



Bat activity and richness in beetle-killed forests in southern British Columbia

KIRSTIE J. LAWSON,* CORI L. LAUSEN, KRISTEN A. MANCUSO, LOGAN A. VOLKMANN, T. J. GOOLIAFF, JENNA HUTCHEN, KRISTINE J. TEICHMAN, ANGELINA J. KELLY, AND KAREN E. HODGES

University of British Columbia Okanagan, Department of Biology, Science Building, 1177 Research Road, Kelowna, British Columbia V1V 1V7, Canada (KJL, KAM, LAV, TJG, JH, KJT, AJK, KEH)

Wildlife Conservation Society Canada, P.O. Box 606, Kaslo, British Columbia V0G 1M0, Canada (CLL)

* Correspondent: kirstie.lawson09@gmail.com

Wildlife species exhibit changes in behavior, population dynamics, and abundance after disturbances to forests. In western North America, large swathes of dead trees have resulted from unusually large outbreaks of bark beetles (*Dendroctonus* spp.) over recent decades. For bats, these tree mortality events could be either negative or positive, depending on whether cavities and crevices for roosting increase in response to beetle outbreaks and how the food supply is affected. It is therefore important to determine bat presence and activity in areas with many beetle-killed trees. We examined bat species richness in the southern interior of British Columbia, Canada, in areas with light and severe beetle-kill. We identified six bat species from acoustic recorders; the federally endangered little brown myotis (*Myotis lucifugus*) had the most detections. Although we surveyed stand-level vegetation, we found no systematic difference between areas identified from government aerial surveys as having had high or low beetle-kill within the previous decade. Neither beetle-kill severity nor the fine-scale vegetation that we measured correlated with bat presence or activity. We conclude that bats in this region use beetle-killed forests and that the severity of beetle-killed trees is neither adversely affecting bat presence or activity, nor enabling increased use by bats of affected forest stands in comparison to activity levels found in other high elevation forests.

Keywords: activity, bark beetle, boreal forest, British Columbia, habitat, little brown myotis, *Myotis lucifugus*

Bat species are declining globally (Mickleburgh et al. 2002). Population losses are often tied to habitat loss; however, the habitat preferences of many bat species within certain habitats, such as beetle-killed forests, remain poorly understood. Bats select habitats that contain roosts and prey, and in which they can navigate easily. In western coniferous forests of North America, dead or dying trees may provide high-quality roosting sites because of their sloughing bark (Barclay and Brigham 2001; Kalcounis-Rüppell et al. 2005), and stands with dead trees may provide important open foraging habitat for bats (Randall et al. 2011). Bark beetle infestations are increasing across western North America (Alfaro et al. 2015), killing coniferous trees and potentially creating high-quality habitat for bats. However, it is unknown if bats preferentially use forest stands affected by bark beetles, and if so, whether the intensity of infestation affects use of stands by bats.

Bark beetle infestations reduce canopy cover (Stone 1995; Allen et al. 2006), which may improve flight paths for bats as well as the ability to echolocate and forage for prey (Brigham et al. 1997). Many forest-dwelling bats in North America are

aerial hawkers of insects and may therefore benefit from foraging opportunities in open forest (Nagorsen and Brigham 1993; Stone 1995). If beetle-killed stands produce higher insect abundance, then these forests may attract bats. Of the 19 species of bats in Canada, 16 roost in trees (Lacki et al. 2007), and many bats use snags in early to intermediate stages of decay (Vanhof and Barclay 1996; Parsons et al. 2003; Baker and Lacki 2006). Thus, many forest-dwelling bats may benefit from increased snag abundance in beetle-killed stands (Fenton et al. 1994; Kunz and Lumsden 2007).

