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Influence of forest composition and age on habitat use by bats in southwestern British Columbia.

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Luszcz, T.M.J. and Barclay, R.M.R. Influence of forest composition and age on habitat use by bats in southwestern British Columbia.

ABSTRACT

Habitat use by bats in forests varies with environmental variables, clutter and prey availability, but few studies have looked at habitat use as a function of forest composition and forest age across a range of elevations. We examined factors influencing habitat use of forest-dwelling bats in southwestern British Columbia using ultrasonic detection. We measured activity of three bat foraging-guilds in four forest types and three age classes from May to August 2000 and 2001. Habitat use varied with forest composition and stand age, but not always as we predicted. Activity of open-habitat foragers (large bats) was greatest in higher elevation forests and in young forests. In contrast, activity of the gleaner *Myotis evotis* (H. Allen, 1864) was greater in lower elevation black cottonwood (*Populus balsamifera trichocarpa* (Torr. & A. Gray) Brayshaw) and cedar-hemlock stands. *M. evotis* activity also increased with increasing forest age. Activity of edge and gap insectivores (*Myotis* Kaup, 1829) was greater in black cottonwood stands and old IDF stands than in other forest types. The probability of detecting foraging *Myotis* was highest in black cottonwood stands. *Myotis* activity did not show a clear pattern with forest age. Our results demonstrate the importance of black cottonwood riparian forests to foraging *Myotis* bats, as well as the importance of older, low-elevation forests.

Keywords: bats, *Myotis*, habitat use, foraging, echolocation, forest composition, forest age, black cottonwood, elevation.

INTRODUCTION

Understanding how bats are influenced or constrained by their environment at multiple scales helps to predict their distribution and habitat use. For example, at the landscape scale, increased elevation, as with latitude, is often associated with a decrease in bat diversity and activity (Grindal et al. 1999; Willig et al. 2003; Linden et al. 2014), likely because of lower temperatures and insect biomass (McCain 2007; Stevens 2013; Wolbert et al. 2014). Some species occur over a wide range of elevations (e.g. the Long-eared Myotis, *Myotis evotis* (H. Allen, 1864), and Little Brown Bat, *M. lucifugus* (Le Conte, 1831); Fenton and Barclay 1980; Manning and Jones 1989), whereas others are more restricted (e.g. Yuma Myotis, *M. yumanensis* (H. Allen, 1864); Nagorsen and Brigham 1993).

At the stand scale, the degree of habitat structure and heterogeneity of a habitat is hypothesized to be the most important environmental constraint to foraging bats (Schnitzler and Kalko 2001; Estrada-Villegas et al. 2012). When foraging, bats must avoid obstacles, and discern between echoes from prey and echoes from surrounding clutter (Fenton 1990). Clutter refers to the amount and types of obstacles to a flying bat that may also interfere with detection of echoes from a prey target. Flying through cluttered habitats requires greater manoeuvrability and agility (Norberg and Rayner 1987), as well as an echolocation-call structure that minimizes overlap of outgoing pulses and incoming echoes (Fenton 1990). Large bats with long narrow wings are fast, less manoeuvrable flyers that generally use open, uncluttered habitats (e.g. Big Brown Bat, *Eptesicus fuscus* (Palisot de Beauvois, 1796)), whereas, small bats with short broad wings are usually manoeuvrable, agile flyers that can exploit more cluttered habitats (e.g. *M.*

evotis; Norberg and Rayner 1987). Echolocation calls that sweep over a narrow frequency band are useful for long-range detection of large prey in open habitats, whereas broadband, frequency-modulated calls are suited for short-range detection of small prey in closed or more cluttered habitats (Fenton 1990). Thus, body size, wing morphology, and echolocation-call structure all play a role in determining a bat's foraging ability and access to particular habitats and prey (Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Fenton 1990; Schnitzler and Kalko 2001). Understanding how bats are constrained by morphology and echolocation is especially important in forest management. Bats with the same ecomorphological constraints often forage in similar forest habitats (Schnitzler and Kalko 2001), so it can be valuable to examine bat habitat use in forests by foraging guild (e.g. open space foragers versus edge and gap insectivores versus gleaners; Frick et al. 2009).

The amount and arrangement of clutter of a forest, and thus habitat use by bats, is influenced by factors such as tree-species composition, and stand age or structure (Thomas 1988; Krusic et al. 1996; Kalcounis et al. 1999; Jung et al. 2012). For example, deciduous forests with species such as aspen and cottonwood (*Populus* sp. L.) are different from coniferous forests in their structural heterogeneity and amount of clutter (Oliver and Larson 1990). They are often less cluttered at mid-canopy height than coniferous forests, which may partially explain the greater bat activity observed in deciduous or partially deciduous forest types (Krusic et al. 1996; Kalcounis et al. 1999). Furthermore, many deciduous species, such as black cottonwood (*Populus balsamifera trichocarpa* (Torr. & A. Gray) Brayshaw) are usually associated with water bodies, which are preferred foraging locations for many bats (Fukui et al. 2006; Swystun et al.

2007), and therefore may be a particularly attractive forest type to foraging bats. Forest age can also have a significant effect on bat habitat use, likely because of differences in amount and arrangement of clutter and roost availability (Hayes and Loeb 2007). In general, young forests are dense and relatively structurally homogeneous, often presenting larger amounts of clutter to bats. Bat activity is often greater in mature or old growth forests, likely due to a higher density of suitable roosts, combined with more structural heterogeneity, more openings, and less clutter (Thomas 1988; Crampton and Barclay 1998; Jung et al. 2012). Because climatic variables (e.g. temperature), forest composition, and forest age all affect bat habitat use, it is important to examine all of these factors together when attempting to understand bat habitat preferences in forests.

The majority of the world's bat species are associated with forests, the loss and degradation of which is a major issue (Hutson et al. 2001). In British Columbia, forests comprise 70% of the province, and almost half of them have been (or will be) logged (Austen et al. 2008). Alteration of age-class and tree species distributions, and removal of roost trees can negatively affect bat biodiversity in forests. A better understanding of what matters for bats in forests can enable land managers to manage for these biodiversity values for the long term.

