when intraspecific competition is high (Van Horne 1983, Pulliam and Danielson 1991). Despite the

benefits of using movement data, they are difficult to collect, especially for elusive and wide-ranging species such as solitary carnivores.

We evaluate the movement patterns of Pacific marten (*Martes caurina*) in relation to three factors: stand type, sex, and season. Martens are an indicator species (Thompson 1991, Bissonette and Broekhuizen 1995) due to their association with forested patches with a multi-layer canopy and large snags, logs, and trees (Spencer et al. 1983). Marten populations may decline sharply with relatively small amounts (<30%) of habitat loss and fragmentation (Chapin et al. 1998, Hargis et al. 1999). Such declines presumably occur because open areas negatively affect landscape connectivity (Cushman et al. 2011, Moriarty et al. 2011, Moriarty et al. In review) and likely increase the distances that martens move. We examined how martens perceived stand types that represented a gradient in forest complexity. We divided our study area into three types: (1) structurally "complex" stands were characterized by multistory, dense conifer vegetation with little or no history of management in the last 50 years and that often contained both vertical and horizontal structural diversity; (2) structurally "simple" stands 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. In previous studies, martens have been shown to avoid openings (Heinemeyer 2002, Cushman et al. 2011), but those studies did not determine whether martens select simplified stands or whether these stands are permeable during daily movements.

Martens are sexually dimorphic; males are about one third larger than females (Merriam 1890). Therefore, we expected a physiological difference in movement capacity where males would be able to move faster and travel farther than females. We also anticipated behavioral

differences between males and females, due to the differences in body size and social structure. Moreover, given that females and males often have overlapping territories (Hawley and Newby 1957), behavioral differences may limit intersexual resource competition, although this proposed niche partitioning has not been empirically confirmed for martens or closely related species such as fisher (*Pekania pennanti*) (Powell and Leonard 1983).

Seasonally, martens likely move more during summer than winter as observed in European pine martens (*Martes martes*) (Zalewski et al. 2004). Summer movements may be associated with increased availability of food resources, presence of predators, and reproductive responsibilities (females raise kits, males reproduce with multiple females). During winter, when most prey and predators hibernate or migrate to different elevations, martens have fewer resources and predators, lack reproductive responsibilities, and may experience increased thermoregulatory stress due to cold temperatures and precipitation. Marten movement patterns have been described only during winter via snowtracking studies (e.g., Hargis and McCullough 1984, Andruskiw et al. 2008, Cushman et al. 2011, Cheveau et al. 2013). However, functional connectivity in the southern Cascade Mountains in California is most restricted by simplified forest structure or openings during summer months (Moriarty et al. In review). Therefore, comparing winter and summer movements required use of GPS collars, the first time this spatial technology has been deployed on martens.

We conducted three sets of analyses for the purpose of understanding marten movement. First, we characterized movement patterns and daily and hourly movement rates to summarize potential seasonal and sex-related differences. Second, we evaluated movement-based stand use and selection from individual utilization distributions for each season, specifically testing whether use of stand types differed. We hypothesized stand type use would differ due to

consequences of forest structure for marten foraging and predation avoidance, with foraging occurring most often in complex stands (Andruskiw et al. 2008). As such, we predicted both that home ranges would have a disproportionate amount of complex stand types compared to the landscape (second order selection), and within home ranges, martens would use complex stands more than available (third-order selection). Lastly, we quantified motion variance, speed, and sinuosity. Because martens forage actively for small mammals in downed woody material and other complex environments (Andruskiw et al. 2008), requiring frequent changes of speed and direction: (1) movement would increase in complexity (sinuosity, motion variance) when traveling through stands with increased structural complexity, (2) speeds would increase during the summer when reproductive activities occur in all stand types, and (3) females would move slower compared to males, especially in areas with increased risk such as openings and simple stands (Moriarty et al. *in review*).

METHODS

Study Area

This research was conducted in Lassen National Forest (LNF), California, where marten populations were monitored over 8 previous years (Figure 1., Zielinski et al. *In press*). This area also was part of a 13-year effort to intensively manage forests with a primary focus on fuel reduction treatments that result in forest simplification (Owen 2003, Pinchot Institute 2013). Elevations in this region ranged from 1500-2100 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. Mean annual snow depth in winter was 134 cm (California Department Water Resources, 1981-2014).

Study Design

To ensure that we were studying martens exposed to a gradient of stand types, we divided the landscape into 61 6.2 km² hexagons (Figure 1) and stratified our live trapping effort. Using a 3-km grid, we evenly distributed trapping effort among hexagons with either >60%, 40-59%, or <40% of the area occupied by complex stands. We used modified Tomahawk live traps (Model 108, Hazelhurst, Wisconsin, USA) to catch martens, employed chemical anesthesia (Mortenson and Moriarty *In press*), 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 five minutes (Quantum 4000 Micro-Mini, Telemetry Solutions, Concord, California, USA) only on individuals that previously wore VHF collars to minimize risk of losing GPS collars. We collected telemetry data (VHF triangulations and other point locations) weekly and, for GPS, during one to eight days per season when the marten was moving due to limited battery life (Moriarty and Epps *In press*). We restricted our movement analyses to GPS locations with average predicted accuracy and standard error (SE) of 28±7m (Moriarty and Epps *In press*). We included in our sample only martens that were >2 years old because we were interested in the movement behavior of the segment of the population most likely to affect sustainability (Buskirk et al. 2012).

GPS collars provided several challenges. First, we did not deploy GPS collars on females during critical reproductive periods (from the first trimester of pregnancy through denning (February-July) and we were reluctant to deploy GPS collars on most of our adult females

because the collars would have exceeded 5% of their body weight in many instances. Thus, we were unable to report on female marten movement during a period when it may have been relevant, and our sample size for females is small and biased towards heavier animals. Second, we deployed our collars opportunistically when they were available, rotating 1 to 6 collars between individual martens when they became available from the manufacturer. There were a few occasions when we collected data on several martens simultaneously. Lastly, we collected movement data over short periods of time during each deployment (3-9 days) because of short battery life.

Stand Use and Selection

We used Brownian Bridge Movement Models (BBMM) to (1) infer habitat selection from the probability of use within each marten's seasonal home range and (2) describe motion variance (Horne et al. 2007a), or variation in speed and/or sinuosity, within each stand type. BBMMs estimate the expected movement path of the individual from random walks between successive pairs of locations (Horne et al. 2007a). These movement models incorporate both expected location accuracy and the time between two points to create utilization distributions, or the probability of use (Marzluff et al. 2004). We used compositional analysis as described by Aebischer et al. (1993) to test whether home ranges were selected disproportionately in areas with larger amounts of complex stands compared to the overall study area (second-order selection, Johnson 1980). We defined the study area by creating a 750m buffer around both the sampling grid and all marten home ranges, thereby including our survey area where martens were trapped as well as all marten use areas as defined by the utilization distributions. We expect this landscape representation to be conservative for this analysis because martens could

move anywhere within our depiction of the landscape, even across study areas potentially, and some areas within each study area might have also had martens that were not detected.

Next, we used the utilization distribution as a weighted probability surface and conducted a compositional analysis to test whether stands within a home range were used disproportionately to their occurrence (third-order selection, Johnson 1980). We performed these compositional analyses in package `adehabitatHS` in R (Calenge 2006) which follows recommendations by Aebischer et al. (1993). When evaluating third-order selection, we assumed that all stand types within a home range were available (Fretwell and Lucas 1969) because we only collected data on adult martens, assumed to be dominant within their home range and having complete access to resources, although we also acknowledge heterospecific competition between other carnivores with overlapping ranges could occur. Analyzing for selection also assumes that each stand type is accessible (Garshelis 2000), which is reasonable because martens move considerable distances within their home range in a short time period (Moriarty, unpubl. obs.).