Relatively few studies have documented bat habitats in forests in British Columbia (BC), Canada (Parsons et al. 2003; Luszcz and Barclay 2016), and none of these studies examined the importance of beetle-killed trees or stands. We are aware of only three studies that have investigated the effect of forest pathogens on bats; the evidence is equivocal about whether bats select beetle-killed stands (Randall et al. 2011; Mehr et al. 2012; Kortmann et al. 2017). In the midst of unprecedented large-scale bark beetle outbreaks in BC (Aukema et al. 2006; Alfaro et al. 2015), and large-scale salvage-logging operations

that often follow (Dhar et al. 2016), it is critical that we understand the extent to which bats use these habitats. This need is exacerbated by the looming threat of the invasive pathogen *Pseudogymnoascus destructans*, the cause of the highly lethal white-nose syndrome, which is currently the leading cause of bat mortality in eastern North America (Gargas et al. 2009; O'Shea et al. 2016). In March 2016, white-nose syndrome was discovered in the state of Washington, United States (Lorch et al. 2016), raising serious concerns for its emergence in neighboring BC. A better understanding of which bat species are using which habitats may be beneficial to future conservation efforts if white-nose syndrome spreads into BC.

We investigated the use of beetle-killed stands by bats in the southern interior of BC. Our objectives were to 1) determine bat species richness in beetle-killed stands in this region, 2) compare the relative activity of bats in stands with light versus severe beetle-kill, and 3) investigate whether habitat attributes at the stand level were correlated with bat activity. We hypothesized that sites with higher snag densities, but more-open tree canopies, would increase shrub cover and food for bats while also enabling easier flying through more-open canopies. We expected that stands with higher beetle-kill would have more snags and more-open canopies, and we thus predicted greater bat species richness and activity in forest stands that were more severely affected by bark beetles. We expected more pronounced effects for generalist species like little brown myotis (Fenton and Barclay 1980) and big brown bats (*Eptesicus fuscus*—Kurta and Baker 1990), as these species have fewer restrictions to a particular food source or habitat types.

MATERIALS AND METHODS

Study area.—Our study took place on federally owned crown land in the Thompson-Okanagan Region in the southern interior of BC. This region is biologically diverse, with lower elevations containing some of the northernmost sagebrush steppe (*Artemisia* spp.) in North America, and higher elevations supporting dry and montane forest types. The region supports at least 14 of the province's 16 bat species (Nagorsen and Brigham 1993). We focused on montane forests composed primarily of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). These forests have been heavily impacted by industrial timber harvest, cattle ranching, and mining, and contain extensive road networks (iMap BC 2016a). Large (> 5,000 ha) wildfires occurred in the region in 2003, 2009, and 2015 (iMap BC 2016b).

We used iMap BC (2016a, 2016b, 2016c) to assess spatial data for forest stands affected by beetles, wildfires, or timber harvest (see Supplementary Data SD1). Polygons that identified beetle-killed stands were based on standardized aerial surveys conducted by the BC Ministry of Forests, Lands, and Natural Resource Operations (Resources Inventory Committee 2000; Aukema et al. 2006). The foliage of beetle-killed conifers fades to red in the year following the attack, then gray 2 years later, making recent infestations readily identifiable from the air. We selected stands of mature forest that were at least 40

ha and had not been harvested, mined, or burned. We chose sites that had been affected by bark beetle (*Dendroctonus* spp.) outbreaks within the last 10 years that resulted in either light beetle-kill (1–10% tree mortality) or severe beetle-kill ($\geq 30\%$ tree mortality). Ideally, we would have also sampled mature forest sites with no recent beetle-kill, but no such sites existed; all sites had received some beetle damage within the previous decade. In areas where multiple overlapping outbreaks had occurred, we classified stands based on the highest severity outbreak within our 10-year window. We verified forest cover and tree mortality by examining satellite imagery in Google Earth (2016), and by inspecting each stand on the ground. We selected stands that were accessible by road, and we placed bat detectors 50–100 m from the nearest road or cut block to reduce potential edge effects (Schnitzler et al. 2003). Site elevations were 1,335–1,710 m (mean 1,482 m).