Few studies have combined forest composition and age across an elevational gradient in their examination of habitat use by bat foraging guilds (but see Krusic et al. 1996; Loeb and O'Keefe 2006). The three main bat foraging guilds in forests of British Columbia are open-space foragers (large bats with lower frequency echolocation and fast, less manoeuvrable flight), edge and gap insectivores (*Myotis* species (Kaup, 1829) with high frequency calls of shorter duration and manoeuvrable flight), and gleaners with

shorter duration high frequency calls and highly manoeuvrable flight that allow them to glean insects from vegetation in cluttered or open habitats (e.g. *Myotis evotis*).

We predicted that activity of all guilds would be greater in black cottonwood stands than in coniferous forests because of black cottonwood's proximity to riparian areas and its lower stem density. Within conifer-dominated forests, we predicted the greatest large bat and *Myotis* activity would occur in warmer, lower elevation forests compared to cooler, higher elevation sites, whereas activity of the gleaning bat, *M. evotis*, should not differ as much because of their adaptability to a range of elevations and environmental conditions. Within any given forest type, we predicted that bat activity would increase with forest age because of greater structural heterogeneity, less clutter and increased roost availability. We expected that forest age would have a stronger effect on the open-space foraging guild (large bats) than on edge and gap insectivores, and that the gleaner, *M. evotis*, would be least affected by forest age, as it is able to exploit cluttered habitats. Open-space foragers should be excluded from young, dense forests, whereas small, agile species should be able to use forests of all ages and clutter profiles. We collected data using ultrasonic detection to test our predictions of habitat use by the three bat foraging guilds. Using an information theoretic approach, we developed a set of hypotheses (models) to test our predictions of habitat use and determine what set of variables are most important in predicting bat habitat use in forests in relation to forest composition and age.

MATERIALS AND METHODS

Study Area

Our study took place in the northern Skagit watershed in southwestern British Columbia within the Cascade Mountain Range. The latitudes and longitudes bounding the study area are as follows: the most westerly point (49°12'27.31" N, 121°25'27.08" W), easterly point (49°04'00.16" N, 120°42'27.05" W), northerly point (49°15'17.43" N, 121°14'36.80" W) and southerly point (49°00'01" N, 121°04'28.08" W). The elevation of the study area ranged from 460 - 1690 masl. Based on provincial range maps (Nagorsen and Brigham 1993), the local bat community consists of up to 13 species. We conducted all fieldwork in 2000 and 2001, during the period of peak bat activity from mid-May to the end of August.

We used biogeoclimatic subzones to sample different forest types. Biogeoclimatic ecosystem classification (BEC) integrates climate, soil and vegetation data (and therefore elevation) to classify the various ecosystems of British Columbia (Meidinger and Pojar 1991), and thus may be a useful way to assess variation in bat habitat use in relation to forest composition. BEC is widely used in species and ecosystem management in British Columbia. Our study area encompassed four main BEC subzones: Interior Douglas-fir wet warm (IDFww) referred to hereafter as IDF, Coastal Western Hemlock southern dry submarine variant (CWHds1), Coastal Western Hemlock southern moist submarine variant (CWHms1), and Engelmann Spruce-Subalpine Fir moist warm (ESSFmw),

referred to hereafter as ESSF (Green and Klinka 1994; Supplementary Table S1¹). We grouped the cooler CWHms1 with the warmer CWHds1 into one “ecosystem zone”, called CWH here. From within the IDF and CWH ecosystem zones, we separated deciduous black cottonwood stands into their own ecosystem zone, “Bc”. In summary, the ecosystem zones in our study were Bc, IDF, CWH, and ESSF (Supplementary Table S1).¹ The Bc ecosystem zone was comprised of riparian black cottonwood forests, which in our study, had lower large-tree densities, and thus were more open than the coniferous forests of the other ecosystem zones (Supplementary Fig. S1).¹ As a result of their lower tree densities and flat, diffuse crowns (Parish et al. 1996), these stands also had lower canopy closure than IDF or CWH forests (Supplementary Table S2).¹ They also tended to have a more dense shrub layer. Mature cottonwood stands were also taller and had a greater density of potential roost trees than mature stands of the CWH or ESSF zones (Supplementary Figs. S3, S4).¹ Black cottonwood trees are fast growing, and are inherently associated with fungal decay (Peterson et al. 1996), so these stands generally have a high density of wildlife trees, but a shorter overall lifespan. The IDF ecosystem zone dominates low to mid elevations in south-central British Columbia (Meidinger and Pojar 1991). Forests in the IDF range from open to closed canopy, and are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn ex D. Don). Mature forests of the IDF were taller than in the other coniferous ecosystem zones (Supplementary Fig. S4).¹ The CWH ecosystem zone is found at low to mid elevations on

¹ Supplementary Tables S1, S2, and S3 and Figs. S1, S2, S3 and S4 are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0167>.

steep slopes, and is on average the rainiest BEC zone in BC, although the Skagit Valley includes some of the driest portions of this zone. Forests in this zone are dominated by western hemlock, with Douglas-fir, western red cedar, and variable amounts of Amabilis fir (*Abies amabilis* Douglas ex J. Forbes). Forests in the CWH zone tend to have a deep, dense tree canopy, and a sparse shrub and herb layer (Meidinger and Pojar 1991). The ESSF zone is the uppermost forested zone in most of BC's interior, and it is predominantly in mountainous terrain (Meidinger and Pojar 1991). In our study area, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) were the dominant species in this zone. Forests of this zone tended to have slightly lower canopy closure than other coniferous zones although not significantly (Supplementary Table S2).¹

Study Design, Field Methodology and Echolocation Call Analysis

To confirm species presence and to collect reference echolocation calls, we captured bats using mistnets placed along flyways used by foraging or commuting bats in all ecosystem zones (see Luszc 2004 for details on capture methods and results). As we released bats, we recorded reference calls, tracking them with a spotlight to maintain recording contact for as long as possible. We released bats into a variety of habitats to mimic the different sizes of forest gaps encountered in our study.