Stand-specific Movement Patterns

BBMMs can be used to incorporate animal movement and quantify selection, and can also provide a metric of motion variance that represents changes in speed and sinuosity (Nielson et al. 2013) providing opportunities to evaluate temporal aspects of habitat selection (Byrne et al. 2014). We estimated stand-specific Brownian bridge motion variance for each individual during summer and winter to quantify changes in movement patterns. Motion variance provides an index allowing broad comparison of changes in movement, but does not separate between speed and sinuosity. Thus, we conducted separate analyses to quantify speed and sinuosity within

each stand type and thereby determine which factor may have affected motion variance. Speed was quantified as the kilometers (km) traveled per hour (hr), calculated as the distance traveled between two locations in the same stand divided by the time elapsed between the two locations. Sinuosity was the total distance traveled within a stand divided by the linear distance between the two points where the animal entered and departed the stand (e.g., Maletzke et al. 2008). To characterize distance traveled, speed, and sinuosity, we went through a series of steps to ensure we only evaluated consecutive locations along a path. We defined a path as sequence of locations with at least three 3-D locations which had expected accuracy of 28m regardless of stand type (Moriarty and Epps *In press*) and a maximum of 10 minutes between each point. We converted the path into segments, where a segment represented a continuous piece of a path within a particular stand type, by first changing the point estimates to polylines using GME (Beyer 2014), then using ArcMap editor tool to place points every 5m along each line. We added path attributes and stand type to each evenly spaced point (5m) using the Spatial Join tool in ArcMap 10.1 (ESRI, Redlands, California, USA) and then analyzed the path segments to calculate sinuosity. We used this path- and then point-based procedure to allow for the possibility that martens could entirely cross contrasting stand types within a 5-minute period, resulting in potential bias if only actual GPS locations were used. Daily and hourly distance traveled, path lengths, and within-stand direct distance and sinuosity estimates were calculated in program R (R Core Team 2013). BBMMs and motion variance were calculated using R package BBMM (Nielson et al. 2013).

We evaluated movement patterns of our three responses (i.e., Brownian bridge motion variance, speed, and sinuosity) in relation to stand type (complex, simple, open), sex (male, female), season (summer, winter), and all combinations of these variables using linear mixed models that included marten as a random effect (package nlme, R Core Team 2013). We

compared models using Akaike's information criterion (AIC) using the function `lme` which penalizes for additional covariates in mixed-models (Müller et al. 2013).

Ethics Statement

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 & ACUC 2011) and the Association for the Study of Animal Behaviour (ABS 2012).

RESULTS

We captured 54 martens (37 male, 17 female), of which 38 (26 male and 12 female adults) were radio collared and 25 were GPS collared. We calculated seasonal home ranges and utilization distributions for 22 individuals with greater than 50 3-D locations: 15 males (11 summer and 12 winter home ranges, 7 paired during both seasons) and 7 females (5 summer, 4 winter, 2 paired during both seasons). Each home range was a mosaic of the three stand types (Table 1). We obtained 8,964 marten locations distributed in complex (66%), simple (29%), and open (5%) stand types. We obtained 550 movement paths from those 22 martens during 2010-2011 (summer) and 2010-2013 (winter). On average, there were 25 paths/individual (range = 5-59) with 58.9 ± 1.9 km of path data per individual ($\bar{x} \pm \text{SE}$). The average path length was 2,401 m (range = 152-12,475 m). We extracted 35,327 path segments within stand types to evaluate sinuosity.

The distances that males moved each day ($7.7 \pm 0.2 \text{ km}$) were marginally greater than those of females ($6.1 \pm 0.2 \text{ km}$, $F = 3.03$, $P = 0.07$) and there was no difference in average daily distance by season (Figure 2a, $F = 0.58$, $P = 0.44$, 2-factor ANOVA, males and females combined). The maximum recorded daily distance moved for females and males was 11.4 and 27.2 km, respectively, and martens moved greater than 2km within an hour 8% of the time ($n=156$ instances). The proportion of the day when we recorded martens moving with path data was similar for both males and females ($F = 1.82$, $P = 0.17$) and differed by season, in that females moved less during summer than winter (Figure 2b, $F = 9.2$, $P < 0.01$).

Martens exhibited second-order selection, selecting home ranges with a disproportionate amount of complex stands and avoiding openings when compared to the study area. This implies that on a landscape level, only the percentage of openings affected the placement of marten home ranges; however, simple stands were marginally avoided compared to complex stands (Table 2). Martens also exhibited third-order selection, using complex stands within their home range more frequently than available (Table 2b), suggesting that they avoided both simple stands and openings.

We observed significant differences in marten movement patterns among stand types within home ranges. First, motion variance was lowest in complex stands and increased significantly in simple stands and openings (Table 3, Figure 2a). This suggests that martens moved consistently in complex stands, and speed, sinuosity, or both varied more in simple stands. An even greater increase in the variance of speed and sinuosity was observed in openings relative to complex stands (Figure 2a). Second, martens moved most slowly in complex stands, averaging 1.30 km/hr ($SD = 1.12$), as compared with simple stands ($x \pm SD = 1.46 \pm 1.23 \text{ km/hr}$) or openings ($1.37 \pm 1.19 \text{ km/hr}$, Table 3, Figure 2b). Travel speeds across openings had increased

variation, likely contributing to the high motion variance (Figure 2a). We interpret this behavior as an inconsistent series of stops and sprints in openings. Last, the difference in distance ratio representing the amount of complexity within a path was highest in complex stands where the average ratio (1.45) reflected 145m of movement within every 100m of straight line distance (Figure 2c). In openings, martens moved very linearly resulting in values close to 1. Sinuosity was highest in complex stands, lowest in openings, and in between in simple stands (Table 3, Figure 2c). In sum, the increase in motion variance in stands with decreasing complexity was due both changes in speed and sinuosity, but potentially most influenced by changes in speed.

A combination of stand type, sex, and season best explained our response variables for all metrics of movement except sinuosity, which was best described by stand type alone (Table 4). Motion variance was similar for both sexes ($t = 1.24$, $P = 0.23$) and during both seasons ($t=0.31$, $P = 0.76$). With sex and season constant, motion variance significantly increased in openings ($t = 4.52$, $P < 0.01$) and simple stands ($t = 2.97$, $P < 0.01$) compared with complex stands (Figure 3a). Speed was greater for males than females ($t=2.61$, $P=0.02$) and both sexes moved faster during winter than summer ($t=-14.03$, $P<0.01$). Speeds generally increased in stand types with decreased complexity (simple $t= 2.90$, $P < 0.01$, open $t=0.06$, $P=0.95$, Figure 3b). During winter, females rarely entered openings ($n=5$ locations), and during summer, decreased speeds in open areas probably occurred because the majority of open locations were in talus patches which provide foraging opportunities. Sinuosity was highest for females ($t=-1.37$, $P = 0.11$), especially in complex stand types, and did not differ by season for either sex ($t=0.65$, $P=0.52$). Sinuosity decreased in simple stands ($t=-4.65$, $P<0.01$) and openings ($t=-5.25$, $P<0.01$) compared to complex stands (Figure 3c).

DISCUSSION

Martens selected stand types with increased structural complexity and exhibited behaviors suggesting stand-mediated responses to foraging strategies and predator avoidance. The amount of movement we observed requires large energetic expenditures (Taylor et al. 1970), indicating that martens must carefully select resources. We hypothesize martens' more deliberate movement through complex stands may have indicated greater foraging or resource use in those stands, as expressed by more consistent and typically slow sinuous movements. In contrast, martens largely avoided openings and simple stands. Their behavior in these stands included increased speed and direct linear movements, especially in openings. The combination of stand use and behavior within stands provides opportunities to identify potential mechanisms correlated with martens' choices and propose methods to increase marten use within managed stands.

