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# Post-fire movements of Pacific marten (*Martes caurina*) depend on the severity of landscape change

Logan A. Volkmann\*  and Karen E. Hodges

## Abstract

**Background:** Wildfires and forestry activities such as post-fire salvage logging are altering North American forests on a massive scale. Habitat change and fragmentation on forested landscapes may threaten forest specialists, such as Pacific marten (*Martes caurina*), that require closed, connected, and highly structured habitats. Although marten use burned landscapes, it is unclear how these animals respond to differing burn severities, or how well they tolerate additional landscape change from salvage logging.

**Methods:** We used snow tracking and GPS collars to examine marten movements in three large burns in north-central Washington, USA (burned in 2006) and central British Columbia, Canada (burned in 2010 and 2017). We also assessed marten habitat use in relation to areas salvage-logged in the 2010 burn. We evaluated marten path characteristics in relation to post-fire habitat quality, including shifts in behaviour when crossing severely-disturbed habitats. Using GPS locations, we investigated marten home range characteristics and habitat selection in relation to forest cover, burn severity, and salvage logging.

**Results:** Marten in the 2006 burn shifted from random to directed movement in areas burned at high severity; in BC, they chose highly straight paths when crossing salvage-blocks and meadows. Collared marten structured their home ranges around forest cover and burn severity, avoiding sparsely-covered habitats and selecting areas burned at low severity. Marten selected areas farther from roads in both Washington and BC, selected areas closer to water in the 2006 burn, and strongly avoided salvage-logged areas of the 2010 burn. Marten home ranges overlapped extensively, including two males tracked concurrently in the 2010 burn.

**Conclusions:** Areas burned at low severity provide critical habitat for marten post-fire. Encouragingly, our results indicate that both male and female marten can maintain home ranges in large burns and use a wide range of post-fire conditions. However, salvage-logged areas are not suitable for marten and may represent significant barriers to foraging and dispersal.

**Keywords:** Boreal forest, Carnivores, Fire ecology, Habitat use, Home ranges, Landscape management, Montane forest, Movement ecology, Salvage logging, Wildfire

## Background

Landscape change is a global and pervasive threat to forest ecosystems [1]. In western North America, disturbances from timber harvest, insect epidemics, and wildfire have caused substantial changes to boreal, sub-boreal, and montane conifer forests (hereafter, “western forests”) over the past 50 years [2, 3]. Large (> 10,000 ha),

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stand-replacing wildfires are a primary driver of succession in western forests, but such fires were historically rare, typically recurring on timescales of >100 years [4, 5]. With climate change, these extreme fire events have become increasingly common [6–8], and are likely to play a pivotal role in reshaping North American forest communities [9–11].

Post-fire, the pattern and severity of landscape change matter to wildlife [12–14]. Although fire is a major, beneficial driver of succession in many forests, some forest-associated birds [15], amphibians [16], and mammals [17] respond negatively to post-fire changes in habitat structure. Wildfires change forests by opening the canopy and reducing the structural complexity from trees, snags, coarse woody debris (hereafter, “deadfall”), and understory vegetation [4, 18]. For species that specialize in late-seral (mature and old-growth) habitats, post-fire landscapes may contain fewer suitable habitats. The loss of large trees, for example, reduces the availability of sites for foraging [19], shelter [20], and reproduction [21] within the first few years post-fire. The continued decay and loss of snags post-fire may negatively impact cavity-nesting species over longer timescales [22–24]. However, large wildfires leave a heterogeneous footprint in forests as some areas burn more intensely than others [25]. Some residual habitats in the form of surviving trees, snags, and deadfall persist for decades post-fire, offering prospects for wildlife persistence and recolonization [26–28].

In addition to this complexity, management activities on burned landscapes may further alter the quality of residual habitats. Post-fire salvage logging—the harvest of dead or fire-damaged trees—is a widespread secondary disturbance in fire-prone regions such as British Columbia (BC), Canada [29]. Like wildfire, salvage logging removes forest structure to varying degrees, creating a patchwork of highly-disturbed and residual habitats. However, salvage logging entails a more intensive removal of trees, snags, and deadfall, leaving fundamentally different conditions for wildlife [30, 31]. Critically, it is unclear how many species respond to salvage logging compared to wildfire and conventional timber harvest, despite the increasing prevalence of salvage logging in western forests [32, 33].

Forest specialists such as Canada lynx (*Lynx canadensis*) [34], fishers (*Pekania pennanti*) [35], and marten (*Martes americana* and *M. caurina*) [36] are highly sensitive to landscape change from wildfire and timber harvest. These animals disperse large distances and occupy large territories, meaning that the size, shape, and connectivity of residual habitats shape their behaviour post-disturbance. Narrow forest openings are easier to cross than wide ones, and large patches of residual habitat offer more potential resources than small ones. Thus, differing

patterns of burn severity and post-fire salvage logging may affect which parts of the landscape support resident animals [37], serve as travel corridors [38], or entirely exclude certain species [39]. Substantial landscape change post-fire may create ecological traps, where the presence of residual forest structure draws animals into low-quality habitat [40, 41], or perceptual traps, where animals fail to recognize residual high-quality habitat [42].

Marten in particular respond to an array of habitat features across a range of spatial scales, from individual den trees to regenerating cut-blocks [43, 44]. These animals are closely associated with mature and old-growth habitats in western forests, and serve as indicators of ecosystem health in both Canada and the United States [45, 46]. Marten can persist on landscapes altered by timber harvest, using residual forest as “stepping stones” to cross low-quality habitats [47, 48]. They can also use landscapes substantially altered by fire [49–52]. However, habitat features important to marten post-fire have not been clearly identified [53].

On unburned landscapes, marten select home ranges that contain a high degree of structural complexity [43, 44]. Trees, snags, deadfall, and understory vegetation provide critical resources for resting [54], denning [55], avoiding predators [56], and hunting small mammal prey [57]. Within young burns (<10 years post-fire), marten use sites with abundant deadfall [50] and residual trees [49, 58], suggesting that these animals target areas of low burn severity that are more similar to intact forests. Areas more severely disturbed by fire offer less structural complexity and fewer prey such as southern red-backed voles (*Myodes gapperi*) [59], red squirrels (*Tamiasciurus hudsonicus*) [60], and snowshoe hares (*Lepus americanus*) [61]; the same is true of salvage-logged areas [39, 62, 63]. It is still unclear how marten incorporate this heterogeneity into a home range, or how readily they use low-quality post-fire habitats to reach high-quality ones.

We studied marten movements over three winters in north-central Washington, USA, and central British Columbia, where record-setting wildfires have caused substantial landscape changes over the past 15 years (2005–2020). Our objective was to determine how marten respond to landscape heterogeneity post-fire, by (1) characterizing their movements and home ranges in burned areas, and (2) assessing their tolerance of post-fire salvage logging. We hypothesized that marten would respond to residual forest structure within burns, focusing their activity in areas with remnant trees. Given marten avoidance of open habitats, we expected resident animals to avoid both severely-burned and salvage-logged areas, with stronger avoidance of salvage-blocks than residual stands of snags.