Using ultrasonic detection, we measured bat habitat use in forests of three age groups from within each of the four ecosystem zones, for a total of 12 habitat types. We condensed the nine existing forest age-classes (British Columbia Ministry of Forests

2002) into three age groups: young (1 to 60 years old), mature (61 to 120 years old), and old (121 years or older) stands. Black cottonwood is fast growing and rarely exceeds 200 years old (Parish et al. 1996), so our grouping of ages for the Bc ecosystem zone differed: young (1 to 40 years old), mature (41 to 80 years old), and old (81 years old or more). Young forests may have started to self-thin, but they are typically denser than older forests, and they have few to no wildlife trees (Supplementary Fig. S2).¹ Mature forests generally have a well-developed understory of shade-tolerant trees as their main canopy matures and opens up (Meidinger 1999). They have more available wildlife trees than young stands. Old forests tend to have moderate to high structural complexity and patchy regenerating understory. They have a lower density of large and small trees, but a greater density of wildlife trees than young stands (Supplementary Fig. S2).¹ They may have an abundance of veteran trees and well-established canopy gaps with coarse woody debris.

Within the 12 habitat types, we measured bat activity in a random set of stands (polygons) chosen from British Columbia Ministry of Forests vegetation resource inventory (VRI) maps based on tree species composition, age class, stand size and accessibility (see Luszc 2004). Across two years, we sampled bat activity at 170 sites as follows Bc: Young = 15, Mature = 11, Old = 14; IDF: Young = 13, Mature = 14, Old = 12; CWH: Young = 15, Mature = 13, Old = 25; ESSF: Young = 11, Mature = 13, Old = 14. In a representative subset of stands, we quantified clutter by measuring density of small trees, large trees and potential roost trees, as well as height of the main tree canopy (Luszc 2004) using the point quarter method (Krebs 1989) (Supplementary Table S3, Figs. S1, S2, S3, S4).¹ Potential roost trees (available snags) were live or dead wildlife

trees with a component that would make a potentially suitable bat roost (e.g. cavity, crack, loose bark; Fenger et al. 2006).

Our detection systems were ANABAT II ultrasonic detectors (Titley Electronics, Ballina, N.S.W., Australia), coupled with ANABAT II delay switches and tape recorders (RadioShack, Optimus CTR-115). We put each ultrasonic detection system 1.1 m above the ground, with the microphone facing upward 30° from the horizontal. The detector faced into a natural gap within a contiguous habitat type. A minimum of two observers independently estimated percent canopy closure of the forest surrounding the gap, and the values were averaged. At each detector site, we also measured gap area (m²) and ambient air temperature 30 minutes after sunset to control for these two variables in our analysis. We tallied nightly counts of bat passes (sequences of search phase echolocation calls) as a measure of bat activity, and feeding buzzes as a measure of foraging activity. Further details of our field set-up and definitions can be found in Luszc (2004).

Over two years, we captured eight species of bats for reference calls (Townsend's Big-eared Bat, *Corynorhinus townsendii* (Cooper, 1837), *E. fuscus*, Silver-haired Bat, *Lasionycteris noctivagans* (Le Conte, 1831), California Myotis, *M. californicus* (Audubon and Bachman, 1842), *M. lucifugus*, Long-legged Myotis, *M. volans* (H. Allen, 1866), *M. evotis*, and *M. yumanensis*. We supplemented our reference call library with calls from other bat research in BC. After converting echolocation calls to computer files, we used ANALOOK software to purge call sequences of extraneous noise (*i.e.* pixels) and to measure call morphology (Luszc 2004).

Data Analysis

For echolocation call analysis, we used SAS statistical software (SAS v. 8.01, SAS Institute Inc., 2000). Prior to identifying passes of unknown bats to species or species group using their echolocation call characteristics, we averaged measurements from calls within a pass to obtain one data point per pass, thereby avoiding pseudoreplication (Hurlbert 1984). We used call duration, minimum frequency, maximum frequency and mean frequency to identify passes to species or species groups. Definitions of these attributes measured by ANALOOK software are from Corben and O'Farrell (1999). Based on preliminary analysis (Luszczyński 2004), we used quadratic discriminant function analysis (DFA; PROC DISCRIM; SAS Institute Inc. 1989) to classify echolocation passes to species or species group using three to four measurements of call morphology as predictors of species' membership. We performed DFA in two stages. First, large bats were distinguished from *Myotis* species using duration, minimum frequency, maximum frequency and mean frequency (Luszczyński 2004). Then, we conducted a separate DFA for the *Myotis* species group to separate *M. evotis*. For each pass, DFA produced a probability of group membership for each of the species being considered. We assigned each unknown pass to the species with the highest probability, using jack-knifed classifications, which used all bats in the identification of each individual except the one being identified (Luszczyński 2004). This technique provides a more conservative classification estimate, and it cross-validates the results (Tabachnick and Fidell 2001). All 278 reference calls were correctly classified in the first DFA separating large bats from *Myotis* species. In the DFA for large bats, 85.7% of *C. townsendii* reference calls were correctly classified (Luszczyński 2004). In the DFA for *Myotis*, 95% of *M. evotis*

reference calls were correctly classified, mainly based on the first discriminant function, which accounted for 93% of the variation among species (Luszczyński 2004). Minimum frequency was the most important variable in the first discriminant function. We used the same quadratic DFA's to identify unknown passes to species in our ultrasonic detection data. Only complete data and known species or species groups were retained for the analysis of bat habitat use. Passes for *C. townsendii* were removed from further analysis because this species forages differently than other large bat species, and there were too few passes to analyze them separately. The large bat foraging guild consisted of three species (*E. fuscus*, *L. noctivagans*, and Hoary Bat, *Lasiurus cinereus* (Palisot de Beauvois, 1796), as well as unknown large bats). The *Myotis* foraging guild consisted of four species (*M. californicus*, *M. yumanensis*, *M. lucifugus* and *M. volans*, as well as unknown *Myotis*). We felt justified in adding unknown *Myotis* to this group because calls from our gleaning guild (represented solely by *M. evotis*) made up such a small proportion of the overall dataset.