Martens avoided openings both within the study area and within the home range, as expected from other landscape-scale studies (Hargis et al. 1999, Potvin et al. 2000, Cushman et al. 2011). Our seasonally-specific utilization models suggest that martens selected complex and avoided openings and simple stands similarly in both summer and winter seasons. Likewise, when examining multi-scale habitat associations within two study areas in Oregon and Washington, Shirk et al. (2014) found habitat selection did not change between seasons. Unique to our study was the prevalence of both openings and simple stands. Simple stands were not strongly avoided at a landscape scale. Forest simplification is a relatively new management strategy that has been used a tool for 15 years in this study area and we hypothesize that simplification did not influence second order habitat selection, i.e., at a landscape scale, because simplified stands are still relatively rare on this landscape. As such, each variable must be

present and available for selection to be biologically relevant (Jones 2001). For instance, Cushman et al. (2011) reported that before management, martens selected stands that had the highest amount of prey but did not avoid open stands, which were rare. After the landscape was altered by 240 small forest clearings, martens avoided open stands but selection of stands with high prey density was no longer detectable.

In our study, in contrast to the landscape scale analyses, marten home ranges had a more balanced mixture of all three stand types. At this scale, martens avoided both openings and simple stands. We did not estimate marten occurrence as a function of stand composition and configuration, but average stand composition in marten home ranges ranged from 4-10% openings and 24-33% simple stand types. Marten populations decline in areas with greater than 25% openings (Hargis et al. 1999, Potvin et al. 2000, Fuller 2006), so our observations were well under this threshold. However, it is unknown how much of a home range can consist of simple stands without adverse effects, particularly when openings are also present. Our annual adult survival (63%, unpublished data) was the lowest reported in North America (McCann et al. 2010), potentially suggesting our current home ranges may be nearing a threshold above which martens may not be able to persist. Additional research on marten survival in landscapes that differ in the amount of simple stands is urgently needed.

At a fine scale, we suspect that marten habitat selection was influenced by five motivations including (1) successful foraging, (2) avoiding predation, (3) finding and using rest sites, (4) territory marking, and (5) mating and kit rearing during summer. With our study, we explored the first two motivations in further detail with novel GPS movement data. Within complex stands, martens consistently traveled at slower speeds and with higher sinuosity. We hypothesize that these movement patterns are linked to increased perception of and ability to find

resources. Successful foraging is a critical component of an individual's ability to survive and also is important for population-level stability (Houston and McNamara 2014). Martens consume up to 29% of their body weight each day (Gilbert et al. 2009) and lack of larger-bodied prey items may limit population growth (Carlson et al. 2014) because smaller-bodied prey require more foraging effort. Foraging activities may already consume almost 50% of the day, especially if an animal is raising young, as observed from fishers (Powell and Leonard 1983) and sea otters (*Enhydra lutra*, Thometz et al. 2014). Thus, the ability to successfully forage on high quality prey and reduce energy expenditure is paramount for carnivores such as martens with high energetic expenditures (Scantlebury et al. 2014), especially during times of reproduction. Martens are able to more successfully find and kill prey in complex stand types, despite the availability of similar prey densities in harvested and regenerating stands (Andruskiw et al. 2008) similar to our simple stand type. Andruskiw et al. (2008) hypothesized increased hunting success was correlated with the high abundance of downed logs, which both provided sensory cues for martens and structural complexity that decreased the wariness of red-backed voles (*Myodes* sp.), simultaneously increasing the likelihood of martens capturing voles. Further, martens may need escape cover and resting sites to safely eat their prey once captured, which has been demonstrated with small mammals (Lima and Valone 1986, Phelps and Roberts 1989). Thus, it is expected that martens would benefit from moving within familiar stands that provide access to prey (Spencer 2012) at speeds that allow both perception of these resources and the ability to take prey items to places providing cover.

We suspect that differences in martens' movement behavior among stand types was closely correlated with predator avoidance strategies. Survival is the most important factor affecting population stability in marten populations (Buskirk et al. 2012). In our study, increased

speeds and decreased sinuosity implied that martens perceived more risk when traveling in openings and simple stands, as suggested by Lima and Dill (1990) in their review of behavioral decisions made under the risk of predation. When martens did cross openings, they moved erratically (fast and/or slow) and linearly. Similar movements were reported for a Chilean rodent (*Octodon degus*) while in openings with high predation risk (Vásquez et al. 2002). These findings are also consistent with food titration experiments that demonstrated martens avoided openings and simple stands during summer when predation risk was high even though food was available (Moriarty et al. In review). During this study, bobcat (*Lynx rufus*) appears to be the primary predator as indicated by forensics evaluation of DNA from marten carcasses (Wengert et al. unpublished data, Wengert et al. 2012). Because martens are quite small (600-1000g), coyotes (*Canis latrans*) and goshawks (*Accipiter gentilis*) also would be likely predators (Bull and Heater 2001, Pagel and Schmitt 2013). We hypothesize martens have less escape cover and thus more predation risk in simple stands and openings. Other species such as gray squirrel (*Sciurus carolensis*) and willow tit (*Parus montanus*) will feed in risky areas provided there is some minimal level of cover (Lima and Valone 1986, Hogstad 1988) and we suspect that some martens foraged in simple stands on rare occasions, mainly during summer when ground squirrels (e.g., *Tamias*, *Otospermophilus* sp.) would be available (Moriarty et al. In review). Stand type may both directly (through perceived risk) and indirectly (by cues) influence marten behavior. Drew (1995) observed captive martens changing their behavior and acting more cautiously when predator cues, such as coyote scat, were added to their environment. Stand type was considered an indicator of relative risk, even without knowledge of relative predator densities, as observed in squirrel monkeys (*Saimira* sp., Boinski et al. 2003) and songbirds (Zanette et al. 2011). If predation risk limits marten movement and changes behavior, then

increased structural complexity within the stand, such as residual overstory trees (Heinemeyer 2002), piles of logs and coarse woody material (O'Doherty et al. 1997), and branches or sapling cover near the ground (Hargis and McCullough 1984), may increase marten use of simplified stand types.

The amount and type of movement balancing resource acquisition with predator risk is directly correlated to energetic expenditures (Wilson et al. 2012, Humphries and McCann 2014). We observed consistent daily long distance movements that exceed recorded movements previously recorded for martens (Thompson and Colgan 1994), and also exceeded daily movements of larger carnivores such as bobcats (Newbury 2013). Martens moved similar distances during both seasons and both sexes moved faster during winter. We expected differences during seasons because in summer martens are occupied with reproductive activities; males attempt to mate with multiple females and females care for kits. Similar movement distances during both seasons may indicate that martens used a familiar network of locations to forage and gain resources within their home range. We suspect that increased speeds during winter may reflect decreased prey availability as martens need to search larger areas to meet their energetic needs, as hypothesized by Barton and Hovestadt (2012). The marten diet includes only a few mammalian prey species during winter months (Martin 1994), because ground squirrels hibernate and birds migrate. It is unknown whether movement rates are correlated with snow pack, but martens use more energy during cold periods without snow cover (Gilbert et al. 2009).

We expected females and males to move differently, but that was not the case, perhaps because of high energetic requirements and intra-sexual territoriality requiring both sexes to scent mark and defend territory perimeters. Females moved slightly more sinuously than males, used both complex and simple stand types, traveled at a slower rate, and moved slower during

summer compared to winter. We interpret this movement as representing a localized foraging strategy focused on the highest prey densities. Less sinuosity for males compared to females may represent a different strategy. Males may be motivated to maintain access to females within their territory boundary, similar to males in avian communities (Fretwell and Calver 1969). Males have larger territories and to mark and defend these ranges may require more rapid and directed movements, as reflected in the increased speeds and distances, increased variance in motion, and decreased sinuosity we observed in males. Bobcats exhibit similar sex-related patterns, with females moving more sinuously and slowly compared to males (Newbury 2013). We also noted particular marten movements that appeared to reflect territoriality, or individuals moving along the perimeter of their home ranges, but we did not separate such movement types during this study. New analyses that combine information from both GPS collar movement data and activity sensors may help interpret movement data (Nams 2014), and sex-specific explorations are warranted.

