The influence of habitat structure on the ability to detect ultrasound using bat detectors

Krista J. Patriquin, Laureen K. Hogberg, Bryan J. Chruszcz, and Robert M. R. Barclay

Abstract It has been assumed that habitat differences influence the ability to detect ultrasonic calls produced by bats. This could mask or inflate differences in levels of bat activity among different habitats, possibly resulting in false conclusions about the ecology of bats. We measured the ability to detect 25- and 40-kHz sounds in various forest types in northern Alberta, Canada. We found that sound transmission varied among forest types (deciduous, coniferous, and mixed). Increases in vegetation density among open, thinned, and intact forest patches did not significantly reduce the ability to detect 40-kHz sound. However, it was more difficult to detect 25-kHz sound in intact patches than in thinned patches. These results have important implications for the design and interpretation of studies on habitat use by bats.

Key words Anabat, bats, echolocation, forest, habitat use, sound transmission, surveys

Variation in sound transmission has received considerable attention, especially in studies of animals such as birds, frogs, insects, and whales, in which sound is an important mode of communication (e.g., Wiley and Richards 1982, Römer and Lewald 1992, Penna and Solís 1998, Mercado and Frazer 1999). This research has focused primarily on long-range communication because it plays an important role in mate attraction and establishment and defense of territories. Differences in habitat structure can influence transmission of the relatively low frequencies of sound used by birds and frogs (Morton 1975, Cosens and Falls 1984, Appleby and Redpath 1997, Penna and Solís 1998). Habitat differences may also influence the transmission of ultrasound produced by bats. Indeed, Parsons (1996) found that 40-kHz signals were easier to detect at ground level in the open than in forested "bush." However, no other studies have investigated the influence of habitat structure on sound transmission by bats, likely because of the logistical difficulties associated with generating and detecting ultrasound in the field. Variation in sound transmission also is less likely to be important to echolocating bats than to other animals because of the short range at which echolocation works (Altringham 1996). Habitat-associated differences in sound transmission are important to researchers eavesdropping on echolocating bats, however, and deserve further attention.

With recent advances in technology, many researchers now employ ultrasonic detectors to study habitat use by bats (e.g., Humes et al. 1999, Kalcounis et al. 1999, Law et al. 1999). Detectors receive the ultrasonic echolocation calls of bats and convert them into audible or digital signals. Some assume it is more difficult to detect bats in areas with dense vegetation than in open habitats (e.g., Humes et al. 1999, Law et al. 1999), but most studies make the unstated assumption that bats are equally detectable in all habitats (e.g., Perdue and Steventon 1996, Crampton and Barclay 1998,

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Kalcounis et al. 1999, Sherwin et al. 2000).

Differences in the range at which bats are detectable in various habitats could have important implications for design and interpretation of habitat-use studies. Misinterpretation of results and erroneous conclusions about the ecology of bats could also lead to improper management recommendations. For example, many bats rely on forests for food and shelter, and the influence of logging on habitat use by bats has been the subject of considerable study (e.g., Barclay and Brigham 1996, Crampton and Barclay 1998, Humes et al. 1999, Kalcounis et al. 1999, Law et al. 1999). If bats are not equally detectable in different forest habitats (e.g., conifer vs. deciduous, thinned vs. intact), differences in activity as measured by monitoring echolocation might be difficult to interpret.

The goals of our study were to test the assumption that the ability to detect ultrasound varies among habitats and to measure that variation to determine its potential significance in interpreting measurements of bat activity. We conducted our study in a forested landscape subjected to harvesting. We predicted that sound transmission would be greatest in open habitats (clear-cuts), least in intact habitats (no harvesting), and intermediate in areas of selective thinning (thinned habitat). We conducted our study in 3 forest types (coniferous, deciduous, and mixed), to determine the degree of variation in sound transmission among forests that vary in structure. Our goal was to determine whether differences in detectability are significant enough for researchers to consider in their own studies. We did not set out to estimate factors that generally might be used to correct for detection differences because many variables contribute to variation in sound transmission (e.g., relative humidity, vegetation density, frequency of sound).

