Journal of Mammalogy, 85(2):273–281, 2004

EFFECTS OF CLUTTER ON ECHOLOCATION CALL STRUCTURE OF *MYOTIS SEPTENTRIONALIS* AND *M. LUCIFUGUS*

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The structure of echolocation calls, and the distance over which bats perceive their environment, varies with the amount of structural clutter through which they are flying. Clutter and species had significant effects on the frequency-time characteristics of search-phase echolocation calls of northern long-eared (*Myotis septentrionalis*) and little brown bats (*M. lucifugus*). We tested an a priori derived model that predicted the pattern of differences in echolocation call variable values among clutter categories would provide insight into the relative maximum distances that bat species could perceive using echolocation. Specifically, the model predicted that species adapted to flying and foraging in cluttered habitats would have a shorter maximum perceptual distance than species adapted to flying and foraging in uncluttered habitats. The results supported this model and suggest the clutter-adapted *M. septentrionalis* had a shorter maximum perceptual distance than *M. lucifugus*, a species known to forage in a variety of habitats but mainly in uncluttered areas (i.e., over water). Using calls as the sampling unit, a neural network correctly classified >94% of the echolocation calls to species in high clutter. In medium and low clutter, >82% of the calls were correctly classified to species; however >90% correct classification was achieved by leaving <30% of calls unclassified. Researchers should develop clutter-specific call libraries to improve species classification accuracy for echolocation calls.

Key words: clutter, echolocation, holographic neural networks, identification, *Myotis lucifugus*, *Myotis septentrionalis*, study design

Order Chiroptera contains approximately 25% of the world's mammalian species richness with over 1,000 species worldwide (Fenton 1983; Findley 1993). A characteristic of the more speciose suborder, Microchiroptera (approximately 700 species—Koopman 1993), is their use of echolocation for spatial orientation and target discrimination. The structure of echolocation calls in this group is highly variable and probably a function of species' body size and foraging strategy (Aldridge and Rautenbach 1987; Barclay and Brigham 1991; Fenton 1990; Norberg and Rayner 1987). Species that forage in open, uncluttered habitats use long duration and narrow frequency bandwidth calls, whereas species that forage in cluttered habitats use shorter duration and broad frequency bandwidth calls that are better for precise localization and discrimination of targets from the background (Schnitzler and Kalko 2001). In addition to interspecific variation in echolocation call structure, significant variation can also exist intraspecifically. Such variation can occur among individuals (Betts 1998; Obrist 1995), among populations (Barclay et al. 1999; Thomas et al. 1987; but see O'Farrell et al. 2000), or even among calls of an individual. Individual plasticity in echolocation call structure enables bats to efficiently navigate and localize targets under a range of clutter conditions (Boonman and Jones 2002; Kalko and Schnitzler 1993; Miller and Treat 1993; Obrist 1995; Siemers et al. 2001).

For more than 2 decades ultrasonic detectors have been used as a nonintrusive tool to explore various aspects of bat ecology. There are interspecific differences in echolocation call structure among sympatric species that make ultrasonic detection a powerful tool for understanding habitat associations of individual species. For example, in New Hampshire, United States, Krusic and Neefus (1996; http://www.for.gov.bc.ca/hfd/