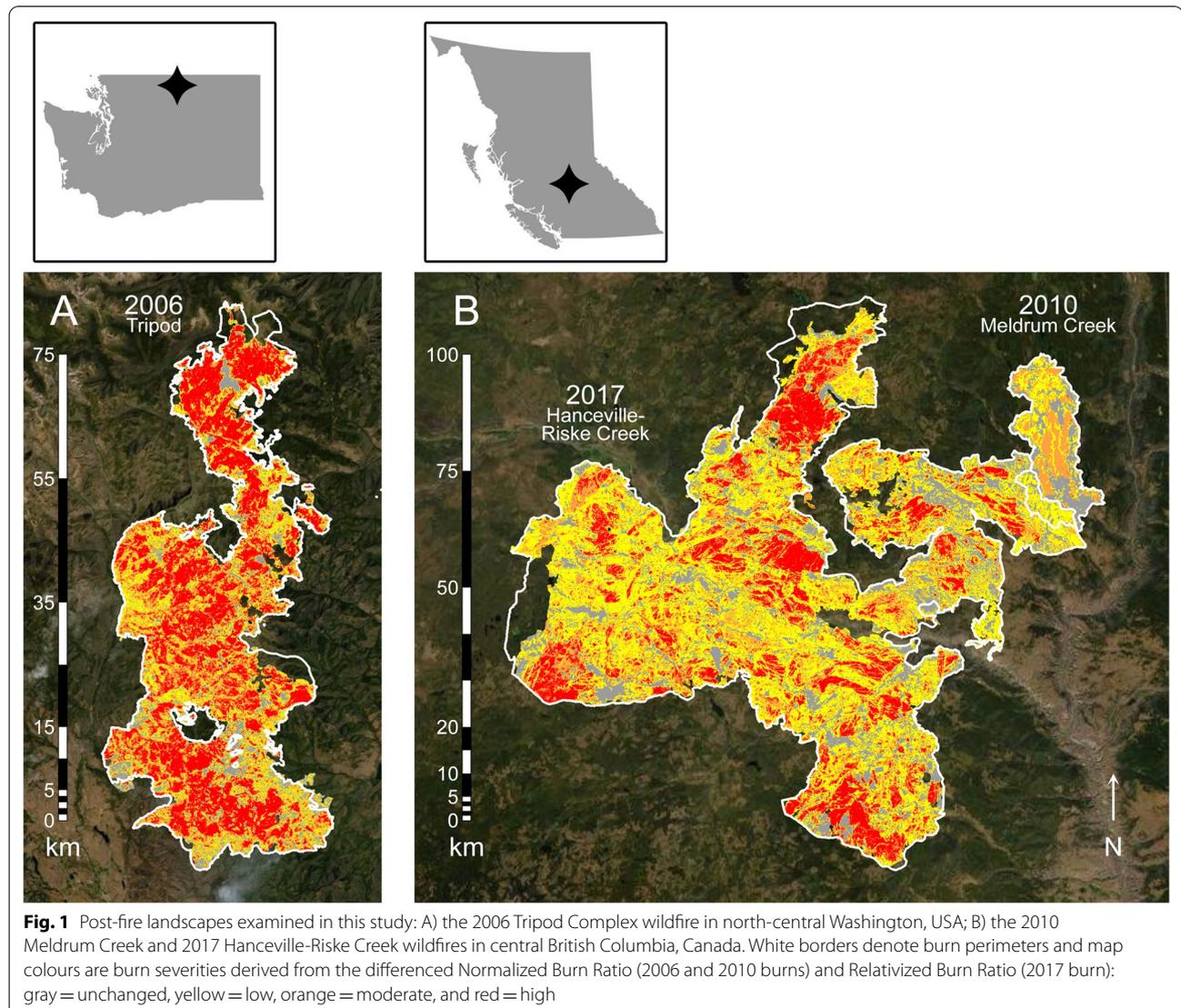
## Methods

### Study areas

We examined marten populations on two post-fire landscapes in Washington (48.790°N, – 119.953°W) and British Columbia (52.071°N, – 122.436°W) that were separated by approximately 400 km. Hereafter we use “Washington” and “BC” to refer to the whole landscape in each region. Our study areas have high-severity fire regimes typical of western sub-boreal and montane forests, with large, stand-replacing fires recurring every 100–300 years on average [4, 5].

The 2006 burn, resulting from the 70,575 ha Tripod Complex wildfire, is situated within the Okanogan-Wenatchee National Forest in north-central Washington (Fig. 1; see Additional file 1: Table S1). This landscape

has rugged topography and a gradient of forest types typical of the northeastern Cascade Range. Prior to burning, much of the study area was mature, highland conifer forest composed of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), with scattered stands of white-bark pine (*Pinus albicaulis*) and alpine larch (*Larix laricina*). The regenerating landscape is dominated by snags, deadfall, and an understory of lodgepole pine and willows (*Salix* spp.). At unburned sites, Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*) intergrade at lower elevations and on south-facing slopes; black cottonwood (*Populus trichocarpa*) and bigleaf maple (*Acer macrophyllum*) occur in drainages. Forests transition to alpine



parkland above ~2100 m, and to shrub-steppe communities below ~1000 m [34]. Our study focused on elevations of 1500–2000 m.

The Okanogan-Wenatchee National Forest is not actively managed for timber harvest, with no logging since 1995. A single north–south access road (NF-39), groomed for snowmobile traffic in winter, runs through the center of the study area. Aside from a ~10 m road buffer cleared of hazard trees, the 2006 burn has seen little human disturbance post-fire. State forests immediately east of the burn contain mature stands and cut-blocks of various ages, but were not sampled in this study.

The 2010 burn, resulting from the 15,553 ha Meldrum Creek wildfire, and the adjacent 2017 burn, resulting from the 239,340 ha Hanceville-Riske Creek wildfire, are situated on multi-use (Crown) land in central British Columbia, including portions of the Chilcotin Military Reserve (Fig. 1; see Additional file 1: Table S1). This landscape has gently rolling topography dotted with small lakes, and elevations of 900–1000 m. Forests in the area fall under the Interior Douglas-fir and Sub-Boreal Pine-Spruce biogeoclimatic zones [64]; prior to burning, the 2010 and 2017 burns contained mostly mature Douglas fir and lodgepole pine, with smaller amounts of Engelmann spruce, white spruce (*Picea glauca*), and quaking aspen. The regenerating landscape is a mosaic of cut-blocks containing patchy regrowth of lodgepole pine, aspen, and willows, interspersed with islands and stringers of residual trees and snags. Large, natural meadows occur in the southern part of the study area. Approximately 15% of the 2010 burn re-burned in 2017.

The BC study area is actively managed for timber harvest and contains an extensive road network. Virtually all stands of fire-killed trees in the 2010 burn, corresponding to areas that burned at moderate to high severity, were salvage-logged between 2010 and 2012. This activity created a series of salvage-blocks covering ~6000 ha and running north–south through the study area. Some selective harvest also occurred in areas that burned at lower severity due to post-fire tree death from mountain pine beetles. Salvage logging at a comparable intensity has taken place in the 2017 burn, beginning in winter 2017–2018.

### Field methods

We examined conditions 10–13 years post-fire for the 2006 burn, 6–9 years post-fire for the 2010 burn, and 0–2 years post-fire for the 2017 burn. Salvage-logged areas of the 2010 burn were 4–9 years old at the time of our study; we did not sample salvage-logged areas of the 2017 burn.

From December to March of 2016–2017, 2017–2018, and 2018–2019, we located marten trails along

snowmobile routes in both study areas as part of a larger survey effort for carnivores on post-fire landscapes [65]. Suitable trails ranged from ~24 h to several days old depending on snow quality. For each trail, working backwards from the marten's direction of travel, we recorded the movement path as a series of straight-line 5 m segments ("steps") marked with pin flags. We georeferenced the trail at its endpoints and at every sixth step (30 m), and measured canopy closure at each of these sites with a spherical densiometer, taking the average of four readings. We prioritized backtracking in areas > 1 km from previously sampled trails to maximize the number of marten in our dataset and to cover as many potential habitats as possible.

Concurrently with snow tracking, we live-trapped marten using single-door, wire mesh live-traps lined with straw and covered with an open-bottom plywood box and fir branches [66]. We targeted low-severity areas of each burn that frequently had marten tracks, spacing trap sites < 1 km apart and > 50 m from roads. We baited traps with chicken or beaver meat and commercial scent lure, and checked for captures every 24 h. We did not operate traps in ambient temperatures below – 20 °C.

Captured marten were transferred to a vinyl and wire mesh handling cone fitted over the front of the trap [67], and then immobilized via mask induction with isoflurane at an initial concentration of 3% in 1 L/min oxygen using a tabletop vaporizer, a type E portable oxygen cylinder, and a Bain non-rebreathing circuit.

After induction, we moved the marten to a tent containing a heating pad and battery-powered space heater. Handling lasted approximately 20 min at an isoflurane concentration to 1–2% to maintain the desired level of anesthesia; we monitored respiration and rectal temperature throughout. We determined the marten's sex and body length, and estimated age via visual inspection of tooth wear. Finally, we attached ear tags (Monel #1) in each ear and fitted adult marten with a store-on-board GPS collar / VHF transmitter (Advanced Telemetry Systems Model G10) weighing approximately 30 g. We programmed collars to attempt a satellite fix every 15–20 min for deployments in winter (December–March), or 90 min for deployments until the following winter. The VHF transmitter aided in recapturing marten, but was not used to obtain location data. Once we were satisfied with collar fit, we discontinued anesthesia and measured body mass using a wool toque and a spring scale. We then released the marten to its place of capture after a recovery time of 10–15 min. We recaptured marten and recovered their collars at the end of each winter field season using the same procedure as above.

**Analyses**

*Mapping*—We mapped burn perimeters and severities in ArcMap using shapefiles from the USGS Geosciences and Environmental Change Science Center [68] and DataBC [69]. Burn severity layers were provided by the Monitoring Trends in Burn Severity project and BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development. Mapping of the 2006 and 2010 burns used the differenced Normalized Burn Ratio (dNBR) [70], whereas the 2017 burn used the more recent Relativized Burn Ratio (RBR) [71]. Although the Relativized Burn Ratio produces a slightly better correlation to field measurements of burn severity, in practice the two metrics have a ~2% difference in accuracy [71]. We analyzed our burn severity layers as rasters with a minimum resolution of 30 × 30 m (0.09 ha). Burn severity classes for these data, based on surface reflectance at ~12 months post-fire for each raster cell, were (1) “unchanged” if no post-fire vegetation change was evident, (2) “low” for <10% overstory tree mortality, (3) “moderate” for 10–70% mortality, or (4) “high” for >70% mortality (Table 1) [70].