GPS collars offer new information about marten movement, which previously has been characterized in North America using snow tracking. Our study suggests that individual paths described in such studies comprised a relatively small percentage of daily movement given that path lengths ranged between 86-2124m (Hargis and McCullough 1984, Heinemeyer 2002, Nams and Bourgeois 2004, Cushman et al. 2011). Although fine scale movement from snow tracking provides information on particular structures such as potential resting sites (Corn and Raphael 1992) and foraging locations (Andruskiw et al. 2008), indices of daily movement expenditures (e.g., distance traveled) available from GPS collars are more likely to be sensitive indicators of habitat quality and energetics required to travel between stand types. The two methods are complementary: for instance, we discovered increased sinuosity in winter paths in complex

stands, as did others using snow tracking (Hargis and McCullough 1984, Heinemeyer 2002, Nams and Bourgeois 2004). However, our use of GPS technology also allowed us to confirm this pattern also in summer. We recommend both GPS data collection and snowtracking in concert to better interpret marten stand use, and we demonstrate that movement patterns from GPS data can provide important additional insights to marten behavior and population level processes.

SYNTHESIS AND APPLICATIONS

Our study suggests that both sexes of martens avoid openings and simple stands when possible, and move more quickly linearly within these stand types. Moriarty et al. (*In review*) found that martens did not consider openings as part of a functionally connected landscape. Even small gaps (<50m) without tree cover decreased the odds of martens using areas adjacent to openings. Instead, martens selected complex stand types which presumably provide access to resources and reduce predation risk. It is necessary to understand how much treatment and over what portion of a home range-sized area can be tolerated by martens. During our study, marten home ranges were comprised of approximately 9% openings and 30% simple stands on average. We propose these quantities could represent maximum levels of non-preferred habitat types that management may create in potential marten home ranges. Although the range of simple stands in marten home ranges was as high as 59%, we also observed low annual survival. Composition and configuration of stand types are beginning to be addressed for the fisher, whose range more closely overlaps forest types where fire risk is greater (Thompson et al. 2011, Zielinski et al. 2013). Thus, experiences with fisher may provide templates for spatially and temporally designing treatments suitable for marten in the future. Both the spatial arrangement of thinned stands and the amount of management over time that an individual marten can endure within a

home range are important to determine for future fuel reduction strategies intended to increase forest resilience to large-scale high intensity fires.

To minimize impacts on martens, we suggest that areas at lower elevations (0-1500 m) should be prioritized for fuels reduction due to the increased departure from normal fire return intervals in those forests. Fire return intervals were historically lower at those elevations (4-22 years, Taylor 2000, North 2012), and martens do not typically occur (Zielinski et al. 2005). In the high elevation forests that support martens, fire return intervals are thought to have remained within the expected range of 83-200 years (Taylor 1993, Taylor 2000) despite fire suppression (Stephens et al. 2007b).

In areas with planned treatments, increasing structural variation within stands may allow martens to travel through future versions of managed stands aimed to reduce fire behavior. Recent forest ecosystem management guidelines (North et al. 2009, North 2012) call for forest simplification designed to mimic variation in stand densities that occur as a result of topography, moisture, disturbance and climate. Creating clusters of differing sized trees, including patches of saplings, and retaining residual logs may both increase areas for marten prey and escape cover and thus better accommodate marten use and movement through managed stands.

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TABLES AND FIGURES

Table 3.1. Marten home range composition. We report the composition of stand types and range within seasonal marten home ranges created using Brownian Bridge Movement Models (mean \pm standard errors (SE)). Size differences between winter and summer are largely due to differing individuals between each season – not an expansion or contraction of individual home range size.

	Female			Male		
	n	Mean \pm SE	Range	n	Mean \pm SE	Range
Summer						
Size (km ²)	5	1.13 \pm 0.2	0.42-1.68	11	3.31 \pm 0.38	1.35-4.92
% Complex	5	54.5 \pm 5.7	42.8-68.6	11	65.7 \pm 2.8	52.9-78.2
% Simple	5	32.0 \pm 4.7	21.3-47.9	11	27.7 \pm 2.6	14.8-43.9
% Open	5	13.5 \pm 3.1	6.6-23.5	11	6.5 \pm 0.9	3.8-10.4
Winter						
Size (km ²)	4	3.34 \pm 0.9	3.11-3.55	12	3.46 \pm 0.44	1.11-5.62
% Complex	4	59.1 \pm 6.1	47.3-72.3	12	62.9 \pm 3.4	39.1-78.5
% Simple	4	34.7 \pm 5.1	23.3-46.4	12	29.6 \pm 2.7	13.1-59.0
% Open	4	6.2 \pm 1.5	3.8-10.4	12	7.5 \pm 1.3	1.7-18.0

Table 3.2. Habitat selection using compositional analysis. Martens selected areas both within the study area (A, second-order selection) and patches within their seasonal home ranges (B, third-order selection, Johnson 1980). Symbols indicate whether the patch in the corresponding row was used more or less (sign+ or -) than expected compared to the patch in the corresponding column. A triple sign (+++ or ---) indicates preference and avoidance, respectively ($P < 0.05$) where a single sign reflects a non-significant difference. The order listed in both columns and rows indicates the direction of selection.

A.

Second-order	Complex	Simple	Open
Complex	0	+	+++
Simple	-	0	+++
Open	---	---	0

B.

Third-order	Complex	Simple	Open
Complex	0	+++	+++
Simple	---	0	+
Open	---	-	0

Table 3.3. Marten behavior in relation to patch type. We described movement using Brownian bridge motion variance, speed, and sinuosity as represented by a distance ratio and evaluated whether these responses changed within stand types that differed in structural complexity. The reference is the complex patch type. We report the coefficient, t-value, and significance (p-value) for each of our behavioral responses.

Response	Patch Type	Coefficient	SE	t-value	p-value
Motion Variance	Intercept (Complex)	10.15	3.94	2.57	0.01
	Simple	13.00	4.34	2.99	0.00
	Open	25.51	5.61	4.54	0.00
Speed	Intercept (Complex)	22.74	1.55	14.58	0.00
	Simple	1.27	0.45	2.77	0.01
	Open	-0.45	0.93	-0.49	0.62
Sinuosity	Intercept (Complex)	1.51	0.06	22.70	0.00
	Simple	-0.20	0.04	-4.66	0.00
	Open	-0.30	0.06	-5.24	0.00

Table 3.4. Movement models and delta AIC and AIC weights (w_i). We described movement using Brownian bridge motion variance, speed, and sinuosity as represented by a distance ratio. Our models included all combinations of patch type (open, simple, complex), marten sex (male, female), and season (winter, summer).