We used the R Programming Environment with the *pscl* library and the *zeroinfl* function (R Core Team 2013) to analyze acoustic data, which involved two stages. We conducted initial analysis using tabular and graphical displays of the data to visualize patterns. We then developed a set of models using an information theoretic approach to test which biological hypotheses have the most support to describe patterns of bat activity. Our data contained a large number of zeros due to nights with no recorded bat activity and as a consequence, the number of bat passes was not normally distributed and could not be transformed to normality (Heilbron 2007). Thus, we modelled the number of counts using a zero-inflated Poisson regression model with two components (Lambert

1992). One component modelled whether bats were present or absent (zero versus non-zero counts). R software `zeroinfl` function actually models probability of absence in the occupancy component. The other component modelled bat activity (passes per hour, or pass rate). An offset term was used to account for night length and passrate was log-transformed. Our covariates were year, ecosystem zone, stand age group, canopy closure, ambient temperature and gap area. To normalize their distributions, percent canopy closure was arcsine square-root transformed, and gap area was log transformed. Elevation was not included as a covariate in the model as it is highly correlated with ecosystem zone, as evidenced from a scatter plot of the two variables. We chose to use ecosystem zone because it incorporates other variables such as climate and vegetation type, in addition to elevation. Using Akaike's Information Criterion for small sample sizes (AIC_c) to determine which combination of variables best predicted habitat use by bats, thirteen models (hypotheses) were fitted to bat activity for each of the three foraging guilds based on biological relevance and predictions. We controlled for temperature and gap area in all models, so they were included in both components. Exploratory analysis revealed no effect of the covariates of interest on bat occupancy, so we were validated in examining effects on bat activity only. We considered models with $\Delta AIC_c < 2$ to be well supported, but we also follow the principles of parsimony (Burnham and Anderson 2002). We analyzed foraging data using logistic regression for *Myotis* species (except *M. evotis*) because only 19% of nights had recorded foraging activity, and we had insufficient foraging data to examine foraging patterns of large bats or *M. evotis*. For all statistical tests, we used an alpha level of 0.05.

RESULTS

In 2000, we detected 1207 passes and 28 foraging buzzes in 518 detector-hours of sampling (2.33 passes per hour; 0.054 buzzes per hour), and in 2001, 2228 passes and 77 buzzes were detected in 942 detector-hours of sampling (2.36 passes per hour; 0.082 buzzes per hour). Less than 4% of echolocation calls were identified to species based on a probability ≤ 0.5 . Of 3435 passes, 7.8% were species of large bats and 92.2% were *Myotis*. Of the overall total, 8.5% of passes were identified as *M. evotis*, 44.3% were other *Myotis*, and 39.4% could only be identified as unknown *Myotis* because the calls were too fragmented to be identified to species.

The three best approximating models (with $\Delta AIC_c < 2$) for activity of large bats all included ecosystem zone, forest age, as well as temperature and gap area, which we controlled for in all models (Table 1). Large bat activity was significantly greater in the ESSF zone than in Bc stands (Table 2). Large bat activity (number of passes per hour) was almost two times higher in the ESSF (95% CI: $1.03 < \mu < 2.80$) than in the Bc ecosystem zone (Figure 1). Large bat activity in mature stands was half that (95% CI: $0.29 < \mu < 0.76$) recorded in young stands, and in old stands, it was one-quarter (95% CI: $0.14 < \mu < 0.41$) that in young stands (Figure 1). Model 6 contained the additional variable 'year', although there was no significant difference in large bat activity between years in the model (coefficient estimate: 0.16 and 95% CI: $-0.23 < \mu < 0.55$). The presence of canopy closure in Model 4 (coefficient estimate: -4.53 and 95% CI: $-15.55 < \mu < 6.50$) resulted in the ESSF no longer having significantly greater large bat activity than the Bc zone (coefficient estimate: 0.42 and 95% CI: $-0.14 < \mu < 0.99$). We followed

principles of parsimony and chose the best model with the fewest variables (Burnham and Anderson 2002).

For *M. evotis* activity, two models (6 and 3) were well supported, with $\Delta AIC_c < 2$ (Table 1). Model 3 was a more complex model with an additional variable (canopy closure), which did not add to (coefficient estimate: -3.27 and 95% CI: $-10.61 < \mu < 4.07$) or change anything in the model. We again chose the simpler model, which included year, ecosystem zone and age, as well as temperature and gap area (Table 2). *M. evotis* activity was almost 1.5 times higher (95% CI: $1.09 < \mu < 1.99$) in 2001 than in 2000 (Figure 2). *M. evotis* activity was significantly greater in Bc and CWH than in IDF or ESSF ecosystem zones (Table 2). *M. evotis* activity (mean passes per hour) in the IDF was one-third (95% CI: $0.24 < \mu < 0.53$) that of *M. evotis* activity in the Bc zone, and activity in the ESSF was just over one-third (95% CI: $0.25 < \mu < 0.61$) that of activity in the Bc (Figure 2). *M. evotis* activity in the CWH (coefficient estimate: -0.16 and 95% CI: $-0.45 < \mu < 0.14$) was not different from that of Bc (Figure 2). *M. evotis* activity in mature forests was more than double (95% CI: $1.3 < \mu < 3.5$) that in young forests, and three times greater (95% CI: $1.9 < \mu < 5.1$) in old forests than in young forests.

The best approximating model for *Myotis* species was the most complex model, including year, canopy closure, ecosystem zone, age, and an interaction between ecosystem zone and age (Table 1). *Myotis* activity decreased significantly with increasing stand canopy closure (Table 3). The effect of stand age on *Myotis* activity differed among ecosystem zones, and because year was a part of the model, we present the results of the interaction by year (Figure 3). *Myotis* activity was greater in 2000 than in 2001 (Table 3). Overall, *Myotis* activity was greatest in the Bc and IDF zones and lowest in the CWH and

ESSF (Figure 3). Activity increased with forest age only in the CWH zone and in old IDF stands (Figure 3). *Myotis* activity in the Bc and ESSF zones did not differ with forest age.

The probability of detecting *Myotis* feeding buzzes varied significantly with ecosystem zone (likelihood ratio test = 11.06, $df = 3$, $p = 0.01$) and was significantly higher in black cottonwood than in any other ecosystem zone (Figure 4). The probability of detecting foraging *Myotis* in IDF or CWH was one-quarter (95% CI: IDF: $0.09 < \mu < 0.85$, CWH: $0.08 < \mu < 0.79$) of what it was in Bc and one-twelfth in the ESSF (95% CI: $0.02 < \mu < 0.54$). The probability of detecting foraging *Myotis* also increased significantly with increasing gap area. The probability of detecting foraging *Myotis* did not vary with forest age (likelihood ratio test = 3.37, $df = 2$, $p = 0.19$) nor stand canopy closure (likelihood ratio test = 0.32, $df = 1$, $p = 0.58$).

For activity of both large bats and *M. evotis*, there was a significant positive relationship with temperature. Unexpectedly, the relationship was slightly negative for *Myotis* activity and occupancy. Activity of large bats and both activity and occupancy of *Myotis* significantly increased with increasing gap area. There was no relationship between *M. evotis* activity and gap area; however occupancy of *M. evotis* increased with an increase in gap area.

