Forest Thinning Changes Movement Patterns and Habitat Use by Pacific Marten

KATIE M. MORIARTY,[1,2] *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

CLINTON W. EPPS, *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

WILLIAM J. ZIELINSKI, *Pacific Southwest Research Station, USDA Forest Service, 1700 Bayview Drive, Arcata, CA 95521, USA*

ABSTRACT Simplifying stand structure to reduce fuel density is a high priority for forest managers; however, affects to Pacific marten (*Martes caurina*) movement and connectivity are unknown. We evaluated whether thinning forests to reduce fuels influenced movements of Pacific marten. We collected movement paths from 22 martens using global positioning system telemetry to evaluate habitat selection and describe movement patterns. We quantified motion variance, speed, and path sinuosity in 3 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 traveled 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 because of their larger home ranges. Martens traveled 0.5–27.2 km/day and an average (SD) of 1.4 (0.4) km/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 over time and movements were more sinuous and slower in complex stand types compared with openings and simple stands. Movement was erratic and more linear in openings than in both complex and simple stands. 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. However, martens avoided stands with simplified structure, and the altered patterns of movement we observed in those stands suggested that such treatments may negatively affect the ability of martens to forage without increased risk of predation. Fuel treatments that simplify stand structure negatively affected marten movements and habitat connectivity. Given these risks, and because treating fuels is less justified in high elevation forests, the risks can be minimized by applying treatments below the elevations where martens typically occur. © 2016 The Wildlife Society.

KEY WORDS animal movement, California, marten, *Martes caurina*, movement, predation, risk, thinning, travel speed, vigilance.

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). For instance, in a patchy landscape, animals are predicted to maximize resource use within the home range by selecting patches with the highest quality resources (Pimm et al. 1985).

Movement patterns reflect strategies to acquire and allocate resources (Van Noordwijk and de Jong 1986, Gaillard et al. 2010, Houston and McNamara 2014), and can provide information about aggregation of resources (Wiens 1976, Seidel and Boyce 2016). For instance, central place foraging patterns, or short forays from a central location, suggest food is localized and has small energetic returns (Giraldeau et al. 1994). For predators, when prey are localized but far from a

centralized location, long-distance foraging bouts punctuated by sinuous movement patterns in areas with anticipated food resources are expected. Conversely, when prey are widely dispersed, searching a large area with less sinuosity is predicted (Barton and Hovestadt 2012). Direct and consistently fast movements reflect traveling through areas with low prey density (Earl and Zollner 2014), and variable speeds combined with sinuous movements correlate with prey searching and pursuit (McIntyre and Wiens 1999, Jonsen et al. 2007). Thus, foraging strategies expressed through movement patterns correlate with areas that provide maximum resources but also minimize predation risk (Lima 1998, Mitchell and Lima 2002, Houston and McNamara 2014). Movement can slow to reflect caution in risky environments (Lima 1987) or can speed up to quickly traverse these areas (Frair et al. 2005). In general, 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 to explore behavioral motivation in different habitats, such data are difficult to collect for small, elusive, and wide-ranging species. North American martens (*Martes* spp.) exemplify this challenge and the potential value of applying the study of movement to understand consequences of landscape modification. Martens are solitary, wide-ranging carnivores, frequently active (Balharry 1993, Thompson and Colgan 1994), consume approximately 25% of their body weight daily (Gilbert et al. 2009), and, because of their small size (~600–1,200 g), experience consistent predation risk (Drew 1995). Martens are considered a management indicator species (Thompson 1991, Bissonette and Broekhuizen 1995) because of their association with forested patches with a multi-layer canopy and large snags, logs, and trees (Spencer et al. 1983). Martens rarely enter openings (Cushman et al. 2011), likely because of increased risk of predation (Moriarty et al. 2015). The ratio between forested patches and openings is critical; marten populations may decline sharply with relatively modest amounts (<35%) of forest loss (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, 2015), and likely increase the distances that martens move. However, little is known about their movement. Snowtracking has been used to study marten movements in winter (Hargis and McCullough 1984, Corn and Raphael 1992, Nams and Bourgeois 2004), and 3 studies have tracked marten movement patterns using telemetry (Balharry 1993, Bissonette and Broekhuizen 1995, Zalewski et al. 2004), but global positioning system (GPS) technology suitably sized for martens and capable of generating much higher resolution data year-round has only been available since 2009 (Moriarty and Epps 2015).

The differential use of habitat by martens, and the dynamics of their movements, are related to the availability of resources provided directly by forest vegetation (e.g., resting locations in trees; Spencer 1987) and indirectly in the form of the prey species associated with different vegetation types. For example, martens appear to be more successful foraging in complex stand types (Andruskiw et al. 2008) than in other types and they consume prey associated with more open forest types (e.g., chipmunks; *Tamias* spp.) during summer compared to winter (Zielinski et al. 1983, Martin 1994). In addition to resources, marten movements are also likely to be influenced by the risk posed by their predators whose abundance and hunting efficiency will vary with different vegetation types. The proportion of marten mortality caused by predation varies by landscape condition, with predation representing 62% (Bull and Heater 2001) to 75% (Raphael 2004, McCann et al. 2010) of mortality events in moderate-to-heavily logged forest compared to 40% (Hodgman et al. 1997) in an intact forest reserve. The composition of predators killing martens in these studies also varied between moderate-to-heavily logged forests and forest reserves, with generalist carnivores including bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) responsible for 71% (Bull and Heater 2001) to 75% (Raphael 2004) of predation events in logged forests versus 40% (Hodgman et al. 1997) in a forest reserve. Thus, variation in landscape structure and composition is expected to affect marten movements by affecting the spatial distribution of resources, such as resting locations and prey, and the threat of predation.

We examined how movements by Pacific martens (*Martes caurina*) reflect their perceptions of stand types that represent a gradient in forest complexity: open stands, stands that are structurally simple, and stands that are structurally complex. The influence of forest complexity on marten movement is particularly relevant because of ongoing efforts to reduce intensity of wildfires by removing fuels such as downed logs, low branches, and small diameter trees. Such treatments have been proposed or applied across North America (Agee et al. 2000, Kalies et al. 2010, Stephens et al. 2012), and result in simplified forest structure. However, the consequences of this new type of forest management on martens, marten movement, and thus stability of marten populations are unknown. As such, we also needed to determine whether martens were selectively using or avoiding differing stand types in our study area. We predicted that martens would make deliberate movements to acquire resources and avoid predation, and these movement patterns would differ by stand type.

Although we predicted stand type to be the primary influence on marten movements, we also predicted that influence would vary through interactions with sex and seasonality. Martens are sexually dimorphic; males are about 33% larger than females (Merriam 1890). Therefore, we expected a physiological difference in movement capacity, whereby males would be able to move faster and travel farther than females, and predicted that willingness to use different stand types would vary by sex because of the different energetic and reproductive constraints. We also expected marten movement and potentially the influence of forest structure on movement to vary seasonally. Seasonal variation in movement has been poorly understood because fine-scale

movement previously could only be assessed via tracking in snow (e.g., Hargis and McCullough 1984, Andruskiw et al. 2008, Cushman et al. 2011, Cheveau et al. 2013). However, martens are likely to move more during summer than winter (Zalewski et al. 2004). During winter, when many sciurid prey hibernate and potential predators likely migrate to lower elevations, martens have fewer resources and predators, lack reproductive responsibilities, and may experience increased thermoregulatory stress due to cold temperatures and precipitation. Thus, in winter, because of changes in risk and resource availability, we expected martens would move less and select complex stands less strictly than in summer.