Data	Model	ΔAIC	w_i
BBMM variance	patch type + sex + season	0	0.80
	patch type + sex	2.88	0.19
	patch type	8.18	0.01
	sex + season	25.18	0.00
	Sex	28.28	0.00
	Season	30.38	0.00
	Intercept	33.58	0.00
Speed	patch type + sex + season	0	0.96
	sex + season	6.5	0.04
	Season	14.4	0.00
	patch type + sex	192.9	0.00
	Sex	199.5	0.00
	patch type	200.7	0.00
	Intercept	206.9	10.00
Sinuosity	patch type	0	0.96
	patch type + sex + season	7.2	0.03
	patch type + sex	11	0.00
	Intercept	25.3	0.00
	Sex	26.6	0.00
	Season	31.1	0.00
	sex + season	32.52	0.00

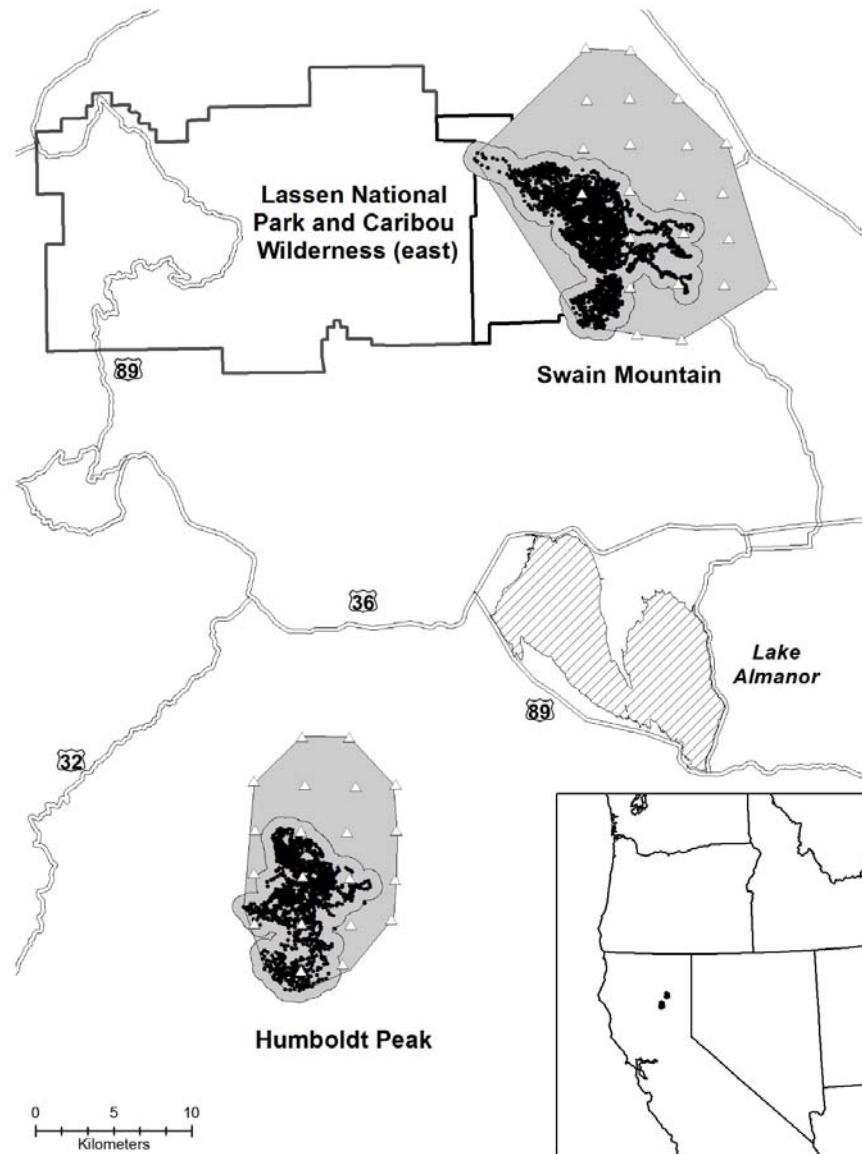


Figure 3.1. Our study occurred in two independent sites (Humboldt Peak, Swain Mountain) within Lassen National Forest, California. Here, we display the study area used for the compositional analysis (grey). White triangles represent trapping locations and filled circles include Pacific marten locations.

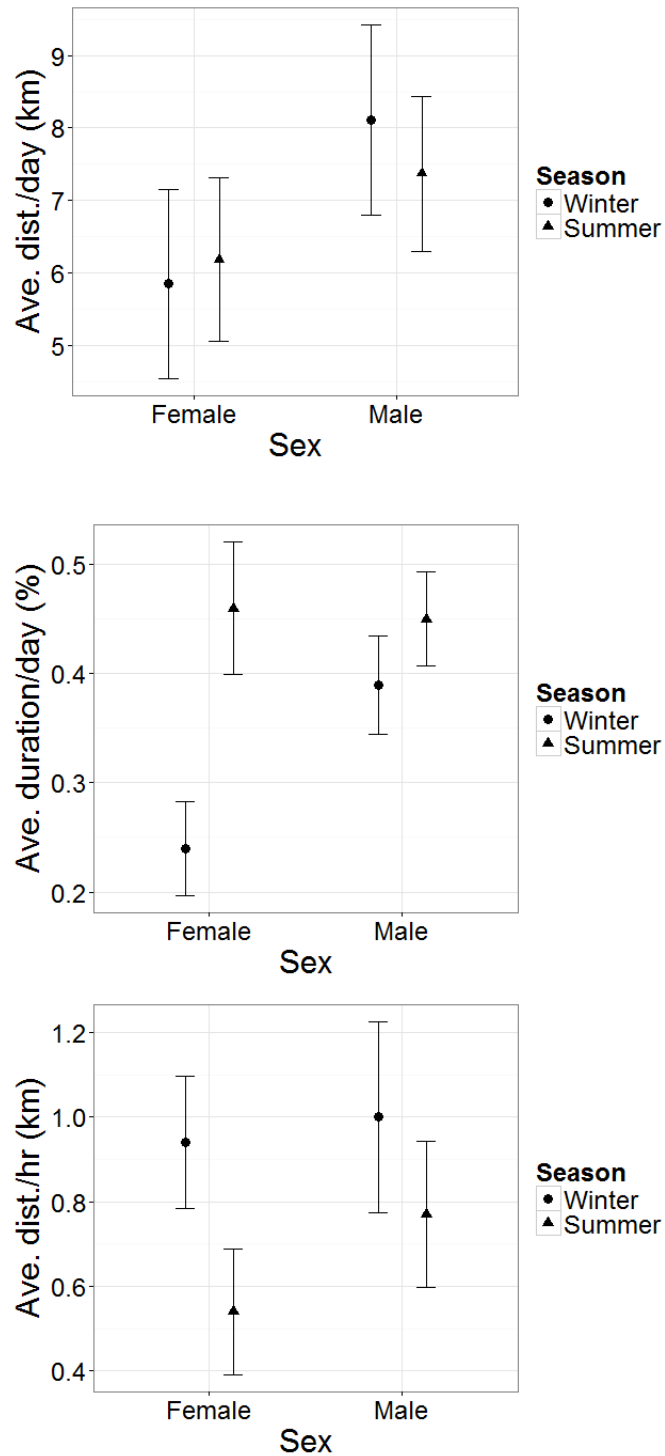


Figure 3.2. Marten movement characteristics: A) Average minimum daily distances traveled. B) Proportion of the day with marten movement and GPS data collected. C) Average distance traveled per hour when the animal was moving. Data were collected from 22 martens in Lassen

National Forest, CA. We show the mean and 95% confidence interval (bars). These data represent minimum values as additional movement could occur between locations and we expect some missed locations due to GPS error.