Methods

Between 27 July and 6 August 2000, we measured the ability to detect ultrasound in open, thinned, and intact forest habitats within the Ecosystem Management by Emulating Natural Disturbance (EMEND) study area in the boreal forest just north of Peace River, Alberta, Canada (56° 40' N, 118° 10' W). EMEND is an experimentally manipulated forest designed to test the impacts of modified harvest regimes on a variety of organisms. We measured sound transmission in 0, 50, and 100% retention patches, where percent retention refers to the percentage of trees remaining after harvest. We sampled one 50% and one 100% patch in each of 3 forest types: deciduous-dominant (balsam poplar [*Populus balsamifera*] and trembling aspen [*Populus tremuloides*]), conifer-dominant (white spruce [*Picea glauca*]), and mixed (aspen and spruce). Tree height was similar in all stands (18–20 m), and tree density was similar in the 100% patches (1,225–1,350/ha). Mean tree diameter (dbh) was similar in the 100% patches (20.4–21.0 cm) but larger in the 50% patches, especially the conifer-dominant patch (coniferous 28.0 cm, deciduous 24.5 cm, mixed 22.2 cm [J. Spence, University of Alberta, personal communication]). Although the density of understory vegetation was not measured, conifer stands tended to have fewer shrubs than did the 2 other types (personal observation). Because all of the 0% patches were uniform with respect to potential sources of sound attenuation, we used only one 0% patch (i.e., clear-cut).

Within a patch we mounted a speaker (Technics leaf tweeter, model EAS-10TH400B, Matsushita Electric Industrial Co., Secaucus, N.J.) to the top of an 8.7-m telescopic pole and oriented it down at a 30° angle to the horizontal. Using a gated sine-wave sound generator (Technical Services, University of Calgary), we produced a series of 5 pure-tone bursts of sound (1 sec duration) at either 25 or 40 kHz. In North America these frequencies often are used to distinguish between larger (e.g., big brown bats [*Eptesicus fuscus*] and hoary bats [*Lasiurus cinereus*]) and smaller (e.g., *Myotis* spp.) species of bats, using various types of bat detectors (e.g., Crampton and Barclay 1998). To approximate the typical survey method used in bat-habitat studies (e.g., Humes et al. 1999), we used an Anabat II detector (Titley Electronics, Ballina, Australia) set at sensitivity 8, held 1 m above the ground with the receiver directed at the speaker, and stood 18 m from the base of the pole. We then gradually reduced the amplitude of the pulses until we could not detect any of the 5 bursts. We defined this value as the minimum intensity required for detection, with a lower value indicating easier detection.

Within the 0% patch and the 3 100% patches, we measured the minimum intensity required for detection in 4 arbitrary directions from the base of the speaker-pole. We did this at each of 3 locations at least 20 m apart within each type of patch. Within the 50% patches, 5-m-wide corridors had been created every 20 m by removing all the trees to accommodate equipment required to selectively thin these patches. The appropriate percentage of trees had then been removed from the strips of trees (retention strips) remaining between machine corridors. Therefore, the 50% patches were a series of machine corridors and retention strips alternating across the patch. We placed the speaker-pole in the center of a retention strip and oriented the speaker perpendicular to the machine corridor. We measured the minimum intensity required for detection and then repeated the process with the speaker oriented in the opposite direction. We did this at 3 separate locations at least 20 m apart in each of the patches.

By repositioning the pole 3 times in each patch and measuring in various directions from the base of the pole, we could account for the natural heterogeneity in the number of potential obstacles between the receiver and speaker, which may affect sound attenuation. In total we collected 12 measurements of minimum detection intensity in each 100% patch and the 0% patch, and 6 measurements in each 50% patch. We sampled on days with no wind or rain, between 0900 and 1700 hours.

In the laboratory we converted the amplitude readings from the sound generator to decibels (dB). We placed the speaker 10 cm from the 1.7-cm microphone of a precision sound-level meter (Brüel and Kjær, Copenhagen, model 2209). We produced pulses of sound at amplitudes ranging from the lowest to the highest readings obtained in the field for both 25 and 40 kHz and measured the intensity. We converted dB to microbars (μbar) to provide a nonlog measure of sound intensity (Broch 1971).

Due to heterogeneous variance among treatments, we used restricted maximum likelihood to estimate the variance-covariance structure of the repeated measurement within patches based on a model of heterogeneous compound symmetry (SAS Institute 1999, Version 8.01, Proc Mixed), as this yielded the best AIC (Akaike's Information Criterion) value. We tested for the effects of forest type, patch type, and frequency on minimum required intensity in 50 and 100% patches using a mixed model (SAS Institute 1999, Version 8.01, Proc Mixed). We did not include the 0% patch in this analysis because only 1 forest type was sampled. In this analysis, minimum required intensity was the dependent variable, with forest type, patch type, and frequency as independent variables. All second- and third-order interactions also were included in the model. The location of the pole was nested within patch type, which was a repeated measure in the model. We then performed Dunn-Šidák multiple comparisons (Sokal and Rohlf 1995) between each forest type within each frequency and patch type. For example, we compared the minimum required intensity for 25 kHz in conifer and deciduous forests within 50% patches. We made 12 comparisons in total and adjusted the Type I error rate to $\alpha = 0.004$ (i.e., $\alpha_c = 1 - [1 - 0.05]^{1/k}$, where k = the number of contrasts).