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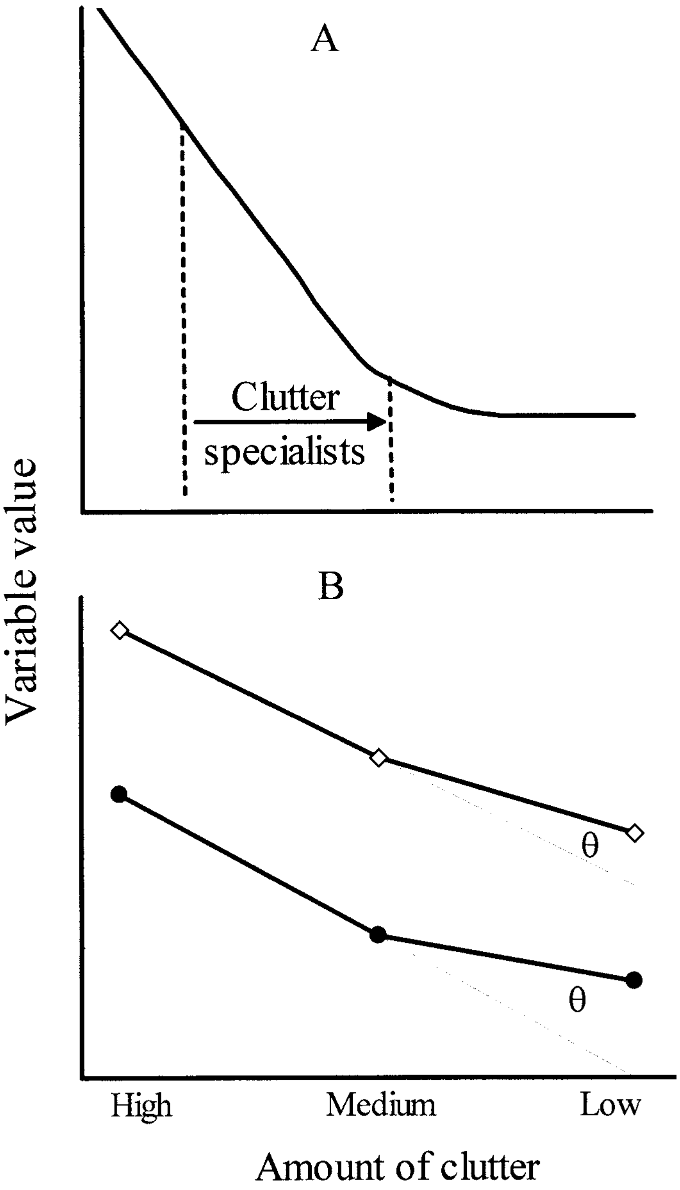

FIG. 1.—A model for predicting the effects of clutter on echolocation call structure for bat species adapted to flying in cluttered and uncluttered habitats. A) Frequency-time characteristics of echolocation call variables that bats alter as they fly from high to low clutter. A line depicting the value of a call variable across clutter should attain an asymptote when the distance to clutter equals the maximum perceptual distance of species. Dashed lines represent the difference in relative value of a variable at researcher-defined medium clutter area for open- and clutter-adapted species. B) Expected pattern of change in echolocation call structure when clutter is recorded categorically for open- and clutter-adapted species. Theta is an estimate of the angle and is calculated by the magnitude of the difference in the echolocation call variable value between medium and high clutter, divided by this difference between low and medium clutter. It should be greater for species that are adapted to flying in cluttered habitats (filled circles) than those adapted to flying in uncluttered habitats (open diamonds).

pubs/docs/wp/wp23.htm, accessed November 2003) had a 100% correct classification rate of echolocation calls for the hoary bat (*Lasiurus cinereus*), red bat (*L. borealis*), big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), and eastern pipistrelle (*Pipistrellus subflavus*). However, some species such as those within the genus *Myotis* may not be reliably identified acoustically such that many investigators are able to identify calls recorded from these bats only to genus (e.g., Erickson and West 2003; Furlonger et al. 1987; Grindal 1999; Hayes 1997; Jung et al. 1999; Zimmerman and Glanz 2000). Other studies have examined entire bat communities (Hecker and Brigham 1999; Krusic et al. 1996; Seidman and Zabel 2001), or guilds (Brigham et al. 1997; Sherwin et al. 2000; Thomas 1988) for patterns of activity using ultrasonic detectors. Unfortunately these approaches overlook functional species-specific habitat associations, and it is not possible to detect temporal changes in activity for individual species, which might be important for less common species (i.e., endangered species). The use of ultrasonic detectors for passively surveying bat communities has potential. However, to reach their full potential, reliable identification of ecologically distinct species such as the little brown bat (*Myotis lucifugus*) and the northern long-eared bat (*M. septentrionalis*) is required, as populations are the functional unit for management and conservation purposes (Meffe and Carroll 1997).

The goal of this research was to examine the effects of clutter (i.e., obstacles in the flight path of bats such as trees) on echolocation call structure. Specifically, we wanted to address 3 questions. First, does clutter affect echolocation call structure? Second, can *M. septentrionalis* and *M. lucifugus* be reliably identified from echolocation calls using artificial neural networks? Finally, could differences in echolocation call structure recorded from areas that vary in the amount of clutter be useful for making interspecific comparisons of foraging strategy, and relative maximum perceptual distance? We predicted that the value of an echolocation call variable affected by clutter would be positively or negatively correlated with clutter, until a threshold distance to clutter is reached, beyond which echolocation call structure does not change further (Fig. 1). At distances to clutter greater than the threshold distance, the bat is flying in uncluttered space (Schnitzler and Kalko 1998). This threshold distance to clutter should represent an estimate of the maximum perceptual distance of the species using echolocation. Species that fly and forage in uncluttered habitats scan larger areas and should have greater perceptual distances, than species that fly and forage in cluttered habitats.