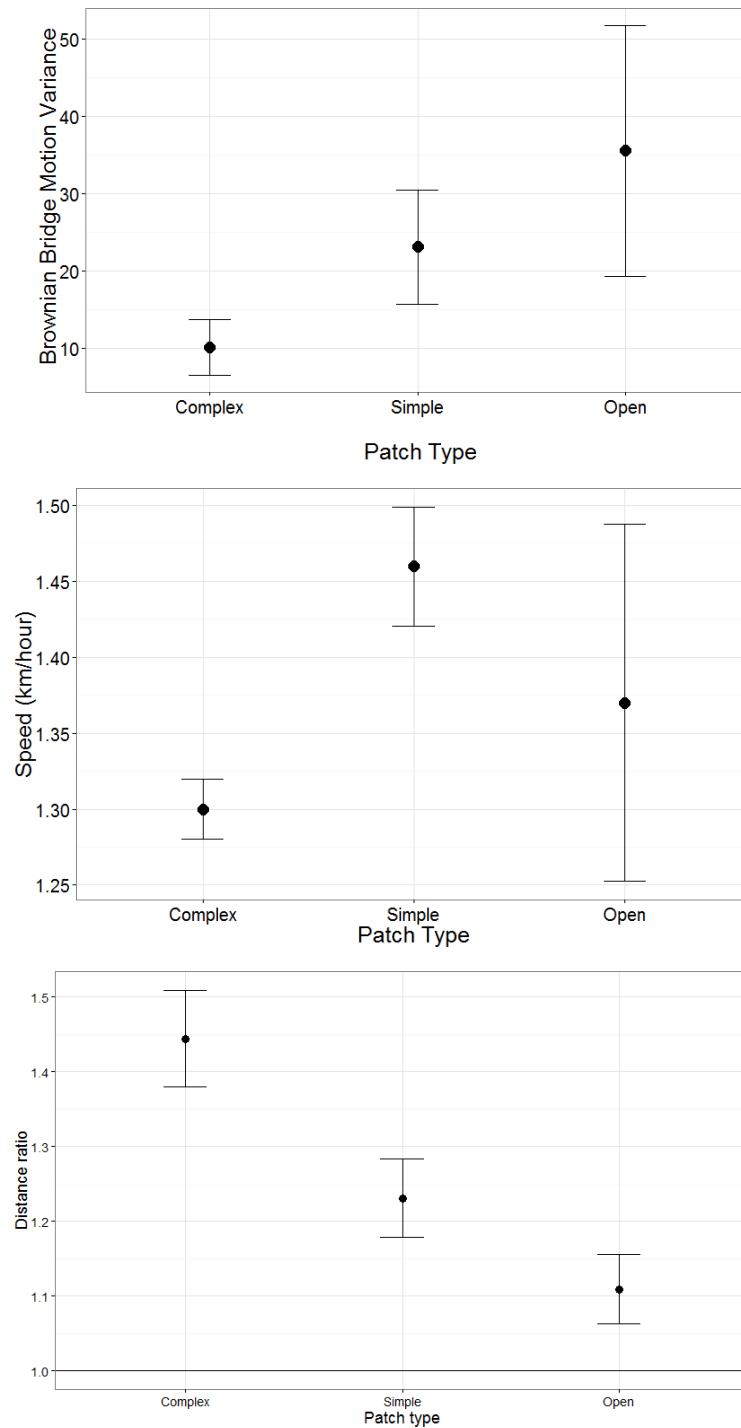
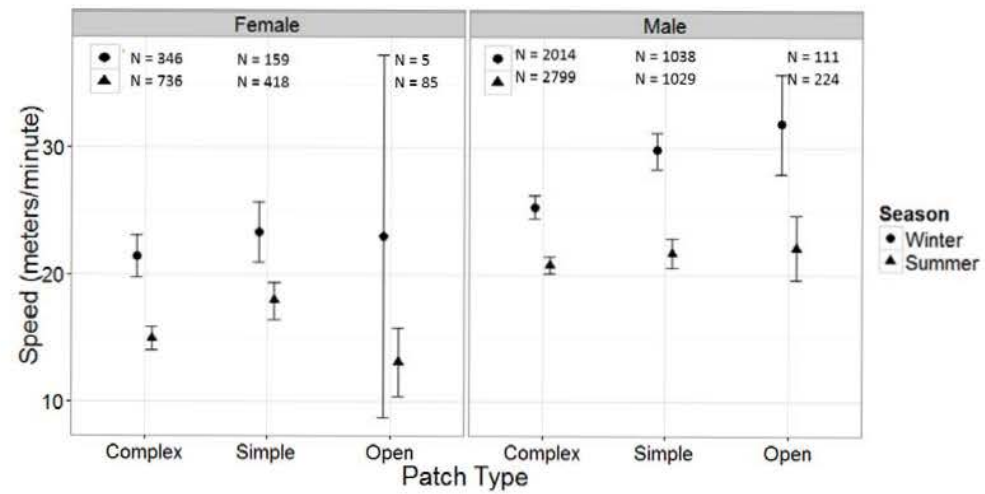
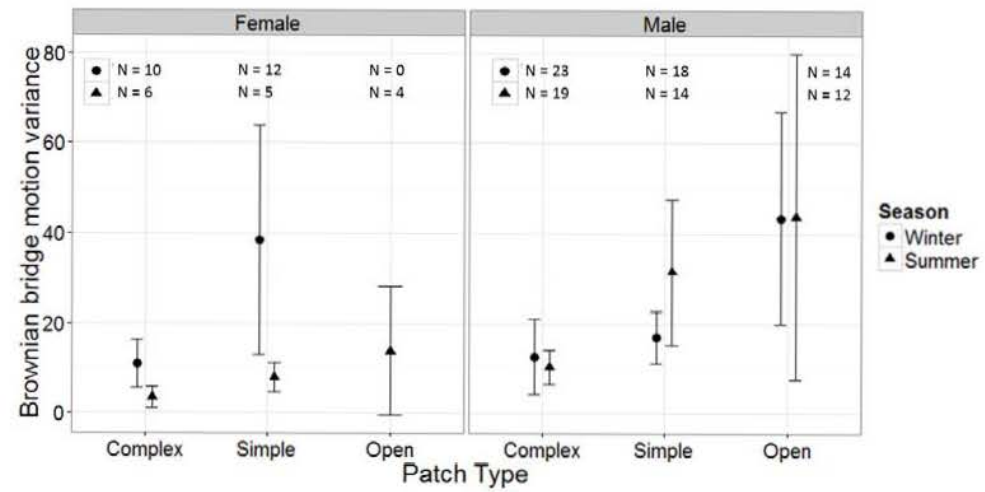


Figure 3.3. Marten movement patterns in patch types that differ in structural complexity

(complex, simple, open) described by three metrics: A) Brownian bridge motion variance reflects the influence of speed and/or sinuosity, an index of movement complexity. B) Speed represents a

conservative estimate of marten velocity, estimated from 8964 two-point segments with locations having estimated accuracy of 28m (n = 5895 complex, 2644 simple, 425 open). C) Distance ratio between the distance traveled and direct distance within each path, where the 35,327 path segments represented (path segments = 16456 complex, 13698 simple, 5173 open). Data were collected from 22 martens in Lassen National Forest, CA. We show the mean and 95% confidence interval (bars).



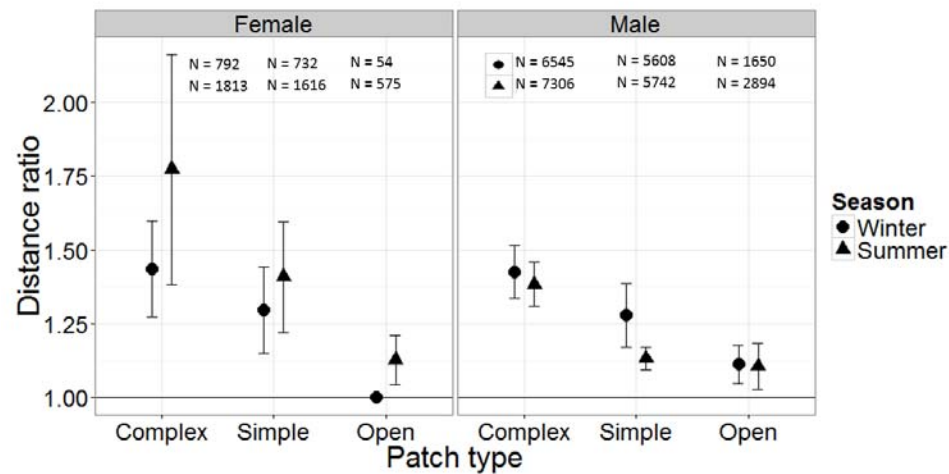


Figure 3.4. Marten movement patterns in patch types segregated by sex (male, female) and season (summer, winter), including (A) Brownian bridge motion variance, with the number of individuals in each category by sex, season, and patch type, (B) Speed in km/hr, with the number of locations with a proceeding 3-D location allowing an estimate of time traveled between locations, and (C) Distance ratio, with the number of path segments within a patch type. We calculated the 95% confidence intervals from the number of individuals (not the number of paths), 7 females ($n = 5, 4$ during summer and winter) and 15 males ($n = 11, 12$ during summer and winter respectively). These data were modeled with marten as a random effect.