We generated custom shapefiles for roads, meadows, and salvage-logged areas using Landsat imagery and maps of 25-year landscape change from the National Forest Information System [3, 72]. The BC study area has a complex history of timber harvest beyond the scope of this study, so we considered treed areas of the 2010 and 2017 burns to be “intact forest,” even if some historical thinning was evident in Landsat imagery. We obtained hydrology shapefiles (streams and lakes) from the Washington Geospatial Open Data Portal [73] and DataBC [74].

In a few cases, marten trails in the 2010 burn extended into the 2017 burn or vice versa. We assigned each trail to a single burn based on where the majority of waypoints fell. For areas of the 2010 burn that re-burned in 2017, we assigned waypoints to the more recent disturbance.

We omitted two trails in the 2010 burn that were < 100 m long.

*Trail Analyses*—We used the R package “trajr” to calculate marten movement characteristics on each trail [75]. Sinuosity *S* expresses the amount of angular change over a given path length, with straight paths approaching *S*=0 and convoluted paths approaching *S*=1 [76]. We estimated sinuosity using corrected methods from Benhamou [77]. For marten, we expected trails in low-quality habitat to have lower sinuosity. For trails that crossed meadows or salvage-blocks, we used ArcMap to measure net displacement *D* and straight-line distance *L* for trail segments within these habitats. We then calculated the straightness index *D/L* for each crossing [78]. Highly straight paths approach *D/L*=1, and we expected marten to behave this way when crossing open areas. In practice, sinuosity and straightness are inversely related to each other [77]; we chose the straightness index to characterize crossings because we lacked a sufficiently large sample of angular change for these trail segments. Because we repeatedly detected marten activity over winter in areas where we back-tracked, we assumed that each trail was an independent foraging bout from a resident animal—in other words, an animal familiar with the landscape rather than merely dispersing through it.

We also used the R package “adehabitat” to determine the extent to which each trail deviated from the null model of correlated random walk, i.e. trail “directedness” [79, 80]. A random walk is characteristic of marten searching suitable habitat for prey, whereas a directed walk implies movement through lower-quality habitat. For this procedure, we first generated 1000 random trails with the same step length, total distance, and turning angle distribution as the original trail (see Additional file 1: Figure S1). We then calculated the mean squared displacement of each random trail and compared this distribution to the mean squared displacement of the original trail using a Monte Carlo permutation test. By definition, a directed walk differs significantly from the null hypothesis of random movement and represents a categorically different behaviour [79]. We therefore considered trails with high directedness (Monte Carlo *P*<0.05) to be instances where marten shifted their foraging behaviour in response to habitat quality; most (62%) of trails that we identified as directed walks had a Monte Carlo *P*<0.01 (see Additional file 1: Figure S2).

We assessed habitat selection along marten trails in terms of post-fire landscape change (burn severity) and landscape heterogeneity. For each georeferenced point along a trail we assigned a dNBR/RBR raster value of 0=unburned, 1=unchanged, 2=low, 3=moderate, or 4=high. To quantify landscape change, we estimated overall burn severity (“burn index”) following methods

**Table 1** Distribution of burn severities on post-fire landscapes in this study

Burn	Burn severity (%)				
	Unchanged	Low	Moderate	High	No Data
<i>Washington</i>					
2006	12.0	22.2	25.1	39.6	1.2
<i>British Columbia</i>					
2010	16.8	44.7	18.8	18.1	1.5
2017	45.2	27.8	27.0	0.1	0.0

Data are derived from the differenced Normalized Burn Ratio (2006 and 2010 burns) and Relativized Burn Ratio (2017 burn): unchanged=no post-fire vegetation change was evident, low = < 10% overstory tree mortality, moderate = 10–70% mortality, and high = > 70% mortality (Key and Benson 2006)

in Roberts et al. [81]. We first calculated the proportions of burn severity classes along each trail using ArcMap, then multiplied these proportions by their corresponding dNBR/RBR raster values (0 to 4, as above); our burn index was the sum of these multiplied values (see Additional file 1: Figure S3). This index ranged from 0 if the trail fell entirely in unburned areas to a maximum of 4 if it crossed areas burned entirely at high severity, with intermediate values indicating moderate or mixed severity.

We quantified landscape heterogeneity (“burn diversity”) for each trail as a total sum of squares, using the proportions of unburned and burned habitat classes calculated above. We rescaled the index to range from 0 if the trail crossed a single habitat type to a maximum of 1 if all habitat types occurred in equal proportion, using the equation:

$$\frac{C - \sum_{i=1}^n (y_i - y)^2}{C} \quad (1)$$

where  $C$  is a scaling factor equal to the theoretical maximum sum of squares if one habitat type dominates among  $n$  available habitat types.

For each burn, we used Grubbs’ test to identify and remove significant outliers among explanatory variables [82], then used Pearson correlations to assess collinearity, retaining variables with pairwise  $R^2 < 0.5$ . We used univariate beta regressions with the R package “betareg” to examine the influence of canopy closure, burn index, and burn diversity on trail sinuosity [83]. We used univariate logistic regressions to examine the influence of these three habitat predictors on trail directedness. We chose a Gaussian distribution for model fit based on inspection of quantile-comparison plots, and pooled our data across all years. We assessed statistical significance with post-hoc Wald tests.

**Home Range Analyses**—We examined marten home ranges as utilization distributions (“kernels”) using the R packages “trajr” [75], “adehabitatLT”, and “adehabitatHR” [80]. We defined each animal’s home range as the area enclosed by a 90% fixed kernel, and its core activity area as the area enclosed by a 50% fixed kernel, using the biased random bridge method [84, 85]. Compared to simple kernels [86], this method models animal movement as a biased random walk and accounts for time lag between successive locations, producing utilization distributions that are more sensitive to travel corridors. To reduce bias from locations where marten were inactive (i.e. resting sites), we defined 23.7 m as the minimum distance between successive locations ( $L_{\min}$ ), based on the estimated location error for a stationary collar at a low-severity site in the 2010 burn ( $N=4498$  locations). We defined 12.5 h as the maximum time lag

between successive locations ( $T_{\max}$ ), which covered > 90% of locations for all animals regardless of fix rate [85]. We selected the diffusion parameter  $D$  and smoothing parameter  $h_{\min}$  based on the total number of locations for each marten. We visualized home range contours and calculated home range overlap using ArcMap.