DISCUSSION

In summary, habitat use by bats in the northern Skagit watershed varied with forest composition and forest age; however, not all patterns were as we predicted.

Ecosystem zone, forest age, temperature, and gap area were important variables in explaining activity of all three guilds (large bats, *M. evotis* and other *Myotis*). Overall, large bat activity was greater in the cooler, higher elevation ESSF than in Bc stands. In contrast, *M. evotis* activity was greater in black cottonwood and CWH stands. Large bat activity was greater in young stands, whereas *M. evotis* activity was greater in mature and old forests. The effect of forest age on *Myotis* activity varied with ecosystem zone. Overall, *Myotis* activity was greater in black cottonwood and IDF stands, and generally lower in CWH and the ESSF. *Myotis* activity was highest in old IDF stands, and in the CWH zone, activity increased with forest age, whereas no effect of forest age was observed in the Bc and ESSF. The probability of detecting foraging *Myotis* was greatest in black cottonwood stands.

Ecosystem zone, forest age, temperature and gap area were the most important variables explaining large bat activity. It is unclear to us why one of the well-supported models included year. We would have expected canopy closure to be a significant variable explaining large bat activity because large bats should be excluded from forests with high canopy closure, but it was not. In addition, contrary to our predictions, activity of large bats was greater in the higher elevation ESSF ecosystem zone than in the lower elevation Bc zone. These differences are unlikely due to different roost availability because in our study area, the density of available roost trees did not differ across ecosystem zone (Supplementary Fig. S1¹), although bat roost preferences may differ from our definition of available roosts. It could also be that preferred prey availability was greater in the ESSF zone, or perhaps the higher activity represents males of large bat species at higher elevations, as has been found in other studies (Grindal et al. 1999;

Cryan et al. 2000). In summer, males spend more time in torpor than reproductive females do, and this could be facilitated by occupying cooler sites at higher elevations (Altringham 1998). The greater activity of large bats in younger forests compared to mature or old forests was also unexpected because younger, denser forests should be unavailable to larger, less manoeuvrable bats (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). In our study, activity of large bats did increase with gap size. Thus, we suggest that we detected the echolocation calls of large bats flying at or above canopy level in the relatively short young forests, whereas we were less able to detect canopy-level bats in older (taller) forests. Other studies have reported greater activity of species of large bats at or above the tree canopy than below it (Kalcounis et al. 1999; Menzel et al. 2005; Muller et al. 2013).

The best approximating model for *M. evotis* activity included year, ecosystem zone, age, temperature, and gap area. It is unclear why *M. evotis* activity was significantly greater in 2001 than in 2000, as there were no significant differences in monthly temperature or precipitation across the two years. Activity of *M. evotis* was significantly greater in Bc and CWH stands than in IDF and ESSF zones. We did not expect this difference because *M. evotis* occupies a range of elevations (Manning and Jones 1989). *M. evotis* in western Oregon frequently foraged in riparian habitats (Waldien and Hayes 2001), and roosts have most often been located in upslope habitats in coniferous trees (or stumps) and rock features (Vonhof and Barclay 1997; Waldien et al. 2000; Nixon et al. 2009). Thus, it is possible that *M. evotis* roosted in the CWH and commuted to black cottonwood stands to forage. The greater activity of *M. evotis* in mature and old forests suggests age suggests that perhaps they were roosting, in addition

to foraging, in these stands. *M. evotis* is a clutter-adapted species that should be able to exploit forests of any age and clutter profile, and foraging near the roost would reduce commuting time. Small home ranges for *M. evotis* have been reported elsewhere (Nixon et al. 2009). The second best model for *M. evotis* also included canopy closure, which was surprising for a clutter-adapted forager, although the ability to manoeuvre in tight spaces does not prevent them from using a more open habitat (Fenton 1990). The lack of an observed effect of canopy closure on the activity of *M. evotis* might be an indication of their ability to deal with a variety of clutter profiles.

Variation in activity of *Myotis* species (excluding *M. evotis*) was best explained by the model that included all variables of interest, as well as an interaction between ecosystem zone and forest age. Our prediction of increasing *Myotis* activity with forest age was only observed in the CWH ecosystem zone. It is unclear why this trend was not observed in ESSF stands, but in Bc stands, the structural attributes of black cottonwood (Supplementary Table S2, Fig. S1)¹, regardless of their age may explain why there was no effect of stand age in these forest types. *Myotis* activity was especially high in old IDF stands. Older forests provide more roosting opportunities for bats because they generally contain a greater density of preferred roost types (Crampton and Barclay 1998; Waldien et al. 2000). Despite not being observed across all ecosystem zones, our results lend some support to our predictions (and others findings, e.g. Thomas 1988; Crampton and Barclay 1998) that old forests, especially lower elevation ones, are important to bats. Overall activity of *Myotis* species tended to be greater in cottonwood stands and IDF than CWH or ESSF stands. A lower density of large trees, lower canopy closure (Supplementary Table S2, Fig. S1)¹, a common association with water (Peterson et al. 1996), and high

emerging adult aquatic insect abundances (Fukui et al. 2006), all likely contribute to making cottonwood stands excellent foraging habitat for bats. Our results confirmed that *Myotis* were more likely to forage in black cottonwood than in other forest types, and similar results have been found for other riparian forests (e.g. Fukui et al. 2006). *Myotis* species may also be using mature and old cottonwood stands for roosting. In our study area and elsewhere, there was a higher density of snags in mature cottonwood stands than in young or old ones (Supplementary Fig. S3¹; Swystun et al. 2007). The old IDF stands in our study were probably also important roosting habitat for *Myotis*, as suggested by Thomas (1988) who found higher bat activity in old-growth Douglas-fir forests. The warmer, lower elevation forests of the Bc and IDF zones appear to be more important than the ESSF to *Myotis*. The higher activity may represent mostly females reproducing in drier, warmer low elevation habitats (Thomas 1988; Barclay 1991; Cryan et al. 2000) in closer proximity to water and thus greater concentrations of emerging adult aquatic insects, which are common prey for bats. Cottonwood forests tend to have lower canopy closure than coniferous forests (Supplementary Table S1)¹, as do old forests compared to younger, more cluttered forests. It is thus not surprising that *Myotis* activity was also influenced by stand canopy closure, decreasing as canopy closure increased.