We hypothesized that stand type use would differ because of different structural elements within stands that influence foraging and predation avoidance, with foraging occurring most often in complex stands (Andruskiw et al. 2008). As such, we predicted that home ranges would have a disproportionate amount of complex stand types compared to the landscape (second-order selection; Johnson 1980), and within home ranges, martens would use complex stands more than available (third-order selection; Johnson 1980). Because martens forage actively for small mammals associated with downed woody material and other complex environments (Andruskiw et al. 2008), requiring frequent changes of speed and direction, we predicted that 1) movement would increase in complexity (i.e., increased sinuosity, increased motion variance) when martens traveled through stands with increased structural complexity; 2) speeds would increase during the summer regardless of stand type because of reproductive activities; and 3) females would move slower than males, especially in areas with increased risk such as openings and simple stands (Moriarty et al. 2015).

STUDY AREA

We conducted this research in Lassen National Forest (LNF), California, where marten populations were monitored over 8 previous years (Fig. 1; Zielinski et al. 2015). California banned fur trapping for martens in 1954 because of the perception that habitat loss and trapping were contributing to species decline (Grinnell et al. 1937). Continued declines were correlated with habitat loss (Schempf and White 1977, Zielinski et al. 2005), and most recently there was concern that thinning for fuel and fire treatments posed a significant threat (Zielinski 2013). This 397-km^2 area was ideal to test these assumptions because this area was part of a 13-year effort to intensively manage forests to reduce fuels (Owen 2003, Pinchot Institute 2013). Prior to fuel reduction efforts in 1999, the predominant management activity was removal of the majority of trees in a stand (i.e., clear cut, shelterwood, seed tree harvest). Following 1999, management also included fuel reduction (e.g., thinning from below), which generally resulted in removal of smaller diameter trees, logs, and understory vegetation. Managed stands often set a goal of retaining 40% overstory canopy cover and the overall product of these treatments appears effective at reducing fire behavior (Moghaddas et al. 2010). Elevations in this region ranged from 1,500 m to 2,100 m. Forest vegetation types included
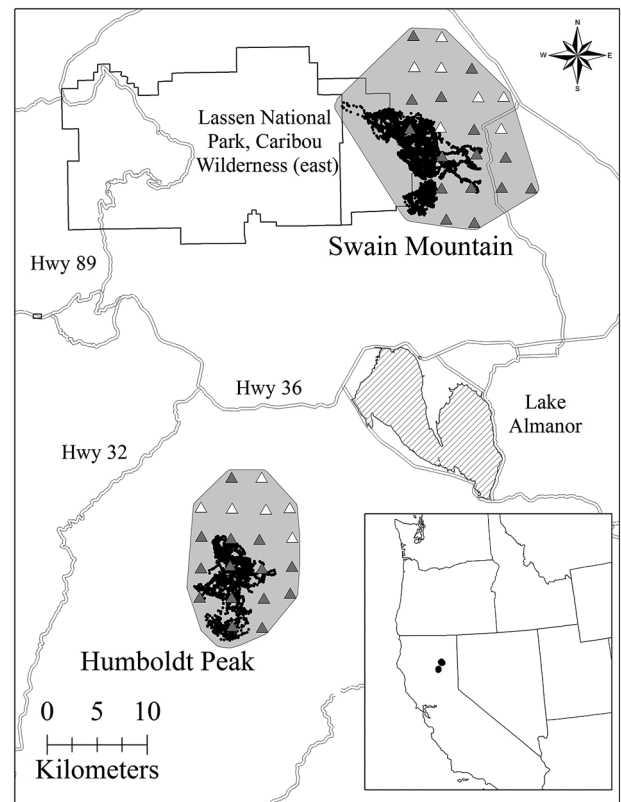

Figure 1. Our study occurred in 2 independent sites (Humboldt Peak, Swain Mountain) within Lassen National Forest, California, USA (Sep 2009–Apr 2013). We display the study area used for the compositional analysis in gray. Triangles represent trapping locations (white = no detection, gray = detection <2 yr prior or capture locations), and filled circles include Pacific marten locations from telemetry.

red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*Pinus contorta*), mixed conifer, and riparian areas. The climate was characterized by short dry summers and cold winters. In the period 2009–2013, the average low and high temperatures measured at 1,890 m were −6°C and 7°C in January and 7°C and 26°C in July. Snow was prevalent between December and May, comprising over 70% of the annual precipitation during an average year. Mean annual snow depth was 134 cm (California Department Water Resources, Harkness Flat Station, 2009–2013).

METHODS

We divided our study area into 3 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 often contained vertical and horizontal structural diversity; 2) structurally simple stands were 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. Stand classifications were created in a geographic information system (GIS; ArcMap v10.1, Environmental Systems Research Institute, Redlands, CA) by combining the most recently available United States

Forest Service vegetation map (CalVeg Existing Vegetation [EVEG]; Northern California Interior 2009 data) with a Forest Service Activity Tracking (FACTS) geodatabase (2012 data) 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 (California Department of Fish and Game 2006) despite loss of both forest cover and understory structure. A change detection analysis using Landsat imagery was conducted and inaccurate polygons were manually updated and modified (R. Martinez, LNF, GIS coordinator, personal communication). Our final product was a map at 30×30-m resolution that classified each stand into 1 of our 3 categories. Simple stands comprised 39% of the total study area ($153.7\,km^2$) and of that category, 18% ($28\,km^2$) were naturally comprising 20–40% canopy cover and minimal understory vegetation (e.g., talus slopes, dry soil types), whereas 82% ($128\,km^2$) resulted from management activities and generally had small diameter trees and understory vegetation removed with a goal of 40% canopy cover. Openings constituted 11% ($43\,km^2$) of the study area and natural openings (5%, $20\,km^2$) included meadows ($14.9\,km^2$), talus lava fields ($3.7\,km^2$), and frozen lakes ($1.4\,km^2$) during winter. Openings created by management (e.g., clear cut, shelterwood harvest) composed 5% ($23\,km^2$) of the study area.

To ensure that we were studying martens exposed to a gradient of stand types, we divided the landscape into 61 6.2-km^2 hexagons within 2 study sites separated by $>20\,km$ (Fig. 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 106, Tomahawk, Hazelhurst, WI) to catch martens, employed chemical anesthesia (Mortenson and Moriarty 2015), and fit adults with a very high frequency (VHF) collar (MI-2, Holohil Systems, Carp, Ontario, Canada). We subsequently deployed GPS collars (Quantum 4000 Micro-Mini, Telemetry Solutions, Concord, CA) on individuals that previously wore VHF collars, and therefore had known home ranges, to minimize risk of losing GPS units. We collected telemetry data (VHF triangulations and other point locations) weekly and, for GPS, during 1–8 days/season for each marten. The GPS collars attempted a location every 5 minutes. To save battery life, we programmed GPS collars to collect locations only when martens were active (Moriarty and Epps 2015). We restricted our movement analyses to GPS locations with average predicted accuracy and standard error (SE) of $28 \pm 7\,m$ (Moriarty and Epps 2015). We included only martens that were >2 years old in our sample because we were interested in the movement behavior of the segment of the population most likely to affect sustainability (Buskirk et al. 2012). Finally, we did not deploy GPS collars on females during critical reproductive periods (Feb–Jul) 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 (Sikes et al. 2011).

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 et al. 2011).

Stand Use and Selection

We used Brownian bridge movement models (BBMM) to infer habitat selection from the probability of use within our study area and each marten's seasonal home range and describe motion variance (Horne et al. 2007), or variation in speed and/or sinuosity, within each stand type. These models estimate the expected movement path of the individual from random walks between successive pairs of locations (Horne et al. 2007). These movement models incorporate expected location accuracy and the time between 2 points to create utilization distributions, or the probability of use (Marzluff et al. 2004).

