



Research Article

Forest Thinning Changes Movement Patterns and Habitat Use by Pacific Marten

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ABSTRACT. Simplifying stand structure to reduce fuel density is a high priority for forest managers; however, effects 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 Millsbaugh 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

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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

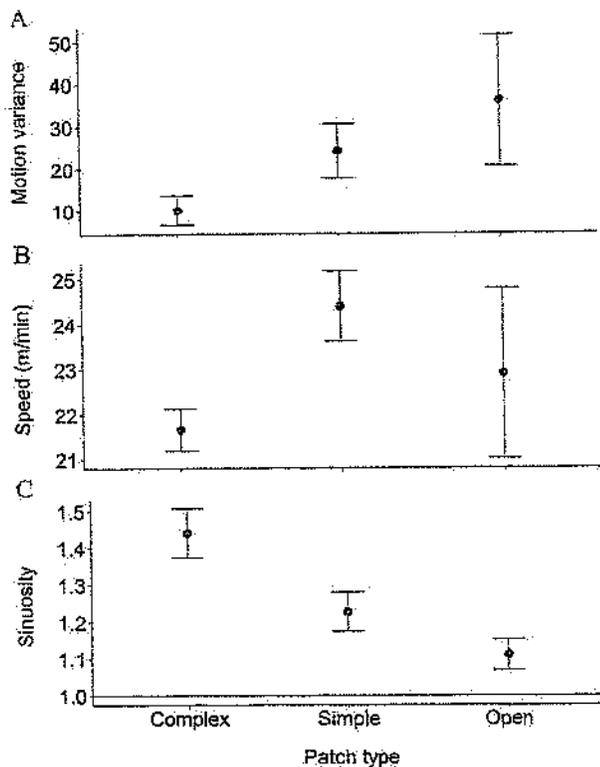


Figure 3. Marten movement patterns differed in stand types with decreasing structural complexity (complex, simple, open) as described by (A) Brownian bridge motion variance, an index of movement complexity that reflects the influence of speed and sinuosity; (B) speed, a conservative estimate of marten 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).

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

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 Information Criterion (Δ AIC) and model weights (w_i).

Response	Model	Δ AIC	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
Speed ^b	Intercept	33.58	0.00
	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
Sinuosity ^c	Stand type	200.73	0.00
	Intercept	206.93	0.00
	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 (Nielsen 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).

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

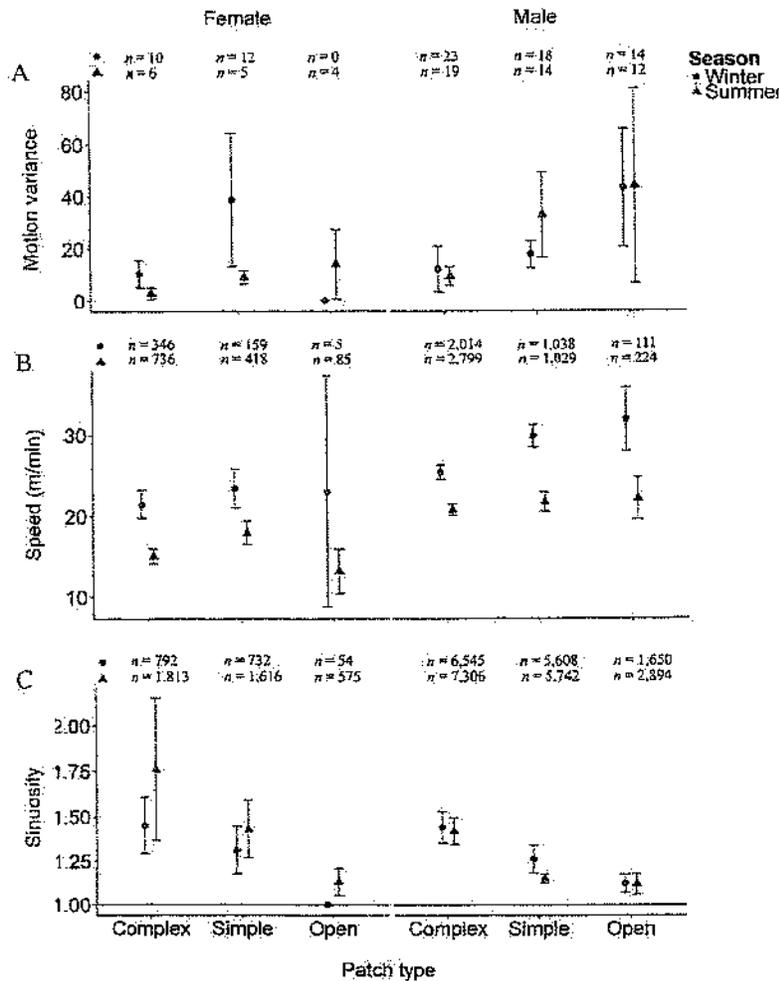


Figure 4. Marten movement patterns in stand types, by sex (F [left], M [right]), and season (summer, winter), including (A) Brownian bridge motion variance, with the number of individuals in each category (n) by sex, season, and stand type, (B) speed (m/min), with the number of locations with a preceding 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 (McCarin 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 (*Glacomys 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
	Intercept	21.62	2.27	9.51	≤0.001
Speed ^b	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
	Intercept	1.51	0.06	22.70	≤0.001
	Simple stand	-0.20	0.04	-4.66	≤0.001
Sinuosity ^c	Open stand	-0.30	0.06	-5.24	≤0.001

^a We calculated motion variance using Brownian bridge movement models in program R (Nielsen 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 gentilis*) 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 (*Sciurus 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 Flovestadt 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