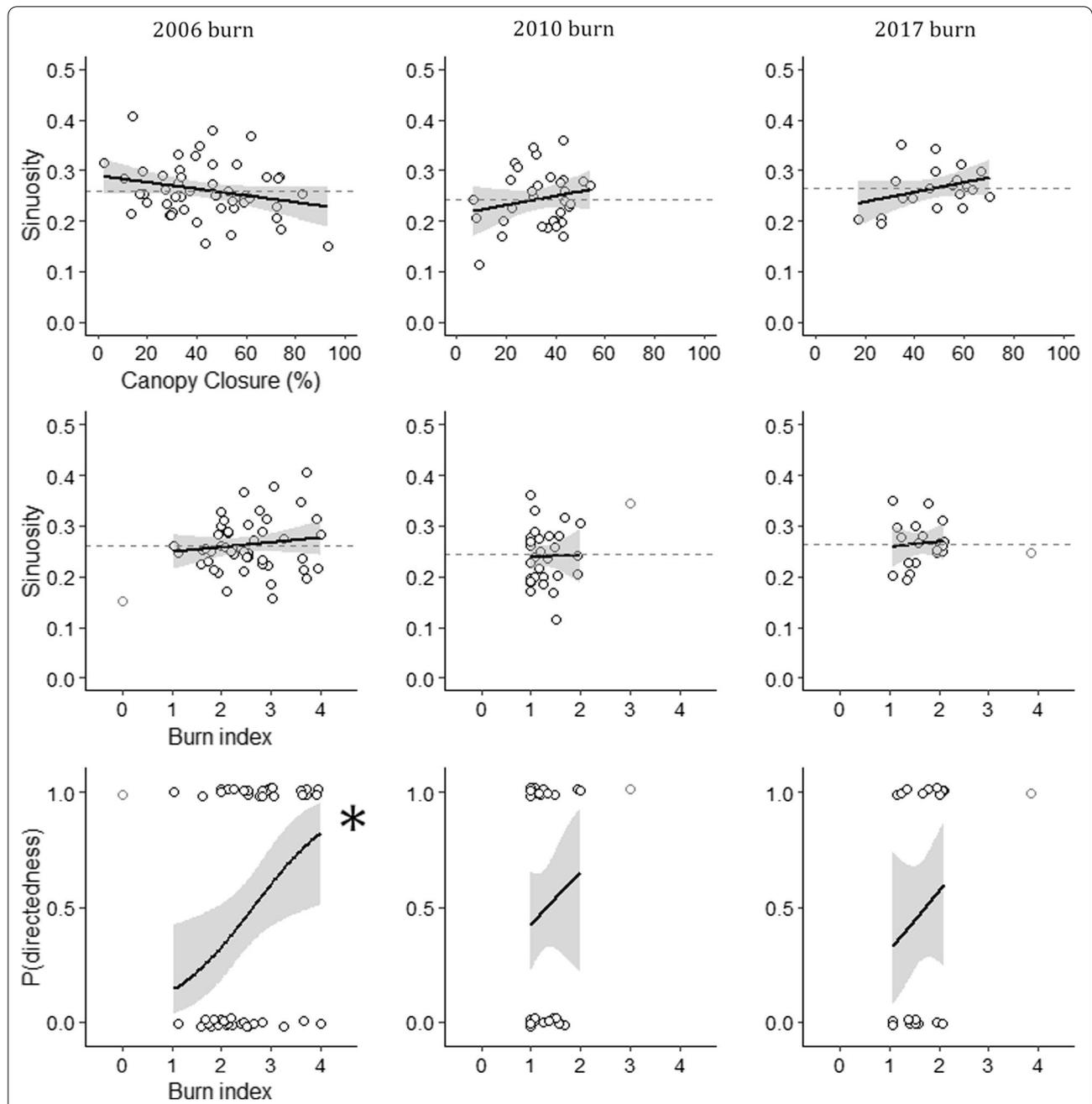
To assess marten habitat selection at the home range scale, we used ArcMap to generate an equal number of randomly-located points (“available” locations) within a convex hull fitted to the outermost locations of each animal (“used” locations). We then assigned the following habitat attributes to each used and available location: (1) cover type (intact forest, meadow, or post-fire salvage), (2) burn severity (unburned, unchanged, low, moderate, or high), (3) distance to the nearest open water (streams or lakes), (4) distance to the nearest natural meadow, (5) distance to the nearest road, and (6) distance to the nearest salvage-logged area for BC. We evaluated marten responses to cover type and burn severity for each animal separately using chi-square post-hoc tests [87]. Likewise, we used logistic regressions to determine individual selection or avoidance of roads, open water, meadows, and post-fire salvage. We use “selected” and “chose” interchangeably in the sections below to describe how marten responded to available habitat features [88].

## Results

Over three winters, we back-tracked 102 marten trails for 65.5 km. Individual trails were 70 to 2200 m long with 14 to 440 5 m steps. Our final dataset included 50 trails covering 24.3 km in Washington; in BC, we back-tracked 33 trails covering 25.2 km in the 2010 burn and 19 trails covering 16.0 km in the 2017 burn. We found marten trails in unburned habitat on only one occasion (2006 burn). Although it was not possible to assign trails to individual marten, the majority of back-tracking took place beyond the home ranges of our collared animals.

Marten in the 2010 and 2017 burns did not significantly alter their movements in relation to canopy closure or burn index (Fig. 2). However, marten in the 2006 burn switched to directed movement in areas of high burn severity ( $N=49$ ,  $Z=2.39$ ,  $P=0.017$ ); they did not respond to canopy closure. Across all burns, marten did not alter their movements in relation to burn diversity (see Additional file 1: Figure S4).

Eight trails in BC crossed post-fire salvage-logged areas at least once, and three trails crossed natural meadows at least once (see Additional file 1: Table S2). Meadows were less common in the Washington study area, and we did not observe marten crossing them. Crossings averaged  $197 \pm 45$  m through salvage-blocks (range 90–595 m,  $N=11$  crossings), and  $267 \pm 100$  m in meadows (range 93–569 m,  $N=5$  crossings). Marten trails were highly



**Fig. 2** Marten movements in response to canopy closure and burn severity on post-fire landscapes, based on linear and logistic regressions. Data are from north-central Washington, USA (2006 burn), and central British Columbia, Canada (2010 and 2017 burns). "Burn index" measures the average burn severity along a marten trail from 0 (entirely unburned) to 4 (entirely high severity). Trails with high directedness, at  $y = 1$ , differ significantly from the characteristics of a correlated random walk, and would be expected from marten moving through low-quality habitats. Dashed lines show sample means; asterisks denote statistical significance. Light gray dots are significant outliers excluded from regressions. X-axis labels apply to all columns

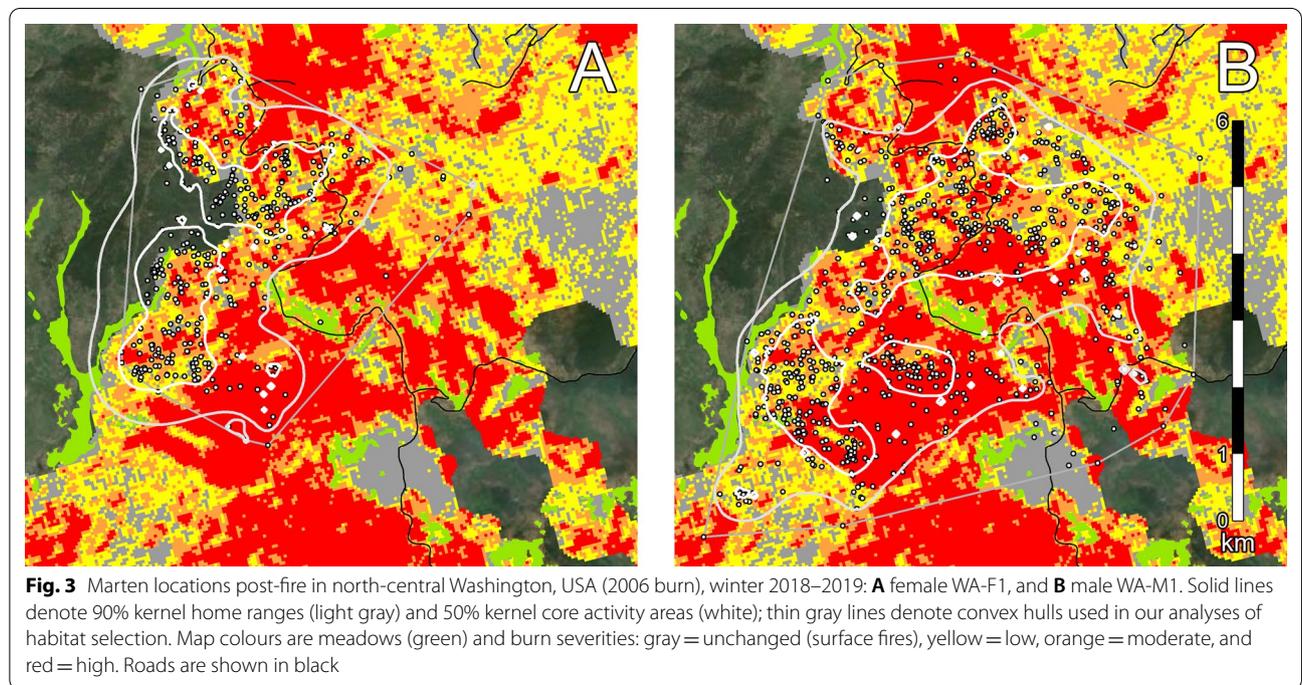
straight in both habitat types, with  $D/L$  averaging  $0.91 \pm 0.04$  in salvage-blocks (range 0.52–1.00,  $N = 11$  crossings) and  $0.89 \pm 0.09$  in meadows (range 0.53–1.00,  $N = 5$  crossings).