Data collection.—We deployed bat acoustic recorders at 16 sites (eight with high beetle-kill, eight with low beetle-kill) from 2 August to 22 October 2016, using Song Meter SM2Bat and SM2Bat+ acoustic recorders and pole-mounted SMX-U1 ultrasonic microphones (Wildlife Acoustics, Concord, Massachusetts). Detectors were programmed to trigger at a signal to noise ratio of 15 dB, with a maximum trigger length of 15 s. Three sites were dropped from all analyses because the recorders failed to record. Within each stand, we searched for small, linear canopy openings ≥ 100 m² to increase the likelihood of obtaining bat calls with minimal clutter (Britzke et al. 2013). We also selected deployment locations < 1 km from a lake or wetland to increase the likelihood of recording bats, as bats often roost near water (Rainho and Palmeirim 2011). We positioned microphones based on the anticipated direction of bat flybys. We monitored four sites at a time (two with light beetle-kill, two with severe beetle-kill), each for a 2-week period, to ensure that data collection covered half of a lunar cycle to account for any variation in activity that might be associated with nocturnal light (Reith 1982; Hecker and Brigham 1999); we moved recorders to new sites on a full or new moon. We programmed each recorder to collect acoustic data for 2 h each after sunset and before sunrise. We recorded files in uncompressed .wav format with maximum file lengths of 15 s and a 2 s trigger window.

In 2017, we recorded habitat data from 11 of the 13 sites for which we had bat records (five low beetle-kill, six high beetle-kill), in order to relate these field data both to the provincial beetle-kill classifications and to bat passes. We were unable to sample two sites: one was clear-cut between 2016 and 2017, and one was not accessible due to poor road conditions. For the 11 remaining sites, from 17 September to 13 October 2017, we characterized the vegetation and structure of each stand using a regularly spaced grid of nine 10-m radius plots centered on the acoustic recording site; plots were separated by 30 m. We measured canopy closure from the center of each plot using a spherical densiometer. We recorded the abundance and diameter at breast height (DBH) of all live overstory trees and snags within 10 m of the center of each plot. We recorded the abundance of saplings (trees < 7.5 cm DBH) within 2 m of the center

of each plot to estimate density. GIS mapping indicated that our sites had not burned within the past 75–100 years, so most snags were the result of insect outbreaks or natural mortality. We estimated the total ground cover (to the nearest 5%) of all shrubs in each 1-m segment of a 10 m × 1 m belt transect oriented due north from the center of each plot. We counted all pieces of coarse woody debris that were > 5 cm in diameter where they intersected the belt transect.

Research followed guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Analyses.—We used Kaleidoscope Pro v. 4.5.4 (Wildlife Acoustics 2016) to auto-classify all acoustic recordings. Output was given in zero-crossing format, which isolates only the strongest signals in each recording. Although this procedure may eliminate some bat calls from the analysis, these signals are typically too faint to reliably identify to species. To classify bat calls, we also ran recordings through custom acoustic filters for characteristic call frequencies of the bats (J. Rae, Wildlife Conservation Society, BC, Canada, pers. comm.) in AnalookW (Corben 2016). We discarded all recordings that could not be identified by either classification technique, and manually verified all remaining recordings. Where possible, we identified calls to individual species. However, as bat calls in high-clutter habitats are often indistinguishable at the species level, we also grouped calls by shared acoustic characteristics into “phonic groups” (Schwab and Mabee 2014). A sequence of calls (pulses) recorded in a 15 s or shorter recording was defined as a bat pass (Loeb et al. 2015), and each pass was classified into 25 kHz bat, 30–35 kHz *Myotis*, 40 kHz *Myotis*, or 45–50 kHz *Myotis* phonic groups (Table 1).

We quantified species richness for each 14-day sampling period using only the calls that we identified to species. We calculated activity rate as the number of passes per 2-h recording period. We quantified activity rate separately for all passes combined, each of the phonic groups, and for the most detected species. We compared species richness and activity rate between low- and high-severity beetle-killed sites using Student’s *t*-tests. Habitat characteristics were compared between areas with light and high beetle-kill severities to assess if there was a difference in habitat structure. We then used linear regressions and *F*-tests to explore correlations between bat passes and stand-level habitat characteristics. We used R v. 3.3.2 (R Development Core Team 2008) and Microsoft Excel for statistical analyses.

Table 1.—Phonic group classifications used for analyzing pass rates of bat species. We individually identified passes to each of six species (indicated by *). Other passes could be classified to within a kHz category, but not to species. Here, we list the species known to occur in the Thompson-Okanagan Region by phonic group; the bats for which some passes could be confirmed to species are shown in bold. Because the 30–35 kHz group contained only one species in this region, we were able to assign all passes in this range to long-eared myotis.