We used BBMM utilization distributions (UD) as a weighted probability surface and performed compositional analysis (Aebischer et al. 1993) to test whether home ranges were selected disproportionately in areas with larger amounts of complex stands compared to what was available in the landscape (second-order selection; Johnson 1980) and to test whether stands within a home range were used selectively (third-order selection; Johnson 1980). We defined the available landscape by creating a 750-m buffer around the sampling grid and all known marten home ranges. We expected martens could move anywhere within the available landscape and compared the composition of stand types in each home range (95% UD) with the overall landscape proportions. When evaluating third-order selection, we compared the proportion of all point locations derived from telemetry (GPS and VHF) in each stand type with available stands comprising the 95% UD home range estimate. We assumed that all stand types within a home range were available (Fretwell and Lucas 1969) because we collected data only on adult martens, assumed to be dominant within their home range and to have complete access to resources, although heterospecific competition with other carnivores could occur. Analyzing for selection also assumed that each stand type was accessible (Garshelis 2000), which was reasonable because martens move considerable distances within their home range in a short time period (Fig. 2). For both third- and second-order selection, we performed compositional analyses in package adehabitatHS in R (Calenge 2006), which follows recommendations by Aebischer et al. (1993).

Stand-Specific Movement Patterns

Brownian bridge movement models can provide a metric of motion variance that represents changes in speed and sinuosity (Nielson et al. 2013) and thus provide opportunities
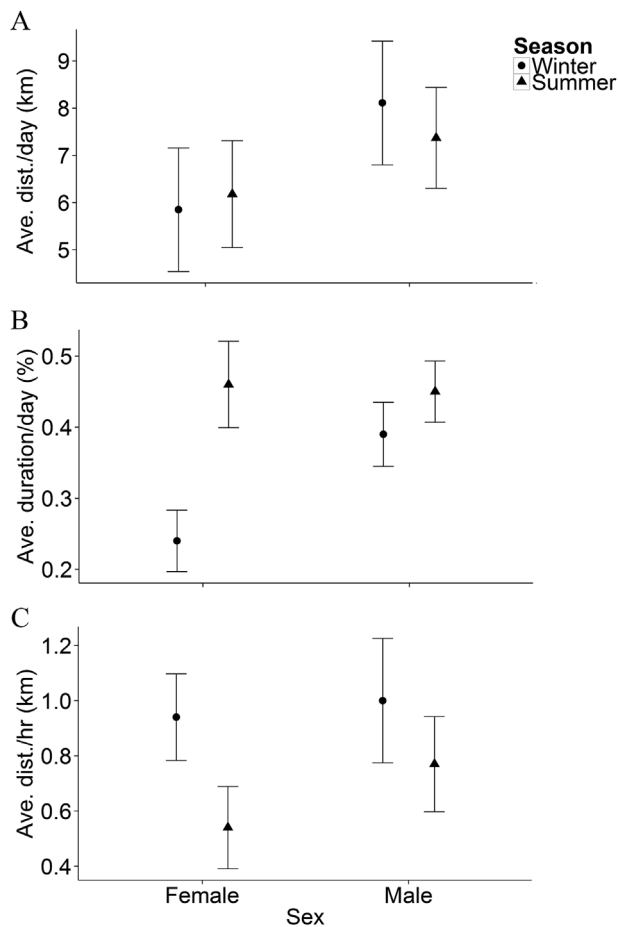
Figure 2. (A) Average (ave.) minimum daily distances (dist.) martens traveled, (B) proportion of the day during which marten movement and global positioning system (GPS) data were collected, and (C) average distance traveled/hour when the animal was moving. Data were from 22 martens in Lassen National Forest, California, USA (Mar 2010–Apr 2013). 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 because of GPS error.

to evaluate temporal aspects of habitat selection (Fieberg and Borger 2012, 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 indexes broad changes in movement but does not distinguish between speed and sinuosity. Thus, in addition to evaluating motion variance, we conducted separate analyses to quantify speed and sinuosity within each stand type to determine which factor may have affected motion variance. We calculated speed as the distance traveled (m) between 2 locations in the same stand divided by the time (min) elapsed. Sinuosity was the total distance traveled within a stand divided by the linear distance between the 2 points where the animal entered and departed the stand (Maletzke et al. 2008). To characterize distance traveled, speed, and sinuosity, we went through a series of steps to ensure we evaluated only consecutive locations along a path. We defined a path as sequence of locations with ≥ 3 3-dimensional locations that had expected accuracy of 28 m regardless of stand type (Moriarty and Epps

2015) and a maximum of 10 minutes between each point; >90% of the data had only 5 minutes between fixes. Although estimates of sinuosity and speed are expected to be biased low when the complete path is not known, we limited the impact of this bias by using those short fix intervals consistently across all 3 habitats. We converted the path into segments each representing a continuous piece of a path within a stand type, by first changing the point estimates to polylines using Geospatial Modeling Environment (Beyer 2014), then using ArcMap editor tool to place points every 5 m along each line. We added path attributes and stand type to each evenly spaced point (5 m) using the Spatial Join tool in ArcMap 10.1 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 we used only actual GPS locations. We calculated daily and hourly distance traveled, path lengths, and within-stand direct distance and sinuosity estimates in program R (R Core Team 2013). We calculated BBMMs and motion variance using R package BBMM (Nielson et al. 2013) and created plots in package ggplot2 (Wickham 2009).

We evaluated whether our 3 metrics of movement patterns (i.e., Brownian bridge motion variance, speed, and sinuosity) varied as a function of stand type (complex, simple, open), sex (male, female), season (snow-free periods [Jun–Nov] or snow cover [Dec–May], as also designated in Moriarty et al. 2011), or all combinations of these variables (7 models) 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) and considered models with ΔAIC <2.

RESULTS

We captured 54 martens (37 M, 17 F), of which 38 (26 M and 12 F adults) were radio-collared between September 2009 and April 2013, and 25 were GPS collared (15 M, 7 F, 2010–2013). We calculated seasonal home ranges and utilization distributions for 22 individuals with >50 3-dimensional 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 3 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/individual ($\bar{x} \pm$ 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. We expected true sinuosity and speed between consecutive points would be greater than estimated sinuosity and speed, leading to a potential negative bias. However, the time between successive locations did not

Table 1. Size and composition of stand types within seasonal Pacific marten home ranges ($\bar{x} \pm$ SD and range) in Lassen National Forest, California, USA (Sep 2009–Apr 2013). Size differences between winter and summer were largely due to differing individuals between each season, rather than an expansion or contraction of individual home range size (K. M. Moriarty, U.S. Department of Agriculture Forest Service, unpublished data).

	Female			Male		
	n	$\bar{x} \pm$ SD	Range	*n*	$\bar{x} \pm$ SD	Range
Summer						
Size (km²)	5	2.0 ± 0.9	1.0–3.3	11	5.0 ± 2.7	1.3–8.9
% Complex	5	57 ± 19	33–75	11	67 ± 10	53–78
% Simple	5	33 ± 18	17–59	11	25 ± 11	12–43
% Open	5	10 ± 4	8–16	11	9 ± 5	1–18
Winter						
Size (km²)	4	3.4 ± 1.3	1.3–4.7	14	6.5 ± 2.3	1.8–11.5
% Complex	4	66 ± 15	43–79	14	63 ± 14	32–81
% Simple	4	29 ± 15	15–51	14	28 ± 12	13–59
% Open	4	4 ± 3	0–6	14	9 ± 7	1–24

differ among stand types, seasons, or sexes. Thus variation in sinuosity or speed between locations would be equivalent among treatments and our results are an underestimate of true travel distance.