We used a separate mixed model (SAS Institute 1999, Version 8.01, Proc Mixed) to test for differences among 0, 50, and 100% patches. In this analysis, minimum required intensity was the dependent variable, and patch type and frequency were the independent variables. We also included all second-order interactions in the model. The location of the pole was nested within patch type, which was a repeated measure in the model. We then performed Dunn-Šidák multiple comparisons (Sokal and Rohlf 1995) between each patch type within each frequency. We made 6 comparisons in total and adjusted the Type I error rate to $\alpha = 0.008$. We repeated this process for each of the 3 forest types separately. To meet normality assumptions, we $\log_{10}$-transformed the data. We present least squares means in all figures.

Results

Minimum sound intensity required for detection varied significantly with forest type, patch type, and frequency ($F = 7.54$, df = 2, 23, $P = 0.002$; $F = 31.30$, df = 1, 17.8, $P < 0.001$; $F = 302.69$, df = 1, 35.8, $P < 0.001$, respectively; Figure 1). All second- and third-order interactions were also significant, including forest type × patch type, forest type × frequency, patch type × frequency, and forest type × patch type × frequency ($F > 7.93$, $P < 0.001$ in every case). Multiple comparisons indicated that for 25 kHz, minimum sound intensity required for detection within 50% patches was significantly higher in deciduous forests than in conifer and mixed forests ($t = 7.98$, df = 9.95, $P < 0.001$; $t = 12.42$, df = 6.72, $P < 0.001$, respectively).

Minimum sound intensity required for detection of 25 kHz within 100% patches was significantly lower in deciduous forests than in coniferous forests ($t = 4.21$, df = 10.5, $P = 0.002$), but not lower than in mixed forests ($t = 2.25$, df = 8.19, $P = 0.04$). In both 50 and 100% patches, minimum sound intensity required for detection of 25 kHz did not differ between conifer and mixed forests ($t = 0.24$, df = 6.65, $P = 0.81$; $t = 2.17$, df = 8.19, $P = 0.06$, respectively).

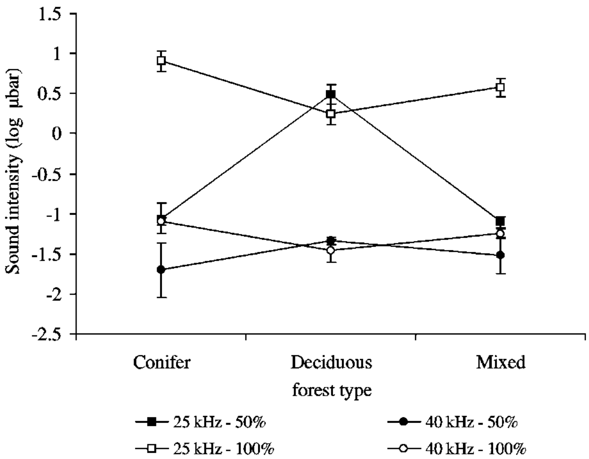

Figure 1. Least squares means (±SE) of log-transformed values of the minimum sound intensity required to detect 25 and 40 kHz in 50 and 100% patches within conifer, deciduous, and mixed forests ($n=6$ and 12 in 50 and 100% patches, respectively). Experiments were conducted near Peace River, Alberta, Canada in July and August 2000.