25 kHz	30–35 kHz <i>Myotis</i>	40 kHz <i>Myotis</i>	45–50 kHz <i>Myotis</i>
Silver-haired bat* (<i>Lasionycteris noctivagans</i>)	Long-eared myotis* (<i>Myotis evotis</i>)	Little brown myotis* (<i>M. lucifugus</i>)	California myotis* (<i>M. californicus</i>)
Big brown bat* (<i>Eptesicus fuscus</i>)		Long-legged myotis (<i>M. volans</i>)	Yuma myotis* (<i>M. yumanensis</i>)
Hoary bat (<i>Lasiurus cinereus</i>)		Small-footed myotis (<i>M. ciliolabrum</i>)	

RESULTS

We obtained 10,145 recordings from 13 sites (seven where beetle-kill was low severity, six where it was high). Auto-classification and filtering identified 1,600 recordings as bat passes; 7,063 recordings were labeled as noise by Kaleidoscope Pro and 1,482 recordings were likely made by animals but could not be classified. Our final data set contained 1,200 recordings auto-identified as bat passes; 400 files were dropped as they were verified as insect calls instead. We were able to identify 354 passes to species, but the rest were resolved only to phonic groups (Table 2). The six species that we identified were little brown myotis, California myotis (*Myotis californicus*), Yuma myotis (*M. yumanensis*), long-eared myotis (*M. evotis*), big brown bat, and silver-haired bat (*Lasionycteris noctivagans*). Little brown myotis had the highest number of passes of any species (Table 2).

Bat species richness and activity did not differ between sites with low beetle-kill and high beetle-kill, nor was there any difference with respect to time of sampling. The mean activity rate at dawn was 2.1 ± 1.5 ($\bar{x} \pm SE$) passes per 2 h. The mean activity rate at dusk was 3.8 ± 2.4 passes per 2 h, but this difference was not significant ($t_{23} = 0.607$, $P = 0.55$). We therefore lumped these time periods (total pass rate) for subsequent analyses of bat passes in stands that had high (1.6 ± 0.7 per 2 h) or low (4.1 ± 3.7 per 2 h) beetle-kill severity; the mean total activity rate for all bats at all sites was 3.0 ± 2.1 passes per 2 h. We found no significant differences in average species richness ($t_{11} = 1.09$, $P = 0.30$) or activity ($t_{11} = -0.61$, $P = 0.55$) between sites varying in beetle-kill severity (Table 2).

Habitat characteristics of high-severity and low-severity beetle-kill sites also did not differ significantly (Table 3). Instead, sites showed high variability for most of the habitat metrics. Activity rates of bats were not significantly correlated to habitat features for all bats combined, at the phonic group level, or when analyzed separately for little brown myotis (Table 4). The only statistically significant result was that bat activity rate for the 25 kHz group increased with the amount of coarse woody debris (Fig. 1).

DISCUSSION

At least six of the 14 bat species known to occur in the southern interior of BC used forest stands that had suffered substantial beetle-kill damage within the previous decade. Although we had predicted that areas with light versus severe beetle-kill

Table 2.—Bat passes for individual species and phonic groups in high- and low-severity beetle-killed stands. Pass rate values are means \pm SEs. *T*-tests are for activity rates.

	Total passes		Activity rate (passes/2 h)		<i>t</i>	<i>P</i>
	High severity	Low severity	High severity	Low severity		
Species						
Little brown myotis	67	93	0.32 \pm 0.16	0.44 \pm 0.44	-0.24	0.82
California myotis	41	54	0.20 \pm 0.07	0.23 \pm 0.12	-0.20	0.84
Long-eared myotis	23	29	0.12 \pm 0.10	0.13 \pm 0.12	-0.06	0.95
Silver-haired bat	27	2	0.15 \pm 0.09	0.01 \pm 0.00	1.78	0.10
Big brown bat	14	1	0.08 \pm 0.08	0	1.02	0.33
Yuma myotis	2	1	0.01 \pm 0.01	0	0.69	0.50
Phonic group ^a						
25 kHz	79	15	0.43 \pm 0.27	0.07 \pm 0.05	1.44	0.18
40 kHz <i>Myotis</i>	161	763	0.82 \pm 0.33	3.59 \pm 3.34	-0.76	0.46
45–50 kHz <i>Myotis</i>	53	77	0.26 \pm 0.10	0.33 \pm 0.20	-0.31	0.76
All bats	316	884	1.63 \pm 0.71	4.11 \pm 3.69	-0.61	0.55

^aWe also had a 30–35 kHz *Myotis* phonic group, but the only species in that group was the long-eared myotis, so we show these data under species instead of phonic group.