Although we recorded relatively little foraging, our study demonstrates the importance of black cottonwood stands to foraging *Myotis*. The fact that the probability of detecting *Myotis* feeding buzzes did not vary with forest age suggests that although mature and old forests contain roosting opportunities, the majority of *Myotis* may be commuting elsewhere to forage (e.g. water bodies, trails and black cottonwood stands).

Fluctuations in insect availability, which we did not measure, also affect bat distribution and habitat use temporally, seasonally and geographically (Barclay 1991; Stevens 2013).

Nightly temperature affects insect activity, and therefore bat foraging activity (e.g. Muller et al. 2013; Wolbert et al. 2014). Activity of both large bats and *M. evotis* increased with increasing ambient temperature. It is unclear why we observed the opposite relationship for *Myotis*. Large bat and *Myotis* activity did increase with increasing gap area, whereas for *M. evotis*, gap area was not a significant influence. Larger openings are less cluttered and have more edge, which is preferred foraging habitat for many *Myotis*, such as *M. lucifugus* (Patriquin and Barclay 2003), and likely less important for the clutter-adapted *M. evotis*. These results further illustrate the importance of controlling for these variables in studies of habitat use by bats.

In summary, we found some support for our predictions regarding variation in activity of the three bat guilds. Large bat activity was higher in the cooler, higher-elevation ESSF zone. In our study area, ESSF (and CWH) stands were shorter than Bc and IDF stands (Supplementary Fig. S4¹), so we may have detected these bats foraging at or above tree canopy height, just as we suggest was the case in young stands where large bat activity was also greater. Measuring activity at different heights would clarify where large bats concentrate their activity (e.g. Menzel et al. 2005; Muller et al. 2013). In contrast to large bats, *Myotis* species were more likely to forage in black cottonwood stands than in any other ecosystem zone, and *M. evotis* used both black cottonwood and CWH more than other ecosystem zones. Cottonwood forests are likely important foraging habitat for bats because they have high insect densities associated with riparian areas

(Fukui et al. 2006), and a more open structure (Supplementary Table S2¹, Fig. S1¹; Peterson et al. 1996; Farid et al. 2006). It is possible that *Myotis* may also roost in black cottonwood stands, particularly mature ones, as they have a high density of available potential roost trees (Supplementary Fig. S3).¹ Although large bat activity did not follow our predictions regarding the effect of forest age, and the relationship of *Myotis* activity with forest age was variable, our results suggest that mature and old forests, especially at lower elevations, are important habitat for *Myotis* spp. and *M. evotis*, as has been found elsewhere (Thomas 1988). Roost tree availability aside, the age of a stand may not be as important to bats as its structure is (Hayes and Loeb 2007). Vegetation structure is thought to be one of the greatest influences on bat distribution and activity at the stand level (Estrada-Villegas 2012). Cottonwood stands attain maturity at a much younger age than coniferous stands (Parish et al. 1996), and similarly-aged coniferous stands can vary in their structural stage depending on their site quality, disturbance history and vegetation type (Meidinger 1999). In hindsight, measuring bat activity in relation to stand structural stage (instead of forest age) may have resulted in clearer patterns of habitat use by bats in the Skagit watershed.

Our results suggest that older forests especially at low elevations, and low elevation riparian forests, are important for bats, yet these habitats are increasingly in short supply. Most logging in British Columbia occurs in low-elevation valleys or slopes, and the interior of the province has more young forest than mature or old forest, likely due to forest fires and logging (Austen et al. 2008). To retain bat populations and their ecological services, forest management should aim to maintain the amount of low elevation forest, especially riparian stands, as well as old forests.

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LITERATURE CITED

Aldridge, H.D.J.N., and Rautenbach, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* 56:763-778.

- Altringham, J.D. 1998. Bats: biology and behaviour. Oxford University Press, New York.
- Austin, M.A., D.A. Buffett, D.J. Nicolson, G.G.E. Scudder, and V. Stevens (*Editors*). 2008. Taking Nature's Pulse: The Status of Biodiversity in British Columbia. Biodiversity BC, Victoria, B.C. Available from: www.biodiversitybc.org [Accessed 3 May 2015].
- Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Anim. Ecol.* 60:165-178.
- Barclay, R.M.R. 1999. Bats are not birds - a cautionary note on using echolocation calls to identify bats: a comment. *J. Mammal.* 80:290-296.
- Barclay, R.M.R., and Brigham, R.M. 2004. Geographic variation in the echolocation calls of bats: A complication for identifying species by their calls. *In* Proceedings of the Symposium on Bat Echolocation Research: tools, techniques and analysis. *Edited by* R. M. Brigham, E.K.V. Kalko, G. Jones, S. Parsons, and H.J.G.A. Limpens. Bat Conservation International. Austin, TX. pp. 144-149.
- Brigham, R.M, Grindal, S.D., Firman, M.C., and Morissette, J.L. 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Can. J. Zool.* 75:131-136.
- British Columbia Ministry of Forests. 2002. Relational Data Dictionary 2.0a for Forest Inventory Planning. Ministry of Forests, Victoria, B.C.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York.
- Corben, C., and O'Farrell, M. J. 1999. Techniques for the effective use of Anabat in identifying free-flying bat species. Anabat System Manual, published by the authors.

- Crampton, L.H., and Barclay R.M.R. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conserv. Biol.* 12:1347-1358.
- Cryan, P.M., Bogan, M.A., and Altenbach, J.S. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *J. Mammal.* 81:719-725.
- Estrada-Villegas, S., McGill, B., and Kalko, E.K.V. 2012. Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. *Ecology*, 93:1183-1193.
- Farid, A. 2006. Using airborne lidar to discern age classes of cottonwood trees in a riparian area. *West. J. Appl. For.* 21:149-158.
- Fenger, M., Manning, T., Cooper, J., Guy, S., and Bradford P. 2006. Wildlife and trees in British Columbia. B.C. Lone Pine Publishing. Vancouver, B.C.
- Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* 68:411-422.
- Fenton, M.B., and Barclay, R.M.R. 1980. *Myotis lucifugus*. *Mamm. Species*, 142:1-8.
- Ford, W.M., Menzel, M.A., Rodrigue, J.L., Menzel, J.M., and Johnson, J.B. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biol. Conserv.* 126:528-539.
- Frick, W.F., Hayes, J.P., and Heady III, P.A. 2009. Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes. *Oecologia*, 158:687-697.
- Fukui, D., Murakami, M., Nakano, S., and Aoi, T. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *J. Anim. Ecol.* 75:1252-1258.