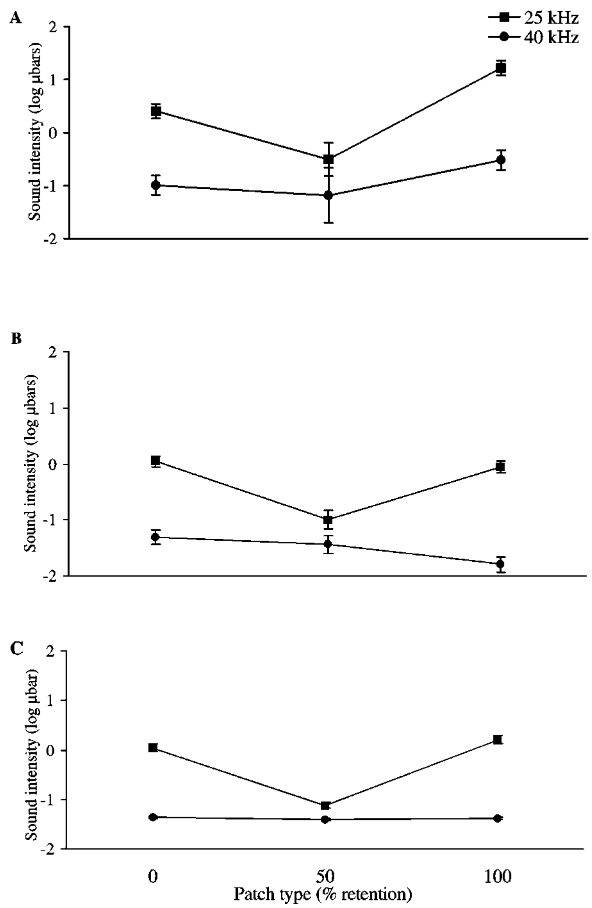

Figure 2. Least squares means (±SE) of log-transformed values of the minimum sound intensity required to detect 25 and 40 kHz in 0, 50, and 100% patches within A) conifer, B) deciduous, and C) mixed forests ($n=12$, 6, and 12 in 0, 50, and 100% patches, respectively). Experiments were conducted near Peace River, Alberta, Canada in July and August 2000.

Multiple comparisons indicated that for 40 kHz, minimum sound intensity required for detection in 50% patches did not differ between conifer and mixed forests, between conifer and deciduous forests, or between deciduous and mixed forests ($t<1.12$, $P>0.28$ in each case). Multiple comparisons also demonstrated that the minimum intensity required for detection of 40 kHz in 100% patches did not differ significantly (using the adjusted α value) between conifer and mixed forests, conifer and deciduous forests, or deciduous and mixed forests ($t<2.62$, $P>0.02$ in each case).

Minimum sound intensity required for detection of 40 kHz did not vary significantly among 0, 50, and 100% patches, regardless of forest type ($t<1.83$, $P>0.09$ in every case; Figure 2). For 25 kHz, it was more difficult to detect sound in 100% patches than in 50% patches in both conifer and deciduous forests ($t=5.01$, df=8.01, $P<0.001$, Figure 2A; $t=4.80$, df=7.89, $P<0.001$, Figure 2B, respectively). Within mixed forests it was more difficult to detect 25 kHz in the 0% patch than in the 50% patches ($t=13.62$, df=15.1, $P<0.001$, Figure 2C). Within conifer and deciduous forests, minimum sound intensity required for detection of 25 kHz did not differ significantly between 0 and 50% patches ($t=2.65$, df=8.01, $P=0.03$, Figure 2A; $t=0.62$, df=6.63, $P=0.56$, Figure 2B, respectively) or between 0 and 100% patches ($t=1.83$, df=14.5, $P=0.09$, Figure 2A; $t=2.65$, df=10.8, $P=0.02$, Figure 2B, respectively). Within mixed forests, there was no significant difference in the minimum sound intensity required for detection of 25 kHz between 50 and 100% patches or between 0 and 100% patches ($t<1.26$, $P>0.25$ in both cases, Figure 2C).

Discussion

We found that ultrasound typical of the frequencies used by echolocating bats was not equally detectable in all habitats. In a study primarily aimed at testing detection differences among detector types, Parsons (1996) also found detection range was reduced in forested "bush" habitat in New Zealand compared to open habitat. The effect of habitat we found was not as we predicted or as assumed in some previous studies (Humes et al. 1999, Law et al. 1999). Differences in forest type influenced the ability to detect 25-kHz sound, but the influence differed with patch type. In thinned forest it was easier to detect 25 kHz in conifer and mixed forests compared to deciduous forests. Sound of 40 kHz was equally detectable in all forest types regardless of patch type. These results differ from those of previous studies that found sound attenuated more readily in coniferous stands than in deciduous stands (Marten and Marler 1977). However, previous studies used sounds ranging from 350 Hz to 11 kHz, considerably lower than the 25 and 40 kHz we used.