Table 3.—Habitat characteristics for forest stands with low- and high-severity beetle-kill. Values are means \pm SEs.

Habitat attribute	High severity (six sites)	Low severity (five sites)	<i>t</i>	<i>P</i>
Canopy closure (%)	85.5 \pm 3.05	87.9 \pm 2.32	-0.61	0.56
Shrub cover (%)	9.3 \pm 1.86	17.6 \pm 6.88	-1.26	0.24
Coarse woody debris (<i>n</i> /transect)	8.4 \pm 2.50	5.8 \pm 1.33	0.87	0.41
Sapling density (<i>n</i> /ha)	8,081.2 \pm 4,211.9	8,824.3 \pm 3,208.0	-0.14	0.90
Tree basal area (m ² /ha)	28.9 \pm 4.37	33.6 \pm 4.27	-0.77	0.46
Snag basal area (m ² /ha)	12.0 \pm 2.79	14.5 \pm 4.07	-0.50	0.63

would vary in snag density and canopy closure, the stands were statistically similar and displayed high variability that was not explained by the aerially classified beetle-kill damage. Similarly, we had predicted stands with low versus high beetle-kill would differ in bat species richness and activity, but they did not; all six species we identified used both kinds of stand and activity rates did not differ between stands. When we analyzed all bat passes together, including those that we could resolve only to phonic group, we still found no activity differences between areas with light versus high beetle-kill. Finally, although we examined a number of habitat features within each stand, only one correlated with bat activity (coarse woody debris and calls by 25 kHz phonic group bats), and that relationship was potentially driven by one outlier site. Collectively, these results suggest that bats use a wide range of beetle-killed forest stands and that the severity of the tree die-offs due to beetle infestation may not directly affect bat presence or activity. Our overarching hypothesis that beetle-kill influenced habitat quality for bats was thus not supported.

Activity rates of bats were quite low, in line with Grindal et al. (1999) who reported < 10 bat passes per hour at high-elevation (1,400–1,800 m) sites in southern BC, in contrast to mid- (1,000–1,400 m) and low-elevation riparian sites that had > 100 bat passes per hour. Our study sites were montane upland forests between 1,335 and 1,710 m elevation (mean 1,482 m; only two sites were below 1,400 m). Because bat activity is generally highest at low-elevation riparian corridors (Grindal et al. 1999), we anticipated low bat activity. Activity rates of bats in

forests vary widely, however, and our rates are still higher than those reported in other forested areas of North America such as in New Hampshire and Maine where Krusic et al. (1996) sampled softwood and hardwood forest stands ranging in age from 10 to 120 years, finding fewer than 5 passes per night. Similarly, low activity rates of bats have been reported in Alaskan old growth rainforests (6 passes/night—Parker et al. 1996) and intact boreal forests of north-central Alberta (1–2 passes/hour—Patriquin and Barclay 2003).

Further, other studies have reported a bimodal distribution of bat activity where the peak feeding activity occurs near sunset, with a smaller second peak in activity occurring before sunrise as bats return to their roost sites before daybreak (Hayes and Gruver 2000). In contrast, we found no difference in bat activity between sunset and sunrise, which suggests that bats in our study area might have foraged similarly at sunrise and sunset, or that bats were roosting in these stands and did not return to roost until close to sunrise. To extend our sampling duration (i.e., total nights in the field), we recorded bat activity only near sunset and sunrise. Thus, we cannot determine to what extent bats remained in these stands during the night to forage, nor can we be certain if bats roosted in these stands. One possible explanation for why bats were just as active near sunrise as sunset is that insect abundance may not have been high enough to satiate bats at dusk, especially since our fall surveys and moderately high elevation sites exposed bats and insects to low ambient temperatures (mean 7 \pm 0.23°C at 30 min after sunset for seven of our sites); insect activity may be reduced

Table 4.—Correlations between habitat characteristics and bat activity rates. For phonic groups, the data include all bat species with passes within that range, both calls we could identify to species and calls that we could identify only to that phonic group. The 30–35 kHz group included only long-eared myotis; we also show little brown myotis separately because we had a high number of passes for them.