The distances that males moved each day (7.7 ± 0.2 km) were marginally greater than those of females (6.1 ± 0.2 km; $F = 3.03$, $P = 0.07$) and there was no difference in average daily distance by season ($F = 0.58$, $P = 0.44$, 2-factor ANOVA, M and F combined; Fig. 2A). The proportion of the day when we recorded martens moving was similar for males and females ($F = 1.82$, $P = 0.17$) and slightly differed by season, with females moving less during summer than winter ($F = 9.2$, $P < 0.01$; Fig. 2B). There was some evidence of less distance moved during summer compared to winter (Fig. 2C). The maximum recorded daily distance moved for females and males was 11.4 and 27.2 km, respectively.

Martens exhibited second-order selection (i.e., at the landscape scale), selecting more complex stands and fewer openings than occurred across the study area at large (Table 2). Simple stands were marginally avoided compared to complex stands. Martens also exhibited third-order selection, using complex stands within their home range more frequently than available (Table 2), suggesting martens avoided simple stands and openings during daily movements.

We explored whether marten movement patterns differed among stand types within their home ranges. First, motion variance was lowest in complex stands and increased significantly in simple stands ($t = 2.97$, $P < 0.01$) and openings ($t = 4.52$, $P < 0.01$; Fig. 3A), suggesting that martens moved consistently in complex stands, and that 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 ($t = 0.06$, $P = 0.95$; Fig. 3A). Second, martens moved slowest in complex stands, averaging (SD) 1.30 km/hour (1.12), as compared with simple stands (1.46 ± 1.23 km/hr) or openings (1.37 ± 1.19 km/hr; Fig. 3B). Travel speeds across openings had increased variation, likely contributing to the high motion variance (Fig. 3A). We interpret behavior in openings as an inconsistent series of stops and sprints. Last, the difference in sinuosity within a path (distance ratio) was highest in complex stands where the average ratio (1.45) reflected 145 m of movement within every 100 m of straight-line distance (Fig. 3C). In openings, martens moved very linearly resulting in values close to 1, significantly differing from observations in complex stands ($t = -5.25$, $P < 0.01$); values in simple stands were intermediate but clearly lower than in complex stands ($t = -4.65$, $P < 0.01$). In sum, the increase in motion variance in stands with decreasing complexity was due to changes in speed and sinuosity, but potentially most influenced by changes in speed.

For our final analysis, where we evaluated the influences of sex, season, and stand type on movement in multivariate linear mixed models, the combination of all 3 variables best explained our response variables for all metrics of movement except sinuosity, which was best described by stand type alone (Table 3). However, effects tests indicated motion variance was similar for both sexes and seasons ($F = 0.65$, $P = 0.52$; Fig. 4A and Table 4). Speed was greater for males than females ($t = 2.61$, $P = 0.02$) and both sexes moved faster during winter than summer ($t = -14.03$, $P < 0.01$; Fig. 4B and Table 4). Speeds generally increased in stand types with decreased complexity (simple $t = 2.90$, $P < 0.01$, open $t = 0.06$, $P = 0.95$; Fig. 4B and Table 4). During winter, females rarely entered openings ($n = 5$ of 1,749 locations) and during summer, decreased speeds in open areas probably occurred because the majority of open locations were in talus patches, which provide foraging

Table 2. Martens in Lassen National Forest, California, USA (Sep 2009–Apr 2013) selected patch types within the study area (second-order selection) and within their seasonal home ranges (third-order selection; Johnson 1980). Symbols indicate whether the patch in the corresponding row was used more (+) or less (−) 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.

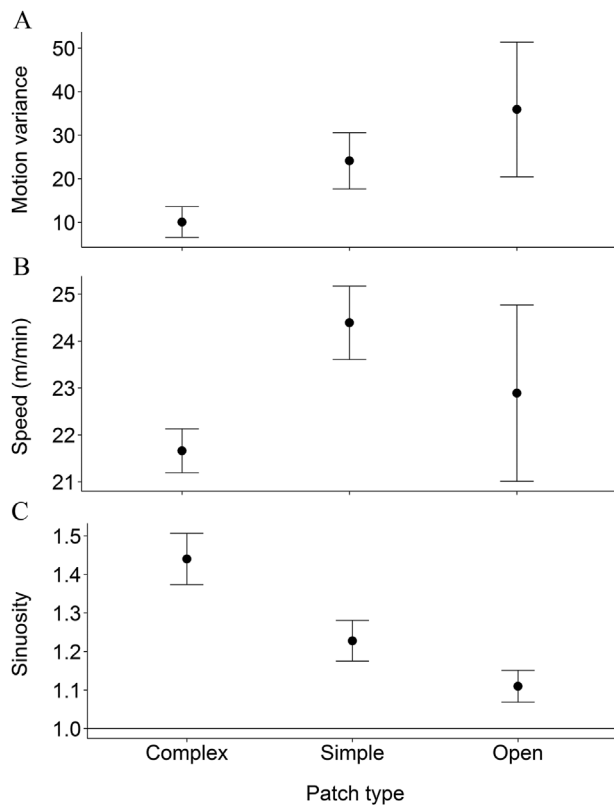|	Complex	Simple	Open
Second-order			
Complex	0	+	+++
Simple	−	0	+++
Open	−−−	−−−	0
Third-order			
Complex	0	+++	+++
Simple	−−−	0	+
Open	−−−	−	0

Figure 3. Marten movement patterns differed in stand types with decreasing structural complexity (complex, simple, open) as described by (A) Brownian bridge motion variance, an index of movement complexity that reflects the influence of speed and sinuosity; (B) speed, a conservative estimate of marten velocity estimated from 8,964 2-point segments with locations having estimated accuracy of 28 m ($n = 5,895$ complex, 2,644 simple, 425 open); and (C) sinuosity between the distance traveled and direct distance within each path ($n = 35,327$ path segments: 16,456 complex, 13,698 simple, 5,173 open). Data were from 22 martens in Lassen National Forest, California, USA (Mar 2010–Apr 2013). We show the mean and 95% confidence interval (bars).

Table 3. Multivariate linear mixed effect models for 3 metrics of marten movement. We described movement of 22 global positioning system (GPS)-collared martens using Brownian bridge motion variance, speed, and sinuosity. We collected marten GPS data in Lassen National Forest, California, USA (Mar 2010–Apr 2013). Our models included all combinations of stand type (open, simple, complex), marten sex (male, female), and season (winter, summer). We present change in Akaike's Information Criterion (ΔAIC) and model weights (w_i).

Response	Model	ΔAIC	w_i
Motion variance[a]	Stand type + sex + season	0.00	0.80
	Stand type + sex	2.88	0.19
	Stand 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[b]	Stand type + sex + season	0.00	0.96
	Sex + season	6.51	0.04
	Season	14.38	0.00
	Stand type + sex	192.90	0.00
	Sex	199.48	0.00
	Stand type	200.73	0.00
	Intercept	206.93	0.00
Sinuosity[c]	Stand type	0.00	0.96
	Stand type + sex + season	7.23	0.03
	Stand type + sex	11.02	0.00
	Intercept	25.34	0.00
	Sex	26.56	0.00
	Season	31.12	0.00
	Sex + season	32.52	0.00

[a] We calculated motion variance using Brownian bridge movement models in program R (Nielson et al. 2013).
[b] Speed represents m/min traveled by martens as recorded from 2 consecutive 3-dimensional locations with expected accuracy <28 m (Moriarty and Epps 2015).
[c] Sinuosity was the total distance traveled within a stand divided by the linear distance between the 2 points where the animal entered and departed from the stand (distance ratio).

opportunities. Sinuosity decreased in simple stands and openings compared to complex stands (Figs. 3C and 4C) and did not differ by season for either sex ($F = 0.65$, $P = 0.52$; Table 3).