An increase in vegetation density (intact vs. thinned forest) did not significantly reduce the ability to detect 40 kHz in any of the forest types. Studies have illustrated that when signalers and receivers are both 1 m above the ground, attenuation of sounds <20 kHz does not differ between open and forested habitat (Marten and Marler 1977). Differences in sound transmission between open and forested habitat occur only if both signaler and receiver are at ground level, and are therefore subjected to ground effect, or if both are at canopy height (Marten and Marler 1977). Our results were not subject to either of these influences; we measured sound transmission 1 m above the ground, with the signal elevated 8.7 m above the ground, which did not place the sound source in the canopy.

In contrast to 40 kHz, transmission of 25-kHz sound was affected by patch type. However, the influence depended on forest type and the effect was not as we predicted. In all 3 forest types, transmission of 25 kHz was best in thinned patches. Transmission was reduced in intact conifer and deciduous forest compared to thinned patches of the same forest type, but contrary to Parsons' (1996) finding, there was no difference in sound transmission between clear-cut and intact patches in any forest type. Indeed, it was more difficult to detect 25 kHz in the clear-cut than in the thinned mixed forest. There were no obvious differences in vegetation structure that help explain detection differences among forest types. The influence of vegetation on transmission of ultrasound is thus not straightforward and is difficult to interpret. One possibility is that at 25 kHz, the canopy cover in thinned patches acted as a ceiling, reflecting sound back into the patch, thereby increasing our ability to detect the sound compared to that in clear-cuts (Morton 1975). Increased vegetation density in the intact patches may have resulted in attenuation and scatter of sound and a decrease in detection ability (Fotheringham and Ratcliffe 1995).

Krista Patriquin sets up an Anabat.

Our results indicate that differences in detectability of echolocation calls across various habitats differ with call frequency. This means some species may be equally detectable across different forested habitats, while others may not. Detection differences also are not simply related to vegetation density, as some have assumed (Humes et al. 1999, Law et al. 1999). Interpretation of activity data will need to take these complexities into account, as is done for acoustic surveys of birds (Richards 1981). For example, habitat selection by bats has been the focus of many recent studies (e.g., Barclay and Brigham 1996, Crampton and Barclay 1998, Humes et al. 1999, Kalcounis et al. 1999, Law et al. 1999), and the influence of disturbances, such as logging, has been of particular interest. A common finding is that more bat activity is detected along the edges of harvested areas than in intact forest (e.g., Crampton and Barclay 1998, Grindal and Brigham 1999). Although habitat selection by foraging bats is one explanation for such findings, differences in the ability to detect bats in different habitats may be an alternative explanation. Ultimately, our understanding of the foraging ecology of bats and development of management recommendations depends on incorporating differences in sound transmission in interpretations of results.

How significant might differences in minimum detection intensity be in terms of the ability to detect bats in different habitats? Using the mean minimum detection intensity for 25 kHz in 50%-thinned conifer stands (0.5 µbar; 68 dB produced 20 m from the detector) and 100% (intact) conifer stands (1.4 µbar; 79 dB) as an example, we estimated the difference in detection range this would results for a bat echolocating at 25 kHz and 120 dB. We included spreading loss and atmospheric attenuation (at 50% relative humidity) in estimating the decline in intensity with distance (see Griffin 1971 for details). Such a bat could be detected at 25 m in the intact forest and 28 m in the thinned forest, an increase of 12%. Although the shape of the detection zone for Anabat detectors is complex and variable (K. Livengood, University of Missouri, personal communication), a simple shape (e.g., cone or sphere) can be used to approximate it. Using such shapes, the volume of air sampled by the detector in the thinned stand would be 40–45% greater than in the intact stand. Using the maximum detection distances for various types of detectors recorded by Parsons (1996), differences in the volume of air sampled in different habitats could be as great as 85%. In other words, even if the absolute density of bats or bat passes was the same in 2 habitats, significantly more may be detected in one habitat compared to another.

Our results suggest that variation in detection of ultrasound across habitats may be considerable, is not straightforward, and needs to be studied further. Until further studies allow us to apply correction factors to account for differences in detectability of bats among habitats, researchers need to consider the potential influence of these differences when designing their studies and interpreting their measurements of habitat use by bats. For studies investigating the use by bats of forest types that differ in vegetation density, detection differences potentially could be minimized by placing detectors in gaps in the forest stands. This would reduce or eliminate variation in detection ability. Likewise, comparisons between open and edge habitats should be less prone to detection differences than comparisons involving greater vegetation differences.

Laureen Hogberg, Krista Patriquin, and Bryan Chruszcz (left to right) erect the speaker pole in a clear-cut.

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