Habitat characteristic	$F_{1,9}$	Adjusted R^2	P
Total pass rate, all bats			
Canopy closure	0.06	−0.10	0.80
Shrub cover	0.55	−0.05	0.48
Coarse woody debris	0.02	−0.11	0.90
Sapling density	0.95	−0.01	0.36
Tree basal area	0.04	−0.11	0.85
Snag basal area	1.60	0.06	0.24
25 kHz pass rate			
Canopy closure	0.32	−0.07	0.59
Shrub cover	1.90	0.08	0.20
Coarse woody debris	18.55	0.64	0.00
Sapling density	0.82	−0.02	0.39
Tree basal area	0.04	−0.11	0.85
Snag basal area	0.66	−0.04	0.44
30–35 kHz <i>Myotis</i> pass rate (long-eared myotis)			
Canopy closure	0.00	−0.11	0.99
Shrub cover	1.30	0.03	0.28
Coarse woody debris	1.96	0.09	0.19
Sapling density	0.87	−0.01	0.38
Tree basal area	0.01	−0.11	0.94
Snag basal area	4.05	0.23	0.08
Little brown myotis pass rate			
Canopy closure	0.11	−0.10	0.75
Shrub cover	0.78	−0.02	0.40
Coarse woody debris	0.00	−0.11	0.99
Sapling density	0.96	0.00	0.35
Tree basal area	0.26	−0.08	0.62
Snag basal area	1.06	0.01	0.33
40 kHz <i>Myotis</i> pass rate			
Canopy closure	0.04	−0.11	0.84
Shrub cover	0.36	−0.07	0.57
Coarse woody debris	0.02	−0.11	0.90
Sapling density	0.79	−0.02	0.40
Tree basal area	0.04	−0.11	0.85
Snag basal area	1.39	0.04	0.27
45–50 kHz <i>Myotis</i> pass rate			
Canopy closure	0.27	−0.08	0.62
Shrub cover	1.60	0.06	0.24
Coarse woody debris	0.46	−0.06	0.52
Sapling density	1.52	0.05	0.25
Tree basal area	0.21	−0.09	0.65
Snag basal area	1.26	0.03	0.29

at lower temperatures (Mellanby 1939). It is also possible that bats foraged outside of the stands and could have night-roosted or continued to forage throughout the night before returning to their roosts at sunrise, if, in fact, our recordings indicated bats emerging and returning to roosts.

We suspect that the forest habitats we sampled may not be as supportive for foraging bats as are lower-elevation sites or sites nearer to standing water. Cooler, higher-elevation roost sites typically support male bats that are solitary and use torpor more often than gregarious females, which seek warmer and lower-elevation roosts (Grindal et al. 1999). Further, our surveys were conducted in fall, so it is possible that seasonal preferences or migration affected the species we detected or the call rates sampled. For example, we might not have detected hoary bats (*Lasiurus cinereus*) due to the limited overlap between our sampling time and their migratory patterns (Cryan 2003);

alternatively, hoary bats prefer deciduous trees for roosting (McClure 1942; Crampton and Barclay 1998) and our study area consisted primarily of conifer trees.

The diversity of bat species at our sites was low. In these forests, there were numerous candidate roost trees available (i.e., with sloughed bark or crevices); however, the habitat was at relatively high elevation, lacked substantial rock crevices, and water was scarcer than in the valley bottoms. These features perhaps reduced the likelihood of detecting some of the other species found in the Thompson-Okanagan Region. For example, we rarely detected Yuma myotis, but previous work in the Thompson-Okanagan found this species primarily in open habitats near water where insect abundance is high (Brigham et al. 1992). Similarly, western small-footed myotis (*Myotis ciliolabrum*) are generally found in dry valleys where they roost in rock crevices or under the loose bark of pines (Holloway and