We obtained 6768 locations from six collared marten (Table 2; see Additional file 1: Table S3): 1187 locations from one male and one female marten in Washington (Fig. 3), and 5581 locations from two male and two female marten in BC (Fig. 4). Locations were primarily over

**Table 2** Characteristics of marten home ranges on post-fire landscapes in north-central Washington, USA (2006 burn), and central British Columbia, Canada (2010 burn)

Marten ID	Dates collared	Fix rate (min)	N days	N locations	Home range (ha)	
					90%	50%
WA-F1	Jan. 16–Mar. 13, 2019	15	56	389	674.4	207.0
WA-M1	Jan. 13–Mar. 17, 2019	15	63	798	1223.3	398.6
BC-F1	Mar. 6–Mar. 25, 2017	90	19	117	1077.6	234.8
BC-F2	Dec. 17, 2017–Mar. 2, 2018	20	75	1181	777.2	153.6
BC-M1	Dec. 18, 2017–Mar. 3, 2018	20	75	1357	1354.3	375.3
BC-M2	Dec. 21, 2017–Mar. 4, 2018	20	73	1182	1345.8	414.4
	Mar. 9–Oct. 28, 2018	90	233	1744	1495.3	464.4

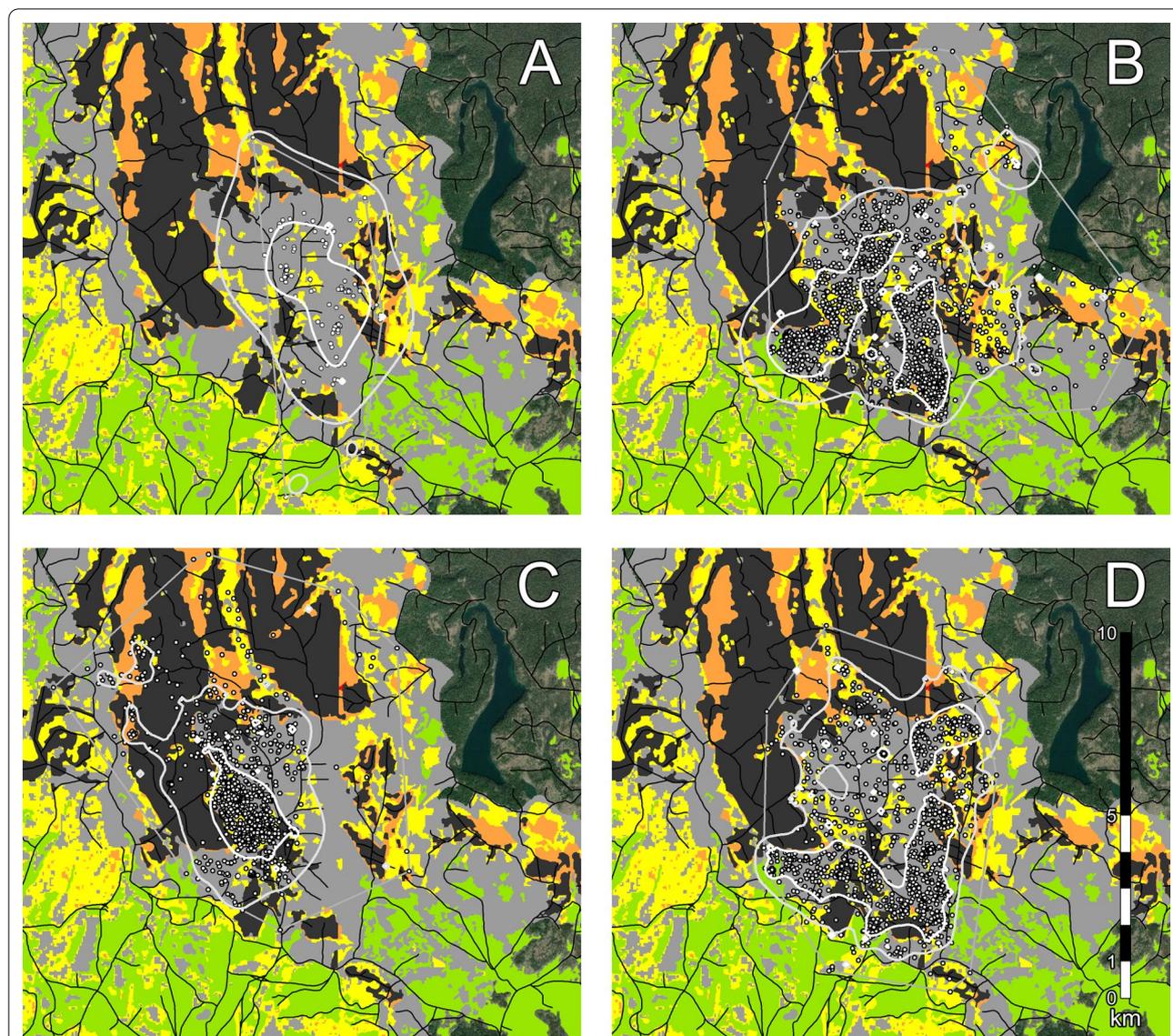
“Fix rate” refers to the time between location attempts. Male BC-M2 was re-collared for the March–October deployment



winter (December–early March), but we also obtained locations after snowmelt (“summer”, late March–October) for one male marten in BC (see Additional file 1: Figure S5).

In both study areas, male marten covered 26–81% more of the post-fire landscape than females (Table 2). Males had winter home ranges averaging  $1307.8 \pm 42.3$  ha, while females averaged  $843.1 \pm 121.0$  ha. Males used core activity areas averaging  $396.1 \pm 11.4$  ha, while female core areas averaged  $198.5 \pm 23.8$  ha. Male BC-M2’s summer home range was similar in size to his winter home range (see Additional file 1: Figure S5).

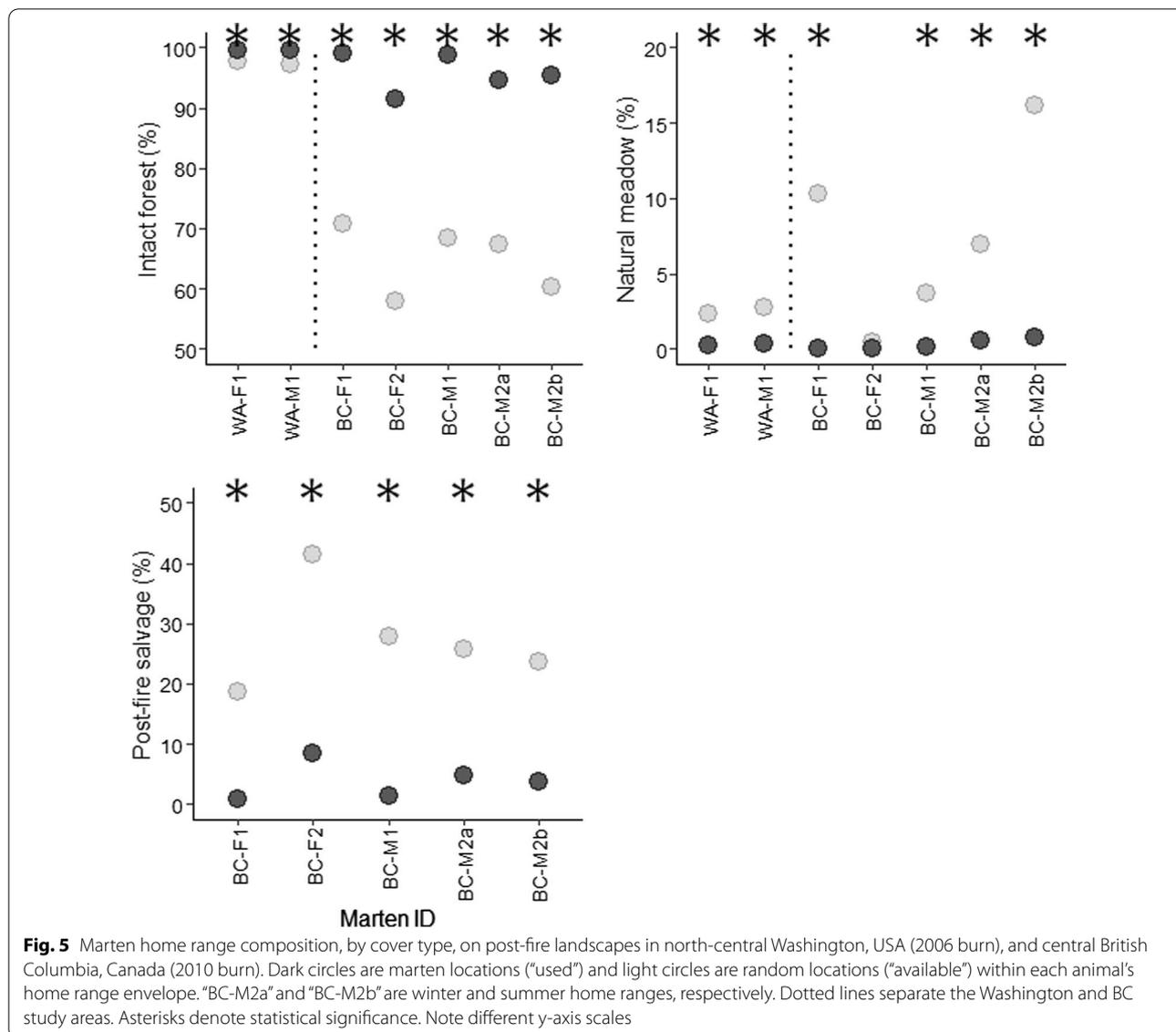
Male and female marten had extensively overlapping home ranges in both study areas (Figs. 3 and 4). In the 2006 burn, 73.6% of female WA-F1’s home range was within male WA-M1’s home range, and 34.4% of her core activity area overlapped with the male’s core activity area. Similarly in the 2010 burn, 69.2% of female BC-F2’s home range was within male BC-M1’s home range, and 55.4% of her core activity area overlapped with this male’s core activity area; 69.2% of her home range was also within male BC-M2’s home range, but only 10.5% of her core activity area overlapped with this male’s core activity area.