CHAPTER 4 : SUMMARY AND DISCUSSION

The research presented in the preceding three chapters highlights the importance of accurate data collection using multiple methods, especially for interpreting the use and behavior of a forest-dependent species that negatively respond to reduced patch complexity. This dissertation elaborates on four primary conclusions.

First, martens do not perceive structurally simple stands as high quality habitat. Martens avoided simple stands year-round, but were willing to travel through them quickly. Simple patches were not avoided as strongly as openings, but these stands were also not used for foraging, resting, or denning. I strongly suspect that there was increased predation risk and fewer opportunities for martens to pursue and obtain prey in simple stands.

Second, I suspect that the landscape is more functionally connected for martens during winters with deep snow cover. During winter, martens travelled into simple stands and openings with incentives, such as bait. I observed similar daily distances traveled during both seasons, but faster movement during winter in all stand types. I inferred that predation risk is lower during winter months with deep snow cover and the combination of snow cover, increased temperature extremes, and less available prey may influence marten movement and behavior.

Third, movement and habitat use did not strongly differ between male and female adult martens but the amount of movement observed by martens was greater than expected. I observed higher percentages of simple stands in female home ranges, and some differences suggesting slightly slower speeds and shorter distances traveled by females compared to males, but these observations were not statistically significant. Because this was the first study to evaluate marten movement using GPS collars, I

revealed that martens traveled an average of 7 km per day, were active half the day, and often traveled at speeds exceeding 1 km per hour. At the extreme, martens moved >2km in an hour 8% of the time. Our longest daily movement was 27 km and our longest continuous path was over 12 km in less than 5 hours. Although I did not use these data to interpret habitat use, increased energetic demands may be a critical component explaining population declines following habitat loss.

Lastly, novel methods provide exciting opportunities to address specific scientific questions, but these methods should be carefully vetted concurrently with previously established techniques and over biologically relevant time periods. I provided three examples that suggest a single technique or approach may provide incorrect or biased conclusions. First, GPS error was often tested using stationary tests, whereby the unit was placed in an area stratified by vegetation cover and topographical obstruction within the study area of interest. In Chapter 1, I showed that depending on where and how a micro-GPS collar was activated produced drastically different performance. Second, food-titration experiments revealed that martens avoid simplified stand types, largely due to predation risk. Martens travelled more readily into these stand types during winter when predation risk decreased and with a bait incentive. Telemetry data confirmed that marten stand use did not change from summer – martens still avoided these stands with the absence of bait. As such, data collected in the winter with baited stations provided biased information on what the animal used and would bias our interpretation of marten habitat. Baited stations provide insight in to species distributions, but our data suggest they should not be used to infer fine-scale habitat relationships, particularly when surveys only occur in winter. Third, martens often are cited as a species whose occurrence is correlated with habitat-related variables at multiple spatial scales. One way to measure marten

habitat use at a fine scale is through snow tracking. Because martens can travel >2 km in an hour and snow tracking generally only occurs for 2 km or less, this method only provides a brief snapshot of marten behavior. I collected data at 5-minute intervals, thus our movement data may be too coarse to relate to very fine-scale needs (e.g., specific habitat elements used for resting and foraging)). As such, interpreting data within the scope of inference and biological relevance requires an understanding of the biology of the animal – often acquired through years of experience.

From this last conclusion I emphasize that through the scientific method, additional questions arise during research. I formulated new hypotheses as I collected additional information and as such, I could not address the multitude of new predictions within this dissertation. Here, I highlight observations and potential limitations not included within this dissertation. I provide considerations that may advance our knowledge of marten ecology and provide management strategies that balance timber harvest with marten habitat needs as I continue into the 21st century.

Marten movement patterns are complex, and I was unable to elaborate on potential social dynamics and implications of memory-related habitat use. I anecdotally observed periodicity in movements, where an individual would revisit locations at similar times, and repeated use of paths by multiple individuals –observations that spanned the course of our study (years). Evaluating the cognitive potential of this species, their use of scent marking and navigation, and how disturbances can influence these cues may be relevant to understanding how martens perceive the landscape. Such cues could be related to population social dynamics through parental learning and habits.

The composition and configuration of patches may affect the ability of martens to occupy a landscape. Marten home ranges were composed of 12-59% simple stands and 0-

24% openings. Additional research should be conducted to understand whether there is a threshold that surpasses a marten's ability to survive in an area with additional fragmentation or habitat loss. With our current knowledge, I suggest managers consider (1) including movement corridors of spatially complex stands adjacent to simple stands and openings, (2) the extended thinning rotation lengths to reduce concurrent impacts within a landscape or home range, and (3) that homogeneous simplification of forested stands could be improved for both martens and their prey by leaving residual ground level structure (e.g. logs, snags) within managed or simplified stands.

Variable thinning, or increasing diversity within stands (North et al. 2009, North 2012, Churchill et al. 2013) provide an opportunity to improve conditions for martens and achieve goals to reduce risk of high-severity and high-intensity fire. Although I was not able to directly measure why martens move to specific features within a landscape, I proposed four primary motivations: (1) prey acquisition, (2) predation risk, (3) survival, (4) reproduction. Homogeneous simplified stands were not as avoided as much as openings, but not selected like complex stands. Increasing specific features at fine scales may provide martens greater opportunities to use stand types designed to reduce the threat of fire, such as foraging sites along downed logs, opportunities to access subnivean space from branches near the ground, or patches of dense sapling cover that provide shelter and food for snowshoe hare. Increasing patches with dense ground cover, large downed logs, and saplings may increase opportunities for martens to successfully forage in stands modified to reduce risks of fire. Further, clustered patches of ground level cover may also provide escape cover for martens, and thus increase survival. Marten den sites may include cavities within large snags, trees, logs, and extremely decayed areas around stumps that create an underground network of passages. Many large diameter trees and

snags are retained or even enhanced with thinning treatments. Retaining these elements may require spring burning, if burning is desired for reducing fine fuels in treated stands. Although I did not provide specific recommendations or prescriptions to diversify simplified stands, these four motivations are predictions explaining potential elements that could positively increase marten movement and stand use. Future research on martens could carefully test how martens use modified and variable stands that were developed to both reduce the risk of fire and provide habitat elements for martens.