DISCUSSION

This study, the first to evaluate fine-scaled movements of martens in summer and winter, demonstrated that marten movements vary strongly across stand types, suggesting that behaviors change sharply as forest complexity declines and may be indicative of foraging strategies and predator avoidance. The amount of movement we observed requires large energetic expenditures (Taylor et al. 1970), indicating that changes to forest structure have significant consequences for energetic balance for these small carnivores. Martens selected stand types with increased structural complexity (Table 2), and in complex stands, martens moved more deliberately, consistently, and slowly (Figs. 3 and 4). We interpret those movements as evidence of increased foraging or resource use in those stands. In contrast, martens largely avoided openings and simple stands. When martens did use

such stands, their movements were faster, more inconsistent, and more direct, especially in openings, consistent with predator avoidance or lower resource availability.

Where most previous studies evaluated marten habitat selection in forest versus openings, our study also directly addressed habitat selection and movement across an intermediate category: simple stands with downed logs and young trees removed in most cases for fuel management. Martens avoided openings at landscape and at home range scales (Table 2), as expected from other landscape-scale studies (Hargis et al. 1999, Potvin et al. 2000, Cushman et al. 2011). However, simple stands were not strongly avoided at a landscape scale but were avoided at the home range scale. We suspect that simplification did not influence selection at the landscape scale because thinned stands are still relatively rare in our study area. Avoidance of a habitat feature may be a function of its prevalence on the landscape (Jones 2001). For example, 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 numerous small forest clearings, martens avoided open stands and selection of stands with high prey density was no longer detectable statistically. Yet, the avoidance of simple stands that we
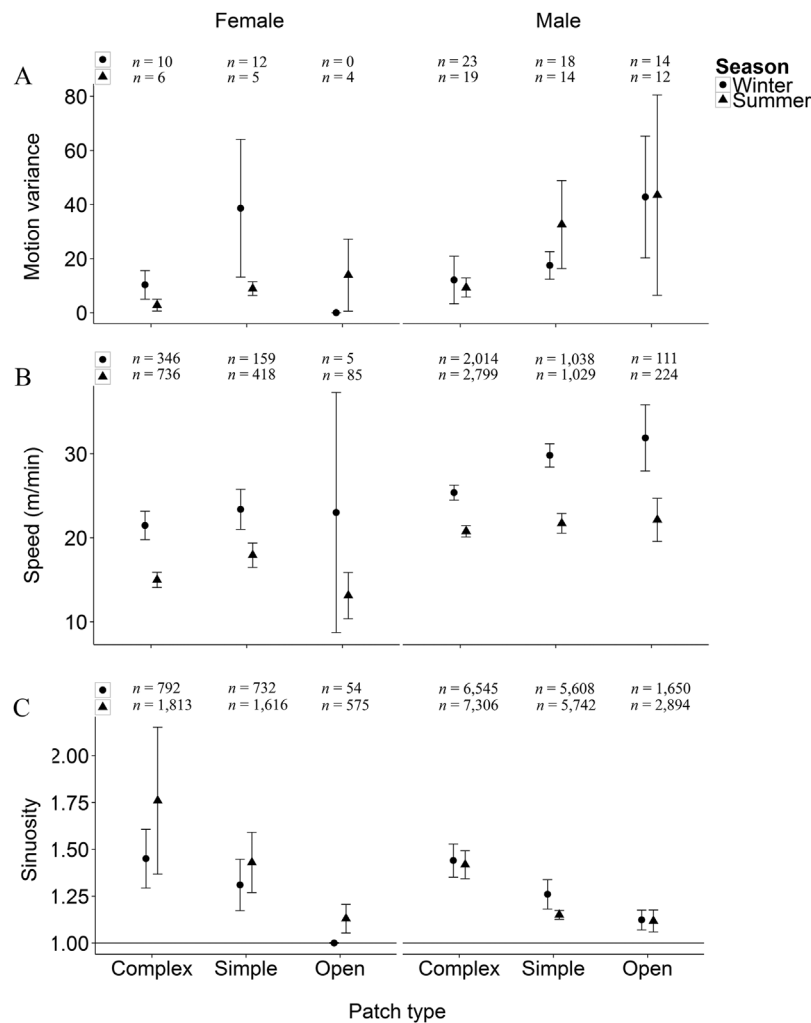
Figure 4. Marten movement patterns in stand types, by sex (F [left], M [right]), and season (summer, winter), including (A) Brownian bridge motion variance, with the number of individuals in each category (*n*) by sex, season, and stand type, (B) speed (m/min), with the number of locations with a proceeding 3-dimensional location allowing an estimate of time traveled between locations (*n*), and (C) sinuosity, with the number of path segments within a stand type (*n*). We calculated the 95% confidence intervals from the number of individuals (not the number of paths), which included 7 females (*n* = 5, 4 during summer and winter) and 15 males (*n* = 11, 12 during summer and winter, respectively) in Lassen National Forest, California, USA (Mar 2010–Apr 2013). We modeled data with marten as a random effect.

detected at the home range scale, and exhibition of movement patterns associated with high-risk and low-resource areas that we observed in those stands, demonstrate that simplifying forest structure changes how martens use landscapes.

Our seasonally specific use models suggested that martens selected complex stands and avoided openings and simple stands similarly in summer and winter. Likewise, when examining multi-scale habitat associations within 2 study areas in Oregon and Washington, Shirk et al. (2014) reported habitat selection did not change between seasons. In contrast, Zielinski et al. (2015) observed a strong seasonal difference in marten detections using non-invasive survey methods; that difference may have altered interpretations of selection in that study. Moriarty et al. (2015) observed a strong difference in seasonal detections in openings when using baited track plate stations but not with telemetry, suggesting that using bait may affect seasonal differences in detection.

Across our study area, marten home ranges were primarily composed of complex stands (39–79%), with significant portions of simple stands (24–33%) but few openings (4–10%). Marten populations typically decline in areas with >25–40% openings (Hargis et al. 1999, Potvin et al. 2000, Fuller 2006), so home ranges in this study were well under this threshold. However, this threshold value, as defined, does not consider the additional presence of simple stands. Our annual adult survival (63%; K. Moriarty, U.S. Department of Agriculture Forest Service, unpublished data) was the lowest reported in North America (McCann et al. 2010), suggesting that the proportion of simple stands or openings in home ranges may be nearing a threshold above which martens may not be able to persist. Similarly, simplification of stands decreased densities of northern flying squirrel (*Glaucomys sabrinus*; Manning et al. 2012), and gap widths as small as 80 m decreased connectivity (Smith 2011, Smith et al. 2013). Spotted owl (*Strix occidentalis*) territories also declined in this region following treatments, despite few

Table 4. Coefficients and effects tests for the best generalized linear mixed effect models, identified by corrected Akaike's Information Criterion (AIC) selection explaining 3 types of movement patterns from 22 martens with global positioning system (GPS) collars. Movement patterns included Brownian bridge motion variance, speed, and sinuosity, as a function of stand type, sex, and/or season. We collected data in Lassen National Forest, California, USA (Mar 2010–Apr 2013).

Response	Variables	Coefficient	SE	t	P
Motion variance[a]	Intercept	4.93	6.69	0.74	0.46
	Simple stand	13.00	4.38	4.51	0.01
	Open stand	25.60	5.67	2.97	≤0.001
	Sex (male)	8.43	6.80	1.23	0.22
	Season (summer)	−1.35	4.43	−0.31	0.76
Speed[b]	Intercept	21.62	2.27	9.51	≤0.001
	Simple stand	1.31	0.45	2.92	≤0.001
	Open stand	0.06	0.92	0.06	0.95
	Sex (male)	7.08	2.71	2.61	0.01
	Season (summer)	−6.76	0.48	−14.03	≤0.001
Sinuosity[c]	Intercept	1.51	0.06	22.70	≤0.001
	Simple stand	−0.20	0.04	−4.66	≤0.001
	Open stand	−0.30	0.06	−5.24	≤0.001

[a] We calculated motion variance using Brownian bridge movement models in program R (Nielson et al. 2013).