**Fig. 4** Marten locations post-fire in central British Columbia, Canada (2010 burn), winters 2016–2017 and 2017–2018: **A**) female BC-F1, **B**) male BC-M1, **C**) female BC-F2, and **D**) male BC-M2. Solid lines denote 90% kernel home ranges (light gray) and 50% kernel core activity areas (white); thin gray lines denote convex hulls used in our analyses of habitat selection. Map colours are meadows (green), post-fire salvage-logged areas (darkest gray), and burn severities: gray = unchanged (surface fires), yellow = low, orange = moderate, and red = high. Roads are shown in black

Unexpectedly, male marten in BC had extensive winter home-range overlap: 75.8% of male BC-M1's home range was within male BC-M2's home range, and 53.6% of male BC-M1's core activity area overlapped with the other male's core activity area. Male BC-M2 used similar areas of the 2010 burn throughout the year; 78.0% of his summer home range overlapped with his winter home range, and 57.7% of his summer core activity area overlapped with his winter activity area (see Additional file 1: Figure S5).

Marten avoided open habitats (Fig. 5). Intact forest accounted for 91.5–99.7% of marten locations in winter ( $\bar{x} = 97.0\%$ ), and all marten used intact forest significantly more than expected from availability ( $\bar{x} = 76.6\%$ ). Natural meadows accounted for 0.0–0.6% of locations ( $\bar{x} = 0.2\%$ ), and five out of six marten used meadows areas significantly less than expected from availability ( $\bar{x} = 4.4\%$ ). In BC, 0.9–8.5% of winter locations occurred in salvage-logged areas. All marten used these areas significantly less than expected from availability

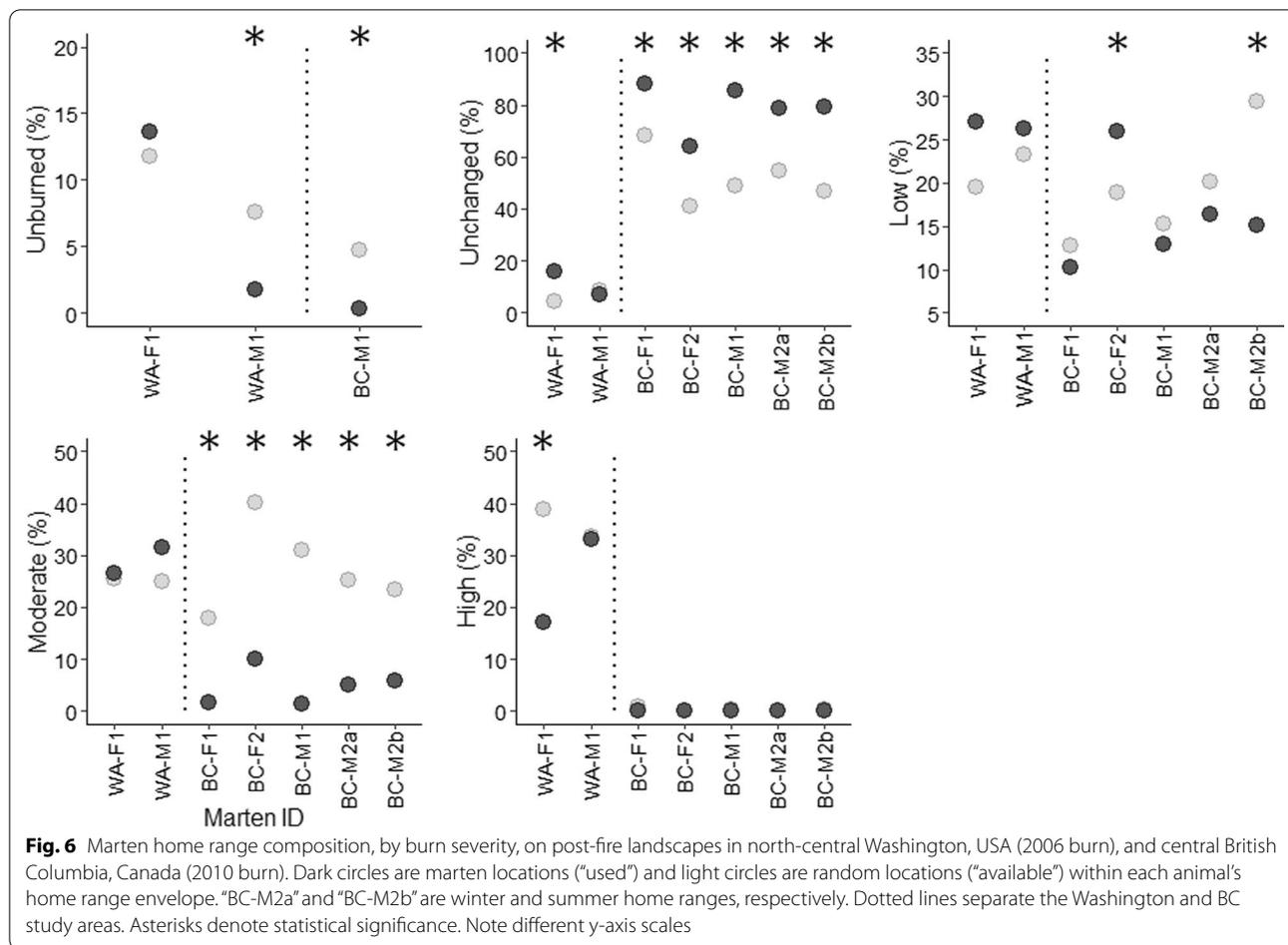


( $\bar{x}$  = 28.5%). Male BC-M2 had similar selection patterns in summer.

Marten responded to burn severity, with stronger patterns of selection in the 2010 burn than the 2006 burn (Fig. 6). In Washington, female WA-F1 used unchanged areas of the 2006 burn significantly more than expected (15.7 vs. 4.4%), and used high-severity areas significantly less than expected (17.2 vs. 38.8%). In BC, unchanged areas of the 2010 burn accounted 64.0–88.0% of all locations in winter ( $\bar{x}$  = 79.0%), and all marten used these areas significantly more than expected from availability ( $\bar{x}$  = 53.2%). Conversely, moderate-severity areas of the 2010 burn accounted for 1.5–10.1% of all locations ( $\bar{x}$  = 4.6%), and all marten used these areas significantly less than expected from

availability ( $\bar{x}$  = 28.5%). Female BC-F2 used low-severity areas of the burn significantly more than expected (25.9 vs. 18.9%), but no other marten showed a significant response. Male BC-M2 had similar selection patterns in summer. Two animals with locations in unburned habitat (males WA-M1 and BC-M1), used unburned locations significantly less than expected (Fig. 6).

Individual marten responded differently to water, meadows, roads, and salvage-logged areas (Fig. 7; see Additional file 1: Table S4). Both marten in the 2006 burn selected areas closer to water compared to random locations, as did male BC-M2 in the 2010 burn (58–258 m closer;  $P < 0.01$ ). Both females in the 2010 burn chose areas farther from water (86–421 m farther;  $P < 0.02$ ) while male BC-M1 showed no significant



patterns. Male WA-M1 in the 2006 burn and female BC-F1 in the 2010 burn chose areas farther from meadows (89–506 m farther;  $P < 0.05$ ). Both males in the 2010 burn chose areas closer to meadows (198–461 m closer;  $P < 0.001$ ), while female BC-F2 showed no significant patterns. All marten except female BC-F2 selected areas farther from roads (38–295 m farther,  $P < 0.05$ ), and all marten in the 2010 burn chose areas farther from post-fire salvage in winter (13–210 m farther;  $P < 0.02$ ). However, male BC-M2’s summer locations were significantly closer to these areas than expected (109–135 m closer;  $P < 0.001$ ).