- Green, R.N., and Klinka, K. 1994. A field guide to site identification and interpretation for the Vancouver forest region. British Columbia Ministry of Forests, Victoria, B.C.
- Grindal, S.D., Morissette J.L., and Brigham, R.M. 1999. Concentration of bat activity in riparian habitats over an elevation gradient. *Can. J. of Zool.* 77:972-977.
- Hayes, J.P., and Loeb, S.C. 2007. The influences of forest management on bats in North America. *In* Bats in forests: conservation and management. *Edited by* M.J. Lacki, J.P. Hayes, and A. Kurta. John Hopkins University Press, Baltimore, Maryland. pp. 207-235.
- Heilbron, D. 2007. Zero-altered and other regression models for count data with added zeros. *Biometrical J.* 36:531-547.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Hutson, A.M., Mickleburgh, S.P., and Racey P.A. 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group., IUCN, Gland, Switzerland and Cambridge, UK.
- Jung, K., Kaiser, S., Bohm, S., Nieschulze, J., and Kalko, E.K.V. 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J. Appl. Ecol.* 49:523-531.
- Kalcounis, M.C., Hobson K.A., Brigham R.M., and Hecker K.R. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *J. Mammal.* 80:673-682.
- Krebs, C.J. 1989. *Ecological Methodology*. Harper & Row, New York.
- Krusic, R.A., Yamasaki, M., Neefus, C. D., and Pekins P. J. 1996. Bat habitat use in White Mountain National Forest. *J. Wildl. Manage.* 60:625-631.

- Lambert, D. 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. *Technometrics*, 34:1-14.
- Linden, V.M.G., Weier, S.M., Gaigher, I., Kuipers, H.J., Weterings, M.J.A., and Taylor, P.J. 2014. Changes of bat activity, species richness, diversity and community composition over an altitudinal gradient in the Soutpansberg range, South Africa. *Acta Chiropterologica*, 16:27-40.
- Loeb, S.C., and O'Keefe, J.M. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *J. Wildl. Manage.* 70:1210-1218.
- Luszcz, T.M.J. 2004. Community structure and habitat use by forest-dwelling bats in southwestern British Columbia. M.Sc. thesis. Department of Biology, University of Calgary, Calgary, AB.
- Manning, R. W., and Knox Jones Jr, J. 1989. *Myotis evotis*. *Mamm. Species*, 329:1-5.
- McCain, C.M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecol. Biogeogr.* 16:1-13.
- Meidinger, D. 1999. Field manual for describing terrestrial ecosystems. Land management handbook No. 25. BC Ministry of Forests and Ministry of Environment, Lands and Parks, Victoria, B.C.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, B.C.
- Menzel, J.M., Menzel, M.A., Kilgo, J.C., Ford, W.M., Edwards, J.W., and McCracken, G.F. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *J. Wildl. Manage.* 69:235-245.

- Muller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Stratz, C., Veith, M., and Fenton, B. 2013. From ground to above canopy - Bat activity in mature forests is driven by vegetation density and height. *Forest Ecol. Manage.* 306:179-184.
- Nagorsen, D.W., and Brigham, R.M. 1993. *Bats of British Columbia*. UBC Press, Vancouver, B.C.
- Nixon, A.E., Gruver, J.C., and Barclay, R.M.R. 2009. Spatial and temporal patterns of roost use by western long-eared bats (*Myotis evotis*). *Am. Midl. Nat.* 162:139-147.
- Norberg, U.M., and Rayner, J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* No. 316:335-427.
- Oliver, C.D., and Larson, B.C. 1990. *Forest Stand Dynamics*. McGraw Hill, Inc., Toronto, ON.
- Parish, R., Coupe, R., and Lloyd, D. 1996. *Plants of southern interior British Columbia*. Lone Pine Publishing, Vancouver, B.C.
- Patriquin, K.J., and Barclay, R.M.R. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *J. Appl. Ecol.* 40:646-657.
- Peterson, E.B., Peterson, N.M., and McLennan, D.S. 1996. *Black cottonwood and balsam poplar manager's handbook for British Columbia*. FRDA Report 250. British Columbia Ministry of Forests, Victoria, B.C.
- R Core Team. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

- Saunders, M.B., and Barclay, R.M.R. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology*, 73:1335-1345.
- SAS Institute Inc. 1989. SAS/STAT User's Guide Version 6, Fourth Edition. SAS Institute Inc., Cary, N.C.
- Schnitzler, H-U., and Kalko, E.K.V. 2001. Echolocation by insect-eating bats. *Bioscience*, 51:557-569.
- Sleep, D.J.H., and Brigham, R.M. 2003. An experimental test of clutter tolerance in bats. *J. Mammal.* 84:216-224.
- Stevens, R.D. 2013. Gradients of bat diversity in Atlantic forest of South America: environmental seasonality, sampling effort and spatial autocorrelation. *Biotropica*, 45:764-770.
- Swystun, M.B., Lane, J.E., and Brigham, R.M. 2007. Cavity roost site availability and habitat use by bats in different aged riparian cottonwood stands. *Acta Chiropterologica*, 9:183-191.
- Tabachnick, B.G., and Fidell L.S. 2001. Using Multivariate Statistics. Allyn and Bacon, Toronto, ON.
- Thomas, D.W. 1988. The distribution of bats in different ages of Douglas-fir forests. *J. Wildl. Manage.* 52:619-626.
- Vonhof, M., and R. M. R. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. *J. Wildl. Manage.* 61:674-684.
- Waldien, D.L., Hayes, J.P., and Arnett, E.B. 2000. Day-roosts of female long-eared myotis in western Oregon. *J. Wildl. Manage.* 64:785-796.

Waldien, D.L., and Hayes J.P. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. *Northwest Sci.* 75:307-314.

Wolbert, S.J., Zellner, A.S., and Whidden, H.P. 2014. Bat activity, insect biomass, and temperature along an elevational gradient. *Northeast. Nat.* 21:72-85.