Myotis lucifugus and *M. septentrionalis* are 6–8 g insectivorous bats, and sympatric throughout most of their range in eastern North America (van Zyll de Jong 1985). *Myotis lucifugus* is an opportunistic predator of many prey types (Belwood and Fenton 1976; Broders 2003a; Whitaker 1972) that it captures by aerial hawking (Faure et al. 1993) in a variety of habitats (Adams 1996; Broders et al. 2003; Jung et al. 1999; LaVal et al. 1977), although activity is probably concentrated in uncluttered areas (Belwood and Fenton 1976; Jung et al. 1999; Saunders and Barclay 1992). *Myotis septentrionalis* is a specialist predator of terrestrial insects (Lepidoptera and

Coleoptera—Broders 2003a), which it captures in flight and by gleaning from vegetation (Faure et al. 1993; Miller and Treat 1993) in cluttered habitats (forest interior—Broders 2003a; Broders et al. 2003; Caire et al. 1979; Jung et al. 1999; Lacki and Hutchinson 1999; LaVal et al. 1977).

MATERIALS AND METHODS

Field methods.—Free-flying bats were captured in mist nets or harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) as part of a study on the ecology of *M. septentrionalis* and *M. lucifugus* in the Greater Fundy National Park Ecosystem, New Brunswick, Canada (45°35′N, 65°03′W) from 1999–2001. For each individual a glow stick (Chemical Light Inc., Vernon Hills, Illinois) was glued (Skin-Bond, Smith & Nephew, Inc., Largo, Florida) between the scapulae and it was released near its capture site and where no other bats were flying. At time of release, all lights in the area were turned out, all personnel were instructed to be quiet, and the animal was placed on a shirt or outstretched hand until it flew away on its own volition (usually within a few seconds). A second person stood approximately 5 m away with a handheld ultrasonic detector (Anabat; Titley Electronics, Ballina, N.S.W., Australia) that was interfaced directly to a laptop computer via a zero crossing analysis interface module. The output volume of the detector set to minimum and the microphone was aimed at the flying bat to record the longest echolocation sequence possible.

One of us (HGB) was present for all releases and characterized all release sites into 1 of 3 clutter categories based on the horizontal distance to the nearest trees. All release sites were inside or in the vicinity of mature forests, and no attempt was made to distinguish sites based upon forest type, age, etc. The definition of clutter used in this study did not incorporate ground structure because the ground at all our release sites was relatively even and unstructured. Low clutter sites had no trees within 10 horizontal m of the release site (clearcuts), medium clutter sites had trees within 3–10 horizontal m of the release site (forest gaps and edges), and high clutter sites had trees within 3 horizontal m of the release site (forest interior and forested trails). Most sequences were recorded while bats flew 2–7 m above the ground. Following release in medium clutter some bats flew near the forest edge (i.e., high clutter), but because the incidence of this was low and it would have been difficult (or impossible) to determine which calls were made in each category, all sequences were categorized based on release sites.

Our animal handling protocols were consistent with those of the American Society of Mammalogists guidelines (American Society of Mammalogists 1998) and approved by the animal care committee of the University of New Brunswick.

Statistical analyses.—One of us (HGB) edited all echolocation sequences manually with Analook software (v4.7J, written by Chris Corben, http://www.hoarybat.com, accessed October 2003) to remove extraneous noise and atypical and fragmented calls. Only unfragmented, search-phase echolocation calls were kept for analysis. Ten variables that were extracted from calls using Analook included call duration (ms), maximum frequency (kHz), minimum frequency (kHz), mean frequency (kHz), frequency of the knee (frequency at the start of the flattest portion of the call; kHz), characteristic frequency (frequency at the end of the flattest portion of the call; kHz), time from start of call to the frequency of the knee (ms), time from start of all to the characteristic frequency (ms), the initial slope (octaves/s), and the characteristic slope (octaves/s; see O'Farrell et al. 2000 for definitions). Because many call sequences were short, and had unfragmented calls interspersed among fragmented ones, a time-between-calls variable was unreliable.