[b] Speed represents m/min traveled by martens as recorded from 2 consecutive 3-dimensional locations with expected accuracy <28 m (Moriarty and Epps 2015).

[c] Sinuosity was the total distance traveled within a stand divided by the linear distance between the 2 points where the animal entered and departed from the stand (distance ratio).

changes in small-mammal communities (Stephens et al. 2014). Simplified stands may not mimic areas killed from natural causes, such as spruce budworm (*Choristoneura fumiferana*), where marten continued to use areas after significant tree mortality (Payer and Harrison 2000). However, areas of natural mortality (e.g., budworm, fire) retain coarse woody material and logs are often used by marten for winter access (Corn and Raphael 1992) and foraging (Andruskiw et al. 2008). Additional research on species associated with structurally complex forests and their survival in landscapes with significant areas of stands simplified by management is urgently needed.

Although marten movement and habitat selection at fine scales likely reflects factors including finding and using rest sites, marking territory, mating, and kit rearing, we assume that acquisition of resources or avoiding predation had the strongest influences on those responses across different stand types. Further, we propose that stand-specific behaviors we observed reflected both of those primary factors. Within complex stands, martens consistently traveled at slower speeds and with higher sinuosity. Such movement patterns may reflect increased perception of and ability to find resources and lower perceived predation risk. Martens are able to find and kill prey more successfully in complex stand types, despite the availability of similar prey densities in harvested and regenerating stands (Andruskiw et al. 2008). Andruskiw et al. (2008) hypothesized that increased hunting success was correlated with the high abundance of downed logs, which 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. Payer and Harrison (2003) suggested retaining coarse woody material >22 cm in diameter. Further, martens may need to use escape cover and resting sites to safely eat their prey once it is captured, as observed for omnivorous rodents (Lima and Valone 1986,

Phelps and Roberts 1989). Thus, we expect that martens would benefit from moving within familiar stands that provide access to prey (Spencer 2012) at speeds that allow perception of these resources, and the ability to take captured prey to places providing cover. Our data on speed, sinuosity, and distance traveled within stand types suggest martens actively foraged predominantly within complex stands.

In open and simple stands, we propose that marten movement behavior strongly reflected predator avoidance strategies, and that martens typically avoided such stands because they presumably lacked adequate cover to escape from predators. During this study, bobcat appeared to be the primary predator as indicated by forensic evaluation of DNA from marten carcasses (Wengert et al. 2013, Integral Ecology Research Center, unpublished data). Coyotes and goshawks (*Accipiter gentalis*) also were predators (Bull and Heater 2001, Pagel and Schmitt 2013). Stand type may influence marten behavior both directly (through perceived risk) and indirectly (by cues). Drew (1995) observed captive martens changing their behavior and acting more cautiously when predator cues, such as coyote scat, were added to their environment. Similarly, stand type may be an indicator of relative risk as observed in squirrel monkeys (*Saimiri* sp.; Boinski et al. 2003) and songbirds (Zanette et al. 2011). When using simple stands, martens increased their speeds and decreased their sinuosity (Fig. 3), suggesting that they perceived more risk. When crossing openings, their speed changed erratically and they moved linearly (Fig. 3). Similar movements were reported for a Chilean rodent, the degu (*Octodon degus*), while in openings with high predation risk (Vásquez et al. 2002). Although lower availability of food in simple stands and openings could also result in less sinuous and faster movement, food titration experiments in the same study area demonstrated that martens avoided openings and simple stands during summer when predation risk was higher even though food was provided (Moriarty et al. 2015). Other

species, such as gray squirrel (*Sciuris carolinensis*) and willow tit (*Parus montanus*), will feed in risky areas provided there is some minimal level of cover (Lima and Valone 1986, Hogstad 1988). In the same manner, we suspect that some martens were willing to incur risk while foraging in simple stands during summer.

Martens moved similar distances during both seasons and both sexes moved faster during winter (Fig. 4B). We expected increased movement and speeds during summer (Zalewski et al. 2004) because 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. Increased speeds during winter may reflect decreased prey availability or increased energetic requirements as martens need to search additional area to meet their energetic needs (Barton and Hovestadt 2012). This study demonstrates that martens travel longer distances than reported (Zalewski et al. 2004), but additional information is needed to understand whether these movements are consistent year round and for juveniles as well as adults.

Contrary to our predictions, female and male movements generally did not differ (Figs. 2 and 4C), perhaps because both sexes have high energetic requirements and defend territory perimeters through scent marking. However, we observed subtle seasonal distinctions that may be related to sex-specific motivation that may be worthy of testing in the future. These observations were not statistically significant (Tables 3 and 4), most likely due to a low sample size for females, but are suggestive of biologically meaningful patterns. Females appeared to move marginally more sinuously than males and traveled at a slower rate, especially during summer when females would be rearing kits (Figs. 2 and 4C). We interpret the combination of speed, variance, and sinuosity as representing a localized foraging strategy focused on the highest prey densities. Males moved slightly less sinuously than females, which may reflect their priority on maintaining large territories that overlap multiple females, similar to male birds (Fretwell and Calver 1969). Male territorial behavior could require more rapid and directed movements, as reflected in the increased speeds and distances, increased variance in motion, and decreased sinuosity. Bobcats exhibit similar sex-related patterns, with males moving less sinuously and faster compared to females (Newbury 2013).

Use of GPS collars offered new information about marten movement, which previously has been characterized in North America primarily using snow tracking. Our study suggests that individual tracks recorded in snowtracking studies comprise a relatively small percentage of daily movement and, thus, may not adequately sample movements. Lengths of average track segments in snowtracking studies ranged between 86 m and 2,124 m (Hargis and McCullough 1984, Heinemeyer 2002, Nams and Bourgeois 2004, Cushman et al. 2011), which at our average reported speed would require only 4–91 minutes to traverse. This compares to an average of 7,620 minutes of movement data/marten from our GPS collars. However, snowtracking has advantages over GPS in that it can identify points of special interest along the movement path such as resting structures (Corn and Raphael 1992) and foraging locations (Andruskiw et al. 2008). Nonetheless, indices of daily movement expenditures (e.g., distance traveled) available from GPS collars are more likely to reflect variation in habitat quality. The 2 methods are complementary. For instance, we discovered increased sinuosity in winter paths in complex stands using GPS collars, as did others using snow tracking (Hargis and McCullough 1984, Heinemeyer 2002, Nams and Bourgeois 2004), but our use of GPS technology allowed us to confirm this pattern in summer. However, GPS collars also have drawbacks. We were unable to deploy GPS collars on females during the denning period and on the smaller females. Technological advances that reduce battery size may make it possible to deploy GPS on all females, not just the largest adults, and for a longer duration. Such opportunities could allow for an empirical demonstration of movement in relation to fitness, testing our assumptions directly. We recommend both GPS data collection and snowtracking be used 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.

MANAGEMENT IMPLICATIONS

Fuels treatments that simplify forest structure (e.g., removal of small diameter trees, downed logs) have negative effects on marten movement dynamics. Thus, the most obvious recommendation to benefit martens is to plan fuels treatments outside of their habitat. Specifically, we suggest that areas at lower elevations (<1,500 m), which is below the typical distribution of martens in the Cascades in California (Zielinski et al. 2005), should be the priority for fuels reduction because of the increased departure from normal fire return intervals in those forests. Fires historically were more frequent at those elevations (4–22 yr; Taylor 2000, North 2012), thus more fuel has accumulated and the risk of crown fires is greatest. In the high elevation forests that support martens, fire return intervals are longer (83–200 yr) and these forests may be considered within their natural fire cycle despite fire suppression efforts (Stephens et al. 2007). Thus, there should be less near-term incentive to thin forests in the elevational zone where martens occur.