**Discussion**

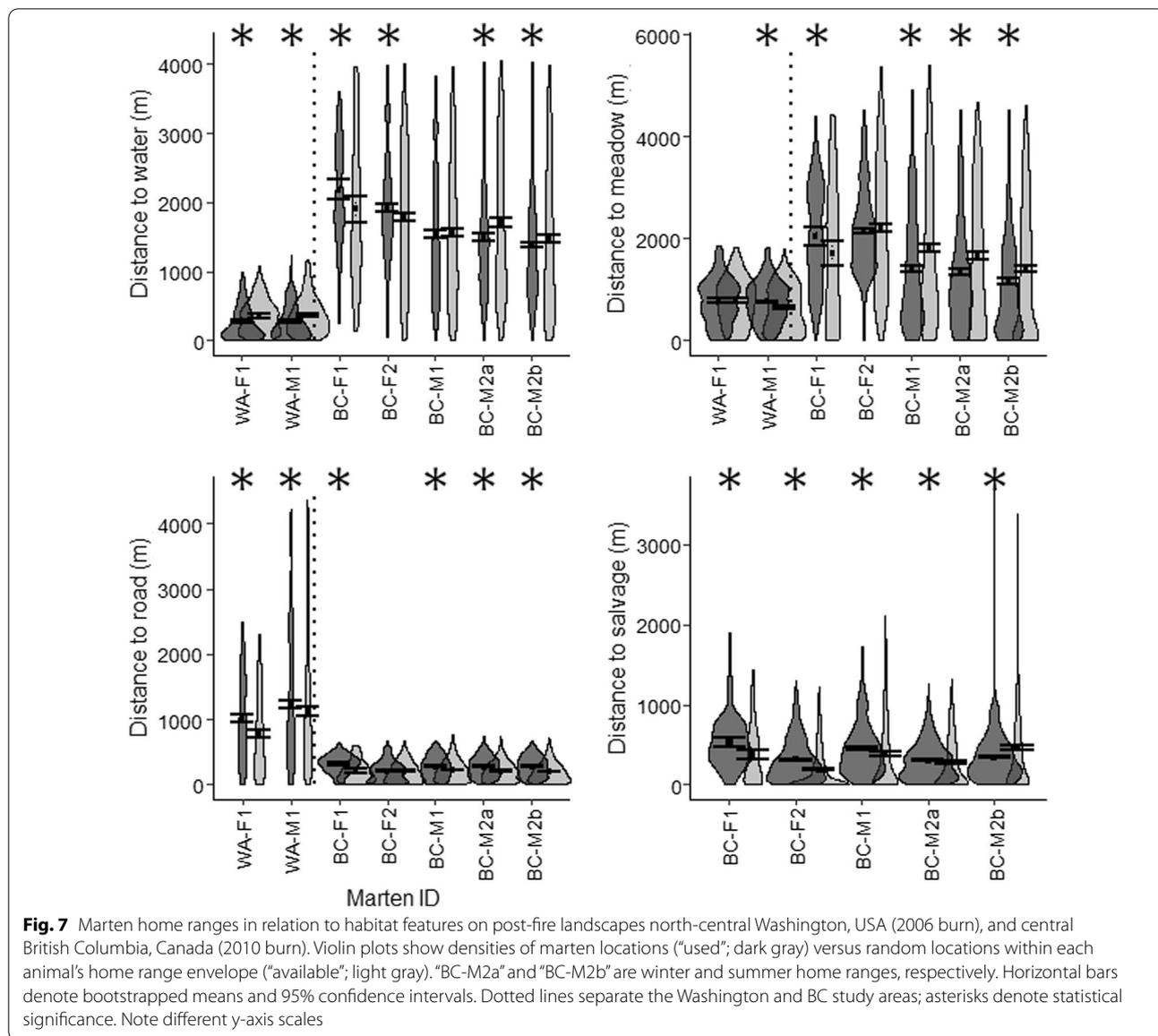
**Marten behaviour in burn mosaics**

In both north-central Washington and central British Columbia, marten used a wide range of post-fire habitats but selected areas more similar to pre-fire conditions. As expected, marten were most active in areas with intact, residual trees and rarely used open meadows or post-fire salvage-logged areas. Marten altered their behaviour

in response to habitat quality, adopting more directed movement through areas burned at high severity. In addition, marten chose home ranges that conspicuously excluded large patches of low-quality habitat.

Previous work has suggested that marten choose specific areas of burned landscapes. Trappers reported that marten were more abundant at the edges of young burns and areas burned at low severity [58]. Marten were most active along waterways and deadfall-rich areas seven years after fire in Alaska [50]. In the Northwest Territories, marten incorporated both burned and unburned habitats into their home ranges [51]. Marten evolved in fire-prone forests and clearly use heterogeneous post-fire landscapes [89]. Our work here indicates that large burns can support resident marten if portions of the landscape are relatively intact.

Local conditions influenced marten behaviour on burned landscapes. Marten in the 2006 burn made straighter movements in severely-burned habitats, where high-intensity fire caused substantial loss of trees, deadfall, and understory vegetation. Previous studies have



shown that fine-scale habitat features affect marten movement [90, 91], and our work here indicates differences in path characteristics at larger spatial scales as well (200–2200 m). Areas of high burn severity have reduced overhead cover and less residual woody structure [19, 25]. Marten crossing these areas are more exposed to predators [56], and have fewer opportunities to access prey and shelter under snow [92]. Although marten sometimes foraged here, their tendency to beeline through open areas is consistent with optimal foraging theory, which predicts that animals minimize their activity in low-quality habitats [48, 93]. We did not see the same shift from random to directed movement from marten in younger burns, suggesting that long-term

changes to the landscape may have a stronger negative influence on marten. Young burns contain more standing timber [94, 95], including damaged cone-bearing trees that may temporarily increase the suitability of severely-burned areas for marten and their prey. Red squirrel populations, for example, may not decline for several years post-disturbance depending on residual seed stores [96, 97].

Post-fire conditions influence marten home ranges as well. Marten in our study had home ranges similar in size to marten in burned black spruce (*Picea mariana*) in the Northwest Territories (11.1 km<sup>2</sup>; 21 years post-fire) [51], but roughly two times larger than marten home ranges in unburned mixed-conifer forests in California (2.3–8.1

km<sup>2</sup>) [98]. Male marten had larger home ranges than females, consistent with the larger size and higher energy requirements of males [98, 99]. Although our sample size is small and we did not collar marten in unburned areas, our results for the 2006 and 2010 burns are consistent with past work showing that marten need larger home ranges on low-quality landscapes [100, 101]. The high home range fidelity of male BC-M2 from winter to summer suggests that marten on burned landscapes need similarly large home ranges throughout the year, as has been seen on other disturbed landscapes [102].

We found substantial home range overlap for adult, resident males in the 2010 burn, which counters earlier statements that marten are territorial towards members of the same sex [98, 103]. This overlap may be a signature of landscape fragmentation forcing marten to share spatially limited resources. Coyotes (*Canis latrans*), for example, share remnant forest patches on agricultural landscapes [104]. Alternatively, male marten may have been competing for access to rare females, as has been documented in male-skewed populations of American badgers (*Taxidea taxus*) [105]. A larger sample of marten home ranges on burned landscapes would help determine which scenario is more likely.

Landscape context may have played a role in how marten responded to large-scale habitat features such as water and openings. Marten in the 2006 burn selected areas closer to water, but marten in the 2010 burn did not. Most water features in the 2006 burn were associated with steep drainages, and would have likely contained more deadfall and thicker post-fire vegetation than the surrounding hillsides [50]. In contrast, water features in the 2010 burn were typically lakes surrounded by gentle slopes. Although marten in both study areas avoided open habitats, marten in the 2010 burn did not respond to meadows and cut-blocks in the same way. These animals chose areas closer to natural meadows and farther from salvage-logged areas, suggesting a difference in habitat quality between the edges of meadows and the edges of cut-blocks [36].

Marten used all burn severities, but selected areas affected only by surface fires (unchanged) or burned at low severity. Our results agree with past work indicating the importance of these areas for marten [58], and support the view that marten will use severely-burned areas if enough residual structure is present [50]. Because burn severity reflects vegetation change [70], low-severity areas are more likely to retain habitat features suitable for marten: a closed canopy, large trees, and a structurally complex understory. Burn severity also shapes the distribution of marten prey including red-backed voles [59], red squirrels [60], western gray squirrels (*Sciurus griseus*) [106], and snowshoe hares [61]. Our detection of marten

throughout all three burns is encouraging, as it suggests that even recent severely-burned areas can provide habitat structure and connectivity. In large burns, however, it seems likely that residual trees play a major role in determining where marten persist and establish home ranges.