For question 1, individual sequences were used as the sampling unit to calculate summary statistics and do the statistical analysis of the effects of clutter on echolocation call structure. Therefore, a recaptured individual subsequently released in the same clutter category as its previous release were not considered independent, and data were combined as 1 independent release. However, if an individual was subsequently released in a different clutter category the sequence was considered independent. The effects of 2 variables, clutter and species, on echolocation call structure were assessed using a 2-way analysis of variance (ANOVA) for each call variable in Systat software (v9—Wilkinson 1998). Call variable values for this test were averaged values of each independent release for each variable (Siemers et al. 2001). Various plots of the model residuals were done to ensure ANOVA assumptions were not violated (Sokal and Rohlf 1995).

For question 2 we used artificial neural networks (Murray 1995) to identify species from echolocation calls. Artificial neural networks have been used extensively in ecology (Chon et al. 1996; Findlay and Zheng, 1999; Guégan et al. 1998) and have recently been used to identify bat species from echolocation calls, with improved results relative to more traditional statistical approaches (Parsons and Jones 2000; Parsons 2001). Artificial neural networks have at least 2 potential advantages over more standard statistical classification methods: 1) they can detect and extract nonlinear relationships and interactions among classification variables; and 2) inferred patterns and associated estimates of precision do not depend on assumptions such as multivariate normality. On the other hand, artificial neural networks have at least 3 potential disadvantages: the end product is a trained net, not an estimated mathematical relationship between independent and response variables; because an a priori specified model is not fitted to the data, overfitting can be a problem, especially when the number of observations in the training dataset is small; and because most artificial neural networks use some variant of a standard gradient descent for error minimization, there is a tendency for them to get trapped in local minima. We used a class of artificial neural networks called holographic neural networks (HNet2000, HNet2000 Corporation, Toronto, Ontario, Canada—Sutherland 1992). Compared to standard artificial neural networks, holographic neural networks learn faster, are less prone to being trapped in local minima and to overfitting, and they almost invariably show reduced error rates (Sutherland 1995, 1997).

To train and test the holographic neural network, each individual call was considered independent. This approach was used instead of using independent release averages or 1 randomly selected call from each independent release, because of low sample sizes of independent releases and because of the low intercall correlation ($r < 0.40$) in call structure. Further, we were most interested in the neural network as a tool to identify species, and given the high variability within an individual, using all calls would permit training of the net on as much of the species variability as possible. All recorded calls were partitioned into training (70%), and testing (30%) sets. The trained net generated a predicted value between -1.5 and 1.5 for each call of the training set. Predicted values close to -1.5 were likely *M. septentrionalis*, those close to 1.5 were likely *M. lucifugus*, and those near 0 were unknown. By assigning a binary threshold value (e.g., 0), each observation could be assigned to 1 of the 2 species based on its predicted value and the misclassification rates calculated based on these assignments.

However, the best measure of the network's predictive ability was its misclassification rate of calls that were not encountered during training. This rate was estimated by 1) training the net using the

Table 1.—Number of independent releases and unfragmented search-phase echolocation calls for *M. septentrionalis* and *M. lucifugus* in high, medium, and low clutter categories. Most calls were recorded within 2 minutes of release, and at least 85% were recorded using all the same detection system components.

	High	Medium	Low
M. septentrionalis			
Number of releases	18	30	12
Number of calls	232	500	302
M. lucifugus			
Number of releases	17	40	25
Number of calls	319	1050	444

training set; 2) inputting the test set into the trained net; 3) generating predicted values for each call in the test set; 4) using the predicted values along with a threshold value to assign each call in the test set to a species; and 5) calculating the misclassification rate. In this manner, misclassification rates were obtained for both training and test datasets. Large discrepancies between these indicate that the trained net was incapable of "generalizing" from one sample to another.

Although in principle a binary classification problem, an unclassified category was introduced. The unclassified category included all calls with predicted values within a range of values symmetric around 0 (i.e., from $-x$ to x). As $|x|$ increased, misclassification rates decreased but the proportion of calls left unclassified increased. Thus, the optimal $|x|$ is one that balances the benefits of increased classification accuracy with the costs of more calls unclassified.