Where fuels treatments are planned in higher elevation forests within marten habitat, our data suggest that maintaining or increasing structural variation will increase the use of these stands by martens. Strategically increasing structural complexity within managed stands, while increasing resilience from fire (Churchill et al. 2013), will be important for maintaining marten populations. Specifically, creating resources for prey and providing escape cover from predators are important steps toward encouraging marten use of treated stands. Recent forest ecosystem management guidelines (North et al. 2009, North 2012) call for forest management designed to mimic variation in stand densities

that occur as a result of topography, moisture, disturbance, and climate. These guidelines call for the retention of structural complexity in riparian areas and on cooler topographic positions, which should benefit martens. Management will ultimately benefit from future studies that help us understand what proportion of a home range-sized area can be treated to reduce fuels while still providing sufficient habitat for martens and whether compromises can occur within managed areas to reduce threat of fire while providing habitat for martens.

ACKNOWLEDGMENTS

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325.

Agee, J. K., B. Bahro, M. A. Finney, P. N. Omi, D. B. Sapsis, C. N. Skinner, J. W. van Wagtendonk, and C. P. Weatherspoon. 2000. The use of shaded fuelbreaks in landscape fire management. Forest Ecology and Management 127:55–66.

Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk in the American marten. Ecology 89:2273–2280.

Balharry, D. 1993. Social organization in martens: an inflexible system. Symposia of the Zoological Society of London 65:321–345.

Barton, K. A., and T. Hovestadt. 2012. Prey density, value, and spatial distribution affect the efficiency of area-concentrated search. Journal of Theoretical Biology 316:61–69.

Beyer, H. L. 2014. Geospatial Modeling Environment. Version 0.7.2. www.spatialecology.com/gme. Accessed 07 Aug 2013.

Bissonette, J. A., and S. Broekhuizen. 1995. Martes populations as indicators of habitat spatial patterns: the need for a multiscale approach. Pages 95–121 in W. Z. Lidicker, editor. Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis, USA.

Boinski, S., L. Kauffman, A. Westoll, C. M. Stickler, S. Cropp, and E. Ehmke. 2003. Are vigilance, risk from avian predators, and group size consequences of habitat structure? A comparison of three species of squirrel monkey (Saimiri oerstedii, S. boliviensis, and S. sciureus). Behaviour 140:1421–1467.

Brown, J. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Bull, E. L., and T. W. Heater. 2001. Survival, causes of mortality, and reproduction in the American marten in northeastern Oregon. Northwest Naturalist 82:1–6.

Buskirk, S. W., J. Bowman, and J. H. Gilbert. 2012. Population biology and matrix demographic modeling of American martens and fishers. Pages 77–92 in K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk, editors. Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, New York, New York, USA.

Buskirk, S. W., and J. J. Millspaugh. 2006. Metrics for studies of resource selection. Journal of Wildlife Management 70:358–366.

Byrne, M. E., J. Clint McCoy, J. W. Hinton, M. J. Chamberlain, and B. A. Collier. 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83:1234–1243.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

California Department of Fish and Game. 2006. California Wildlife Habitat Relationships 8.1. California Department of Fish and Game, Sacramento, USA.

Chapin, T. G., D. J. Harrison, and D. D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327–1337.

Cheveau, M., L. Imbeau, P. Drapeau, and L. Belanger. 2013. Marten space use and habitat selection in managed coniferous boreal forests of eastern Canada. Journal of Wildlife Management 77:749–760.

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291:442–457.

Corn, J. G., and M. G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. Journal of Wildlife Management 56:442–448.

Cushman, S. A., M. G. Raphael, L. F. Ruggiero, A. S. Shirk, T. N. Wasserman, and E. C. O'Doherty. 2011. Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landscape Ecology 26:1137–1149.

Drew, G. S. 1995. Winter habitat selection by American marten (Martes americana) in Newfoundland: why old growth? Dissertation, Utah State University, Logan, USA.

Earl, J. E., and P. A. Zollner. 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. Ecological Modelling 283:45–52.

Fieberg, J., and L. Borger. 2012. Could you please phrase home range as a question? Journal of Mammalogy 93:890–902.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273–287.

Fretwell, S., and J. Calver. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:37–44.

Fretwell, S., and H. Lucas Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fuller, A. K. 2006. Multi-scalar responses of forest carnivores to habitat and spatial pattern: case studies with Canada lynx and American martens. Dissertation, University of Maine, Orono, USA.

Gabriel, M. W., G. M. Wengert, and R. N. Brown. 2012. Pathogens and parasites of Martes species: management and conservation implications. Pages 138–185 in K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk, editors. Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, Ithaca, New York, USA.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2255–2265.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, Ithaca, New York, USA.

Gilbert, J. H., P. A. Zollner, A. K. Green, J. L. Wright, and W. H. Karasov. 2009. Seasonal field metabolic rates of American martens in Wisconsin. American Midland Naturalist 162:327–334.

Giraldeau, L.-A., D. L. Kramer, I. Deslandes, and H. Lair. 1994. The effect of competitors and distance on central place foraging eastern chipmunks, Tamias striatus. Animal Behaviour 47:621–632.

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

Hargis, C. D., J. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157–172.

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

Heinemeyer, K. S. 2002. Translating individual movements into population patterns: American marten in fragmented forested landscapes. Dissertation, University of California, Santa Cruz, USA.

Heinrich, B. 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 40:235–245.

Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. 1997. Survival of American marten in an untrapped forest preserve in Maine. Pages 86–99 in G. Proulx, H. N. Bryant, and P. M. Woodard, editors. Martes: taxonomy, ecology, techniques, and management. Provenital Museum of Alberta, Alberta, Canada.

Hogstad, O. 1988. Rank-related resource access in winter flocks of willow tit Parus montanus. Ornis Scandinavica 19:169–174.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Houston, A. I., and J. M. McNamara. 2014. Foraging currencies, metabolism and behavioural routines. Journal of Animal Ecology 83:30–40.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

Jonsen, I. D., R. A. Myers, and M. C. James. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Marine Ecology Progress Series 337:255–264.

Kalies, E. L., C. L. Chambers, and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: a meta-analysis. Forest Ecology and Management 259:333–342.

Kennedy, M., C. R. Shave, H. G. Spencer, and R. D. Gray. 1994. Quantifying the effect of predation risk on foraging bullies: no need to assume an IFD. Ecology 75:2220–2226.

Lima, S. L. 1987. Vigilance while feeding and its relation to the risk of predation. Journal of Theoretical Biology 124:303–316.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.

Lima, S. L., and T. J. Valone. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. Animal Behaviour 34:536–544.

Maletzke, B. T., G. M. Koehler, R. B. Wielgus, K. B. Aubry, and M. A. Evans. 2008. Habitat conditions associated with lynx hunting behavior during winter in northern Washington. Journal of Wildlife Management 72:1473–1478.

Manning, T., J. C. Hagar, and B. C. McComb. 2012. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. Forest Ecology and Management 264:115–124.

Martin, S. K. 1994. Feeding ecology of American martens and fishers. Pages 297–315 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers. Comstock Publishers, Cornell University Press, Ithaca, New York, USA.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probalistic measure of space use: forest fragments and Stellar's jays. Ecology 85:1411–1427.

McCann, N. P., P. A. Zollner, and J. H. Gilbert. 2010. Survival of adult martens in northern Wisconsin. Journal of Wildlife Management 74:1502–1507.

McIntyre, N., and J. Wiens. 1999. Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. Landscape Ecology 14:437–447.

Merriam, C. H. 1890. Description of twenty-six new species of North American mammals. North American Fauna 4:1–55.

Mitchell, W. A., and S. L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. Oikos 99:249–259.