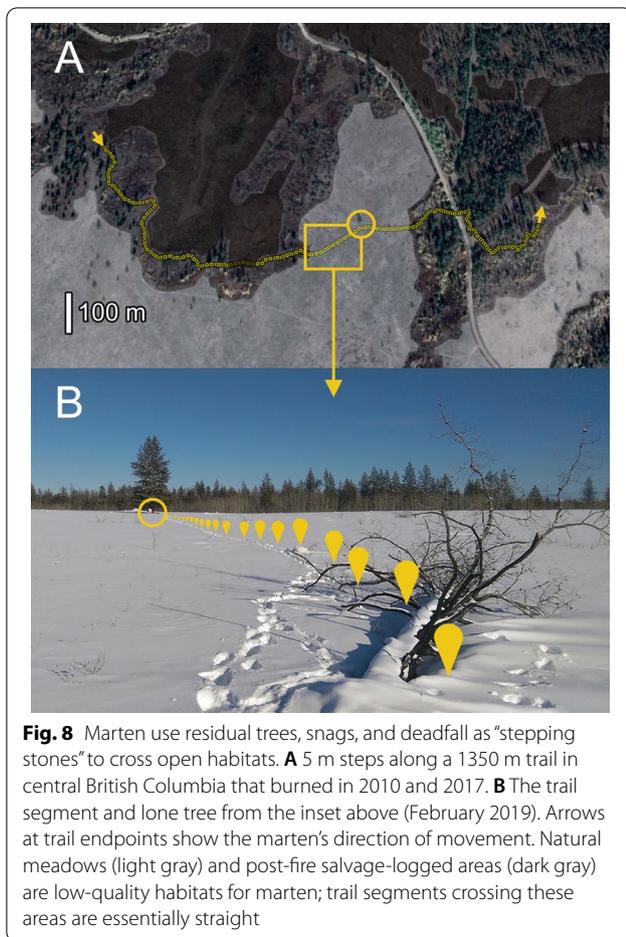
Although marten choose habitats based on prey abundance and accessibility [57, 107], other factors may influence the placement and structure of marten home ranges. Marten may avoid areas of sparse overhead cover due to greater perceived predation risk [56, 108]. Notably, fishers sometimes prey on marten [109, 110] and select similar habitats; thus, competition with fishers in the highly fragmented BC study area may have influenced the distribution of resident marten [111, 112]. In addition, lynx, coyotes, wolves (*Canis lupus*), northern goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*) could all potentially kill marten in our study areas if the opportunity arose. Tracking the activity patterns of other carnivores would help determine how marten factor predation risk into their habitat choices [113].

#### Marten responses to salvage logging

Marten strongly avoided post-fire salvage-logged areas. Salvage-logged areas presented hard edges to marten home ranges that are clearly visible from mapped locations in the 2010 burn. Over three winters of snow-tracking, we rarely encountered marten trails that crossed salvage-logged areas or approached salvage-block edges. Remnant trees, saplings, and slash piles were important landmarks for marten crossing open habitats (Fig. 8), but these features were rare in salvage-logged areas. Marten were also less active near roads, which were extensive in and around salvage-logged areas of the 2010 burn.

We are not aware of any prior studies examining marten home ranges in salvage-logged areas. Indirectly, Steventon and Daust [114] modeled the potential impact of salvage logging on marten after large-scale beetle outbreaks in BC. This work forecast a substantial loss of suitable habitats for marten in the next 20–40 years due to landscape fragmentation, even if conventional timber harvest occurred at lower intensity. Because marten avoid natural openings [89, 115] and conventional clearcuts [36, 47, 48], it is not surprising to see similar behaviour from marten in relation to salvage-logged areas.

Whether marten persist on burned landscapes depends on the quality of residual habitats: females need specific structures for denning [55, 116], whereas males need larger resource patches and larger prey [98, 117]. However, wildfire and salvage logging produce markedly different landscapes [65]. Low overhead cover and low structural complexity make salvage-logged areas unsuitable to both marten and their prey [39]. Road building in salvage-logged areas may also reduce the quality of



nearby uncut stands, as it does in other managed forests [118]. In addition, salvage logging appears to sharply reduce connectivity between residual habitats, validating earlier forecasts of marten declines on these landscapes [114]. Although marten may tolerate a variety of post-fire conditions, salvage logging represents a cumulative disturbance that is substantially worse for marten than the original fire.

#### Future Directions

Under climate change, fire regimes in western North American forests have shifted towards larger, more destructive, and more frequent patterns of burning [119–121]. These shifts are likely to continue [122, 123], and may result in the widespread replacement of forested landscapes with non-forest habitats by the end of the century [8–10]. In addition to habitat losses from fire, further fragmentation via post-fire salvage logging threatens biodiversity in burned forests [31–33]. In the face of such rapid landscape change, it is critical to understand how wildlife use burned landscapes [53, 124] and rethink forest management with fire in mind [125–127].

Although some forest wildlife is well-studied post-fire, important knowledge gaps remain for many species [53, 124, 128]. For marten, we recommend further work to understand the impacts of burn severity and salvage logging on landscape connectivity [129, 130] and population change [114]. Identifying where and when marten cross low-quality habitats would improve our understanding of marten movement ecology, and may help managers better emulate natural disturbance patterns on post-fire landscapes.

Given the limited scope and sample sizes in our study, we recommend further work to determine marten responses to fire and salvage logging more broadly in western forests. Large wildfires are inherently variable and non-replicable disturbances [131], and post-fire habitat conditions are not purely a function of time since fire [61, 132, 133]. Landscape-specific differences in topography, fire history, and management intensity, as well as year-to-year differences in regeneration, snowfall, and prey populations, all influence the conditions that marten encounter post-fire. Although we focus on marten behaviour in winter, when thermoregulation is more energetically costly [134], and deep snow makes foraging more difficult [135], we note that marten may perceive burned habitats differently at other times of year, such as late spring, when den trees become important for raising young [136]. Finally, although we found only modest correlations between habitat variables in our study, the combined effects of burn severity, time since fire, and habitat structure may influence marten behavior more strongly on other landscapes.

We believe that our results are most applicable to marten populations in recently-burned (< 15 years post-fire), pine-fir and spruce-fir forests in the Cascade Range [137] and Blue Mountains of Washington and Oregon [138], and in pine-fir forests of central and south-central BC [139]. We urge further work in boreal and mixed-conifer forests, such as those in the Sierra Nevada mountains, where fire behaviour and salvage logging practices differ.

The strong avoidance of salvage logging by marten raises concerns for other forest specialists. Like marten, female fishers use large, damaged trees and snags for denning [140] and males need large areas of dense forest [141], neither of which may be available on salvage-logged landscapes [142]. Fishers [143], Mexican fox squirrels (*Sciurus nayaritensis*) [144], black-backed woodpeckers (*Picoides arcticus*) [145], and American three-toed woodpeckers (*Picoides dorsalis*) [146] use forests burned at moderate to high severity, but these areas are often salvage-logged. Given the level of avoidance for salvage logging documented here, we recommend greater caution in post-fire landscape planning to protect habitats for wildlife. Residual treed areas are key areas for

marten and other forest specialists, and their preservation should be a high priority.

## Conclusions

Our work provides further insight into marten behaviour on post-fire landscapes. Marten use recently-burned forests, but the inherent heterogeneity within burns strongly influences their habitat choices. Marten alter their movements in response to post-fire habitat quality; lightly-burned areas provide important residual structure for marten and offer suitable conditions for their preferred prey. However, marten avoid severely-burned areas and exclude salvage-blocks from their home ranges. Collectively, our results can inform management decisions that preserve marten habitat as fire and salvage logging change forested landscapes.

## Abbreviations

BC: British Columbia; dNBR: Differenced Normalized Burn Ratio; RBR: Relativized Burn Ratio.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-021-00286-2>.

**Additional file 1. Table S1.** Characteristics of post-fire landscapes examined in this study. **Table S2.** Marten movements when crossing post-fire salvage-logged areas and natural meadows. **Table S3.** Capture dates and physical characteristics of marten in this study. **Table S4.** Marten locations versus random locations in relation to stand-scale habitat features. **Figure S1.** Examples of marten movement behaviour in relation to habitat quality. **Figure S2.** Distribution of marten trails in our dataset along a continuum of trail "directedness". **Figure S3.** Examples of "Burn index" measuring the overall post-fire burn severity on a portion of the landscape. **Figure S4.** Marten movements in response to post-fire canopy closure and landscape heterogeneity. **Figure S5.** Post-fire home range fidelity of male marten BC-M2.

## Acknowledgements

We thank our field assistants Sarah Bird, Taylor Brannock, Jeff Brown, Jordan Cormack, Matt Danielson, Kelly Likos, Erin Morrison, Laura Platt, and Sam Shappas. We thank Dr. Malcolm McAdie for assisting with marten immobilizations. We are grateful to the Department of National Defence for providing safety training and access to the Chilcotin Military Reserve in BC. We thank Becky Cadsand, Mauro Calabrese, Larry Davis, Jeff Lewis, Matt Marsh, and Rich Weir for their local knowledge and guidance on this project.

## Authors' contributions

Both authors designed the study. LV conducted the field work, software coding, and data analyses. LV wrote the first draft of the manuscript, and both authors contributed substantially to revisions. Both authors read and approved the final manuscript.

## Funding

This project was supported by grants from the Habitat Conservation Trust Foundation (HCTF), the Forest Enhancement Society of British Columbia (FESBC), the Skagit Wildlife Research Grant Program (Seattle City Light), the Natural Sciences and Engineering Research Council of Canada (NSERC), and by fellowships from Killam Trusts and the University of British Columbia.

## Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

### Ethics approval and consent to participate

Our animal capture and handling methods were approved by the University of British Columbia's Animal Care Committee (Protocol A16-0114), the Washington Department of Fish and Wildlife (Permit 18-241) and the BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development (Permit WL16-239653).

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no competing interests.

Received: 27 May 2021 Accepted: 20 September 2021

Published online: 09 October 2021

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