Factors that limit marten survival and reproduction likely differ by region, and long-term demographic data are lacking. For Pacific martens living in subalpine and alpine ecotypes, there have been 6 focused research projects on martens highlighted within this dissertation. Geographically from south to north, these studies were located in the High Sierra (Zielinski et al. 2008), Inyo, Tahoe Basin Management Unit (Zielinski et al. 2008), Tahoe (Zielinski 1981, Zielinski et al. 1983, Martin 1987, Spencer 1987), and Lassen (this study) National Forests in California, Winema National Forest (Raphael and Jones 1997, Shirk et al. 2014) and the Blue Mountains (Bull 2000, Bull and Heater 2001) in Oregon, and Mount Baker-Snoqualamie National Forest in Washington (Shirk et al. 2014). These areas provide strategic locations to monitor marten population because they have differing management strategies, vegetation, and climate. This will help to better understand potential changes in marten distributions with a changing climate along a latitudinal gradient. Marten populations decline rapidly, often leading to local extirpations, with as little as 25% forest cover removed within a landscape. Thus, monitoring marten populations provides a canary in the coal mine opportunity for many forest-dependent species. We are fortunate that martens are not yet rare in the Pacific Northwest. However, current petitions to list wolverine, Pacific fisher, and the coastal

subspecies of martens (*Martes caurina humboldtensis*) as Federally endangered suggests that marten population stability should not be taken for granted.

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APPENDIX

EXPANDED METHODS

Our research was conducted at two study sites separated by 23 km in Lassen National Forest (LNF), California (Figure 1). Our study sites included 9.8% wilderness and 30% managed forest in the last 50 years (FACTS 2012). Forest management was historically focused on stand removal, but more recently has been focused on reducing fire hazard and increasing forest resiliency – especially in this region of California where there was a congressional mandate to experimentally simplify large forested areas (USDA 1999).

Data were collected January 2010-April 2013. We defined the summer season as snow-free months (July to November) and winter as periods with snow cover (December to June). Average minimum and maximum temperatures in July are 6.9°C and 29.5°C respectively, and – 6.9°C and 5.3°C in January (Western Regional Climate Center, 1948-2005). Average annual precipitation is 96-253 cm, depending on the location in our study area (Western Regional Climate Center, 1948-2005) and snowdepth varied annually within our study area (S1).

Stand Classification

We classified each forest stand as complex forest, simple forest, or an opening (Table 5.1, 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 were manually updated and modified (R. Martinez, LNF, GIS coordinator, personal communication). Our final product was a map at 30x30m resolution that classified each stand into one of our three categories (Table 5.1). Vegetation characteristics differed between stand types, most prominently between complex and open (Table 5.2). Canopy cover, basal area, shrub cover, sapling cover, and number of sound logs differed between stand types (Table 5.2), confirming a structural difference between our GIS classifications.

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FIGURES AND TABLES

Table 0.1. . Classification of stand types used to assess Pacific marten (*Martes caurina*). We identified three stand types of interest (open, simple, complex) but divided these into subclasses (numbers). We used California Wildlife Habitat Relationships ((Mayer and Laudenslayer 1988) to evaluation vegetation classification. Listed CWHR vegetation types include lodgepole pine (LPN, *Pinus contorta*), ponderosa pine (PPN, *P. ponderosa*), Jeffery pine (JPN, *P. jefferii*), red fir (RFR, *Abies magnifica*), white fir (WFR, *A. concolor*), pine and fir dominated Sierra mixed conifer (SMC-P, SMC-F respectively), subalpine mixed conifer (SCN), montane riparian (MRI), mixed chaparral (MCH), perennial grassland (PGS), annual grassland (AGS), and barren (BAR). Vegetation sizes include diameter at breast height (DBH) class 1 = <2.5cm, class 2 = 2.5-15cm, class 3 = 15–27 cm, class 4 = 28–60 cm, class 5 = >60 cm, class 6 =>60 cm with multi-layered canopy. Density classes include sparse (10-24% canopy cover), open (25-39%) moderate (40–60%), and dense (>60%).

Patch	Description	Management Event(s) as listed in FACTs	Management Description	CWHR Vegetation Types	CWHR Vegetation Sizes	CWHR Vegetation Density
Open	Recently managed (1) and managed before 2000 (2)	Group selection	Small clearing <2 acres with <60 sq. ft./acre	LPN, MRI, RFR, SCN, SMC-F, SMC-P, WFR	1-5	sparse, open
		Regenerating clear-cut	Complete tree removal			
		Overstory removal	Removal of all merchantable trees			
		Shelterwood harvest	Removal of merchantable trees, but retaining select trees for re-seeding			
Open	Natural openings (3)	NA		AGS, BAR, PGS	NA	NA
Simple	Recently managed (4) and managed before 2000 (5)	Fuels reduction	Understory plants, lower limbs, and small diameter trees removed	LPN, MRI, RFR, SCN, SMC-F, SMC-P, WFR	3-5	open, moderate
		Commercial thinning - no biomass	Variable amounts of merchantable trees removed			
		Commercial thinning - biomass	Merchantable trees removed in addition to small diameter			

			(<12" dbh)			
		Pre-commercial thinning - hand	Small diameter (<12" dbh) trees and understory removed by hand			
		Pre-commercial thinning - mechanical	Small diameter (<12" dbh) trees and understory removed by machines			
		Windthrow fuels reduction	Downed trees, logs, and hazards removed.			
Simple	Managed inconsistently (6)	Salvage logging	Removal of dead and dying trees, often along roads	LPN, MRI, RFR, SCN, SMC-F, SMC-P, WFR	3-5	open, moderate
		Sanitation cut	Removal of dead and dying trees			
		Single tree selection				
		Fire restoration and regeneration				
Complex	Dense managed (7) and unmanaged (8)	Managed includes any activity, but we envision "managed" stands as regenerated forests		ASP, DFR, LPN, JPN, MCH, MHW, MRI, PPN, RFR, SCN, SMC-F, SMC-P, WFR	2-4	moderate, dense
Complex	Predicted high quality reproductive habitat (see Kirk and Zielinski	Managed includes any activity, but we envision "managed" stands as regenerated forests		LPN, MRI, RFR, SCN, SMC-F, SMC-P, WFR	4-6	moderate, dense

	2009) managed (9) and unmanaged (10)					
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Table 0.2. Summary of stand type vegetation characteristics . We collected descriptive metrics collected along food-titration experiments to characterize our stand types (complex, simple, open). We report the average value and standard error ($\bar{x} \pm \text{SE}$).

Metric	Description	Complex	Simple	Open
Overstory	Average canopy cover percent, moosehorn coverscope	49.6 \pm 1.5	26.7 \pm 2.1	3.0 \pm 0.8
	Canopy cover standard error	11.8 \pm 0.2	10.8 \pm 0.5	2.2 \pm 0.5
	Basal area of live trees	217.0 \pm 7.8	127.8 \pm 8.5	37.5 \pm 9.3
	Basal area of snags	24.2 \pm 2.3	10.6 \pm 2.7	4.6 \pm 1.4
	Basal area of live trees >61-cm diameter	47.4 \pm 3.8	22.2 \pm 4.6	8.9 \pm 2.3
	Basal area of snags >61-cm diameter	9.9 \pm 1.2	3.1 \pm 1.1	1.8 \pm 0.8
	Percent dwarf-mistletoe (<i>Arceuthobium</i> sp.) on live trees	3.0 \pm 0.5	1.5 \pm 0.2	1.1 \pm 0.3
Understory	Percent shrub cover	1.3 \pm 0.5	3.8 \pm 1.1	13.8 \pm 2.3
	Percent sapling cover	6.0 \pm 1.0	1.6 \pm 0.5	1.1 \pm 0.4
	Percent understory cover (shrub+sapling)	7.3 \pm 1.1	5.4 \pm 1.2	15.3 \pm 2.5
	Average log diameter (cm) in Brown (1974) decay class 1-3, indicating sound wood	32.4 \pm 1.2	29.3 \pm 1.4	34.2 \pm 2.1
	Number of logs in decay class 1-3 (Brown 1974)	2 \pm 0.1	0.9 \pm 0.1	0.6 \pm 0.1
	Total number of logs	2.9 \pm 0.2	2.1 \pm 0.5	1.1 \pm 0.2