Moghaddas, J. J., B. M. Collins, K. Menning, E. E. Moghaddas, and S. L. Stephens. 2010. Fuel treatment effects on modeled landscape-level fire behavior in the northern Sierra Nevada. Canadian Journal of Forest Research 40:1751–1765.

Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289–2301.

Moriarty, K. M., and C. W. Epps. 2015. Retained satellite information influences performance of GPS devices in a forested ecosystem. Wildlife Society Bulletin 39:349–357.

Moriarty, K., C. Epps, M. Betts, D. Hance, J. D. Bailey, and W. Zielinski. 2015. Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. Landscape Ecology 30:1865–1877.

Moriarty, K. M., W. J. Zielinski, and E. D. Forsman. 2011. Decline of American marten occupancy rates at Sagehen Experimental Forest, California. Journal of Wildlife Management 75:1774–1787.

Mortenson, J. A., and K. M. Moriarty. 2015. Ketamine and midazolam anesthesia in Pacific martens (Martes caurina). Journal of Wildlife Disease 51:250–254.

Müller, S., J. Scealy, and A. Welsh. 2013. Model selection in linear mixed models. Statistical Science 28:135–167.

Nams, V. O., and M. Bourgeois. 2004. Fractal analysis measures habitat use at different spatial scales: an example with American marten. Canadian Journal of Zoology 82:1738–1747.

Newbury, R. K. 2013. A dietary based energetics model for bobcats (Lynx rufus) in a deep snow environment. Dissertation, University of British Columbia, Okanagan, Canada.

Nielson, R. M., H. Sawyer, and T. L. McDonald. 2013. BBMM: Brownian bridge movement model. R package version 3.0. http://CRAN.R-project/package=BBMM. Accessed 20 Sep 2014.

North, M. P. 2012. Managing Sierra Nevada forests; PSW-GTR-237. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Stations, Albany, California, USA.

North, M., P. Stine, K. O'Hara, W. J. Zielinski, and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed conifer forests. USDA Forest Service, General Technical Report, PSW-GTR-220, Albany, California, USA.

Owen, D. 2003. Prescriptive laws, uncertain science, and political stories: forest management in the Sierra Nevada. Ecology Law Quarterly 29:745–802.

Pagel, J. E., and N. J. Schmitt. 2013. American marten remains within Peregrine falcon prey sample in Yellowstone National Park. Journal of Raptor Research 47:419–420.

Payer, D. C., and D. J. Harrison. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: implications for marten. Canadian Journal of Forest Research 30:1965–1972.

Payer, D. C., and D. J. Harrison. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. Forest Ecology and Management 179:145–156.

Phelps, M. T., and W. A. Roberts. 1989. Central-place foraging by Rattus norvegicus on a radial maze. Journal of Comparative Psychology 103:326–338.

Pimm, S. L., M. L. Rosenzweig, and W. Mitchell. 1985. Competition and food selection: field tests of a theory. Ecology 66:798–807.

Pinchot Institute. 2013. Independent science panel report: Herger-Feinstein Quincy Library Group Forest Recovery Act. http://www.pinchot.org/doc/476. Accessed 05 Aug 2013.

Potvin, F., L. Belanger, and K. Lowell. 2000. Marten habitat selection in a clearcut boreal landscape. Conservation Biology 14:844–857.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:S50–S66.

R Core Team. 2013. Version 2.15. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raphael, M. G. 2004. Ecology of the American marten in the Oregon Cascade Range. Proceedings of the 4th International Martes Symposium. The Martes Working Group, 20–24 July 2004, Lisbon, Portugal.

Schempf, P. F., and M. White. 1977. Status of six furbearer populations in the mountains of northern California. USDA Forest Service, Pacific Southwest Research Station and Museum of Vertebrate Zoology, University of California, Berkeley, USA.

Seidel, D. P., and M. S. Boyce. 2016. Varied tastes: home range implications of foraging-patch selection. Oikos 125:39–49.

Shirk, A. J., M. G. Raphael, and S. A. Cushman. 2014. Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). Ecological Applications 24:1434–1444.

Sikes, R. S., W. L. Gannon, and Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Smith, J. T. 2011. Movement and gene flow of northern flying squirrels across an interstate highway. Thesis, Montana State University, Bozeman, USA.

Smith, M. J., G. J. Forbes, and M. G. Betts. 2013. Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). Biological Conservation 168:176–183.

Spencer, W. D. 1987. Seasonal rest-site preferences of pine martens in the northern Sierra Nevada. Journal of Wildlife Management 51:616–621.

Spencer, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93:929–947.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1182–1186.

Stephens, S., J. Agee, P. Fulé, M. North, W. Romme, T. Swetnam, and M. Turner. 2013. Managing forests and fire in changing climates. Science 342:41–42.

Stephens, S. L., S. W. Bigelow, R. D. Burnett, B. M. Collins, C. V. Gallagher, J. Keane, D. A. Kelt, M. P. North, L. J. Roberts, and P. A. Stine. 2014. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. BioScience 64:893–906.

Stephens, S. L., R. E. Martin, and N. E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251:205–216.

Stephens, S. L., J. D. McIver, R. E. J. Boerner, C. J. Fettig, J. B. Fontaine, B. R. Hartsough, P. L. Kennedy, and D. W. Schwilk. 2012. The effects of forest fuel-reduction treatments in the United States. BioScience 62:549–560.

Stephens, S. L., and J. J. Moghaddas. 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. Forest Ecology and Management 215:21–36.

Taylor, A. H. 2000. Fire regimes and forest change in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. Journal of Biogeography 27:87–104.

Taylor, C. R., K. Schmidt-Nielsen, and J. L. Raab. 1970. Scaling of energetic cost of running to body size in mammals. American Journal of Physiology 219:1104–1107.

Thompson, I. D. 1991. Could marten become the spotted owl of eastern Canada? Forestry Chronicle 67:136–140.

Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. Journal of Wildlife Management 58:280–288.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Volume 1. Sinauer Associates, Sunderland, Massachusetts, USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Vásquez, R. A., L. A. Ebensperger, and F. Bozinovic. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behavioral Ecology 13:182–187.

Wengert, G. M., M. W. Gabriel, J. E. Foley, T. Kun, and B. N. Sacks. 2013. Molecular techniques for identifying intraguild predators of fishers and other north American small carnivores. Wildlife Society Bulletin 37:659–663.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, New York, USA.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Zalewski, A., W. Jedrzejewski, and B. Jedrzejewska. 2004. Mobility and home range use by pine martens (*Martes martes*) in a Polish primeval forest. Ecoscience 11:113–122.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduced the number of offspring songbirds produce per year. Science 334:1398–1401.

Zielinski, W. J. 2013. The forest carnviores: fisher and marten. Pages 261–301 *in* J. Long, C. Skinner, M. North, P. Winter, W. J. Zielinski, C. Hunsaker, B. Collins, J. Keane, F. Lake, J. Wright, E. Moghaddas, A. Jardine, K. Hubbert, K. Pope, A. Bytnerowicz, M. Fenn, M. Busse, S. Charnley, T. Patterson, L. Quinn-Davidson, and H. D. Safford, editors. Science synthesis to support Forest Plan Revision in the Sierra Nevada and Southern Cascades. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station Albany, California, USA.

Zielinski, W., K. M. Moriarty, J. Baldwin, T. A. Kirk, K. M. Slauson, H. L. Rustigian-Romos, and W. D. Spencer. 2015. Effects of season on occupancy and implications for habitat modeling: the Pacific marten (*Martes caurina*). Wildlife Biology 21:56–67.

Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. Journal of Mammalogy 64:387–396.

Zielinski, W. J., R. L. Truex, F. V. Schlexer, L. A. Campbell, and C. Carroll. 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. Journal of Biogeography 32:1385–1407.

Associate Editor: Kerry Nicholson.