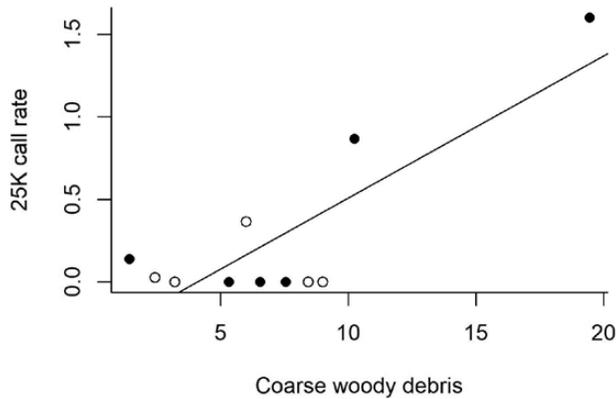


Fig. 1.—Activity rate (passes/2 h) by 25 kHz bats as a function of coarse woody debris (pieces/10 m transect). Black circles (●): high-severity beetle-kill sites; white circles (○): low-severity beetle-kill sites. The line is $y = -0.35 + 0.086x$.

Barclay 2001), habitats that we did not sample. In contrast, we detected silver-haired bats in our study. This species roosts in a range of sites that would be facilitated by bark-beetle damage including woodpecker cavities, crevices, and under bark (Perkins and Cross 1988; Vonhof and Barclay 1996).

Coarse woody debris was the only habitat variable that was correlated with bat activity, and then for only the 25 kHz phonic group, which largely consists of silver-haired and big brown bats. Coarse woody debris supports the life cycles of various insects, including bark beetles (Brown 2000). We measured coarse woody debris and shrubs as potential habitat features that could lead to increased prey abundance. Despite the one correlation (influenced by an outlier), the dominant picture that emerged is that neither shrubs nor coarse woody debris were significant predictors of bat activity, and more work would be needed to see if this one relationship between debris and 25 kHz bats holds elsewhere, as well as to explore our suspected link between debris and insect prey abundance.

We expected sites with high-severity beetle-kill to have greater bat species richness and activity due to increased snag density (Fenton et al. 1994; Kunz and Lumsden 2007) and decreased canopy cover (Brigham et al. 1997; Kortmann et al. 2017), but instead we found no differences. We had selected low and high beetle-killed sites based on annual flights with beetle-kill severity characterized by the onset of beetle outbreaks (i.e., red attack stage). This aerial mapping of beetle-kill severity did not translate to variation in fine-scale vegetation that we measured on site; there were no statistically significant differences in vegetation characteristics between high and low beetle-kill severity, but there was high site variability. This result is similar to work in Oregon that showed that aerial imagery of insect damage correlated poorly with several ground-sampled characteristics (Meigs et al. 2011). These results probably arise because trees also die of other causes, the aerial classifications of beetle-kill are binned into coarse categories, and subcanopy trees could grow quickly after deaths of taller neighbors.

Spun more positively, this lack of a difference in bat activity between high beetle-kill and low beetle-kill areas indicates

beetle-kill severity alone is probably not a major driver of bat presence or activity; other habitat features, such as presence of preferred roost trees (Vonhof and Barclay 1996) or high prey densities (Grindal and Brigham 1999), are likely more explanatory.

Our research contributes to the understanding of habitat use by bat species in montane western coniferous forests experiencing tree dieback. Of particular interest for conservation, the most commonly detected species in our study, the little brown myotis, is federally listed as Endangered (Government of Canada 2017). The little brown myotis has experienced drastic declines in the eastern portion of its range due to white-nose syndrome (Government of Canada 2015), but the species is typically abundant in areas where white-nose syndrome is absent (Government of Canada 2015). However, in 2016, white-nose syndrome was detected in northern Washington, ~320 km from our study area (Lorch et al. 2016). Given the fast rates of spread observed in eastern North America, it is likely that BC bats will experience this disease soon. In that context, it is important to retain known and potential roost sites during land management operations to ensure that forested sites remain suitable for bats. For the little brown myotis, the destruction of roosts and foraging habitat is listed as a threat in its Recovery Strategy (Government of Canada 2015). Our results show that bat populations in BC use beetle-killed forests similarly to rates of use in other high-elevation sites (Grindal et al. 1999) and maintaining these habitats may be important to ensure sufficient roosting and foraging habitat remains for high-elevation bat populations as disease emergence and habitat loss continue to be looming threats.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—GIS layers used to select study areas.

LITERATURE CITED

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