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Table 1. Model fit for activity (with zero-inflation) of large bat species, *Myotis* and *M. evotis*. Displayed are degrees of freedom (K), AIC_c, and ΔAIC_c values, and AIC weights (w_i). Temperature and gap area were included as control variables in each model. temp = temperature, gap = log gap area, and cc = acrsine square root canopy closure. Bold text indicates the best approximating models that were chosen.

Model	Large Bat Species				<i>Myotis evotis</i>			<i>Myotis</i>		
	K	AIC _c	ΔAIC _c	w_i	AIC _c	ΔAIC _c	w_i	AIC _c	ΔAIC _c	w_i
1. year + zone*age + zone + age + cc + temp + gap	19	396.09	7.47	0.01	663.98	5.05	0.04	2976.60	0.00	0.99
2. zone*age + zone + age + cc + temp + gap	18	393.70	5.08	0.03	665.61	6.68	0.02	2985.57	8.97	0.01
3. year + zone + age + cc + temp + gap	13	392.18	3.56	0.06	660.51	1.59	0.24	3033.40	56.80	0.00
4. zone + age + cc + temp + gap	12	390.30	1.68	0.15	664.10	5.18	0.04	3044.90	68.31	0.00
5. year + zone*age + zone + age + temp + gap	18	393.55	4.93	0.03	663.93	5.01	0.04	3025.68	49.09	0.00
6. year + zone + age + temp + gap	12	390.28	1.66	0.15	658.92	0.00	0.54	3116.72	140.12	0.00
7. zone*age + zone + age + temp + gap	17	391.19	2.57	0.10	666.87	7.95	0.01	3025.03	48.43	0.00
8. zone + age + temp + gap	11	388.62	0.00	0.35	663.39	4.47	0.06	3115.06	138.46	0.00

9. year + zone + temp + gap	10	413.12	24.50	0.00	682.67	23.74	0.00	3167.55	190.95	0.00
10. year + age + temp + gap	9	392.99	4.37	0.04	695.01	36.08	0.00	3535.50	558.90	0.00
11. zone + temp + gap	9	411.01	22.39	0.00	688.83	29.91	0.00	3165.35	188.75	0.00
12. age + temp + gap	8	391.20	2.57	0.10	697.11	38.18	0.00	3546.63	570.03	0.00
13. Null Model: temp + gap	6	417.86	29.24	0.00	737.84	78.92	0.00	3552.46	575.86	0.00

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Table 2. Large bat and *M. evotis* regression parameter estimates with lower and upper 95% confidence intervals (in brackets) for best approximating AIC models in the activity portion of the zero-inflated Poisson model, as well as for the base models in the occupancy components.

Variable	Large Bats	<i>M. evotis</i>
Activity		
Intercept	-8.69 (-10.72, -6.66)	-2.63 (-4.10, -1.17)
Temperature	0.18 (0.12, 0.23)	0.10 (0.06, 0.14)
Log Gap Area	0.92 (0.62, 1.22)	-0.13 (-0.36, 0.09)
Year 2001	.	0.39 (0.09, 0.69)
IDF zone	-0.43 (-1.02, 0.16)	-1.04 (-1.43, -0.64)
CWH zone	0.29 (-0.21, 0.78)	-0.16 (-0.45, 0.14)
ESSF zone	0.53 (0.03, 1.03)	-0.94 (-1.38, -0.50)
Mature Forest	-0.75 (-1.23, -0.28)	0.77 (0.27, 1.27)
Old Forests	-1.44 (-2.00, -0.88)	1.14 (0.66, 1.62)
Occupancy (modelling probability of absence)		
Intercept	-3.01 (-7.21, 1.19)	4.28 (0.90, 7.66)
Temperature	0.13 (-0.02, 0.27)	0.06 (-0.06, 0.17)
Log Gap Area	0.20 (-0.41, 0.80)	-1.06 (-1.70, -0.41)

Table 3. *Myotis* regression parameter estimates with lower and upper 95% confidence intervals (in brackets) for best approximating AIC model in the activity portion of the zero-inflated Poisson model, as well as for the base model in the occupancy components.

CC = canopy closure.

Variable	Activity	Occupancy (Absence)
Intercept	0.47 (-0.14, 1.07)	5.62 (2.08, 9.15)
Temperature	-0.05 (-0.06, -0.03)	-0.14 (-0.26, -0.03)
Log Gap Area	0.45 (0.38, 0.52)	-1.00 (-1.64, -0.36)
Year	-0.16 (-0.26, -0.07)	.
Arcsine Square-root CC	-9.98 (-12.74, -7.23)	.
IDF zone	-0.24 (-0.47, 0.00)	.
CWH zone	-1.82 (-2.15, -1.48)	.
ESSF zone	-1.28 (-1.73, -0.83)	.
Mature Forest	0.05 (-0.12, 0.22)	.
Old Forest	0.07 (-0.08, 0.22)	.
IDF * Mature	-0.13 (-0.42, 0.15)	.
CWH * Mature	0.85 (0.42, 1.27)	.
ESSF * Mature	-0.04 (-0.56, 0.49)	.
IDF * Old	0.45 (0.19, 0.72)	.
CWH * Old	1.19 (0.83, 1.56)	.
ESSF * Old	0.04 (-0.46, 0.55)	.

Figure 1. Plot of predicted geometric mean pass rate for large bats by forest age and ecosystem zone in the northern Skagit watershed, British Columbia in 2000 and 2001. Predictions are made at the average temperature and gap area and are adjusted for zero inflation. Ecosystem zones in this and subsequent figures are: Bc = Black cottonwood, IDF = Interior Douglas-fir, CWH = Coastal Western Hemlock, ESSF = Engelmann Spruce-Subalpine Fir.

Figure 2. Plot of predicted geometric mean pass rate for *Myotis evotis* by forest age and ecosystem zone for a) 2000 and b) 2001 in the northern Skagit watershed, British Columbia. Predictions are made at the average temperature and gap area and are adjusted for zero inflation.

Figure 3. Predicted geometric mean pass rate for *Myotis* by forest age and ecosystem zone for a) 2000 and b) 2001 in the northern Skagit watershed, British Columbia. Predictions are made at the average temperature, gap area and canopy closure and are adjusted for zero inflation.

Figure 4. Predicted probability of encountering foraging *Myotis* in the northern Skagit watershed, British Columbia in 2000 and 2001. Predictions are made at the average temperature, and gap area.