All holographic neural network misclassification results reported here are for bootstrapped classification. In this procedure, we randomly partitioned the dataset into training and testing sets for 1,000 trials, with training and testing occurring independently in each trial. Each trial produced a different trained net and a different misclassification rate for both training and test sets. The end result was a distribution of 1,000 misclassification values for training and test sets. Because HNet2000 performs better when the number of observations in each class was approximately equal (Sutherland 1995), and our dataset had more calls for *M. lucifugus* than *M. septentrionalis*, we resampled (without replacement) the training set for *M. septentrionalis* in each trial to ensure an equal number of observations for each species in the training set.

The same suite of call variables were used to identify species in each clutter category. The suite of call variables used for identification was reduced to 7 by eliminating variables with low interspecific variation, high correlation with other variables, and low importance as determined by the coefficients of the response of the network cells to the stimulus elements. The classification results obtained using the reduced set of variables was compared to those obtained using all variables for 6 random selections of test and training sets to ensure the reduction in the number of variables did not significantly reduce classification results. In all cases, the increase in the test misclassification rate for the reduced suite of variables was negligible (all <1.2%). The 7 variables that we selected were call duration (ms), maximum frequency (kHz), minimum frequency (kHz), characteristic frequency (kHz), time from start of call to the characteristic frequency (ms), the initial slope (octaves/s), and the characteristic slope (octaves/s).

For question 3, theta (Fig. 1b) was estimated for all 7 call variables for each species. Theta was estimated using call variable averages calculated using Monte Carlo methods where 1 call was selected for each independent release. Relative differences in maximum perceptual distances between species were assessed by comparing the estimates of theta for all call variables.

RESULTS

There were 2,847 unfragmented search-phase echolocation calls from 142 independent releases analyzed (Table 1). As predicted, the mean of each echolocation call variable, except minimum frequency, was correlated, either positively or negatively, with clutter for both species (Fig. 2). For each species, high clutter calls were of shorter duration (for both species, they were only 60% as long as low clutter calls) and had greater slope and frequency bandwidths than those recorded in low clutter. Similarly, for each clutter category, *M. septentrionalis* calls were shorter with greater slopes and frequency bandwidths than *M. lucifugus*. ANOVA revealed significant variation in echolocation call structure among clutter categories and between species for all 7 call variables (all P values <0.0001). The interaction term was significant ($P < 0.05$) only for minimum frequency.

Theta was greater for *M. septentrionalis* than *M. lucifugus* for 6 of the 7 call variables (Table 2). The theta for the 7th variable, minimum frequency, was spurious because *M. lucifugus* actually had a slightly higher minimum frequency in low clutter than in medium clutter (Fig. 2), and therefore does not follow the same pattern as other call variables. According to the model presented in Fig. 1, these results indicate that maximum perceptual distance of *M. septentrionalis* was shorter than that of *M. lucifugus*, suggesting that *M. septentrionalis* was more adapted to flying in more cluttered habitats than *M. lucifugus*.

Within each clutter category, interspecific differences in proportion of calls misclassified and unclassified was minimal so we do not present species-specific rates. Further, there was no difference in the proportion of calls misclassified or unclassified for medium and low clutter, so they were combined for presentation (labeled medium-low). Invariably, misclassification rates were lower for the training set than the testing set (Fig. 3). Using binary classification, misclassification rates for the test datasets were 5.7% and 17.5% for high and medium-low clutter, respectively. Using an unclassified category with outer bounds of the category $|x| = 0.3$, the misclassification rates dropped to 3.5% and 11% with unclassified rates of 7% and 22% for high and medium-low clutter test datasets, respectively.

DISCUSSION

Our results showed that there were statistically significant, characteristic changes in echolocation call structure among clutter categories for *M. septentrionalis* and *M. lucifugus*. The amount of clutter was inversely related to call duration and positively related to slope and frequency bandwidth of calls. These characteristic changes optimize target discrimination in different clutter situations (Schnitzler and Kalko 2001), and permit interspecific comparisons of foraging strategies and relative maximum perceptual distances. *Myotis lucifugus* commutes and forages in a wide variety of clutter situations (LaVal et al. 1977). The range of distances that this species must perceive as a result of the variety of clutter situations it experience should require high plasticity in echolocation

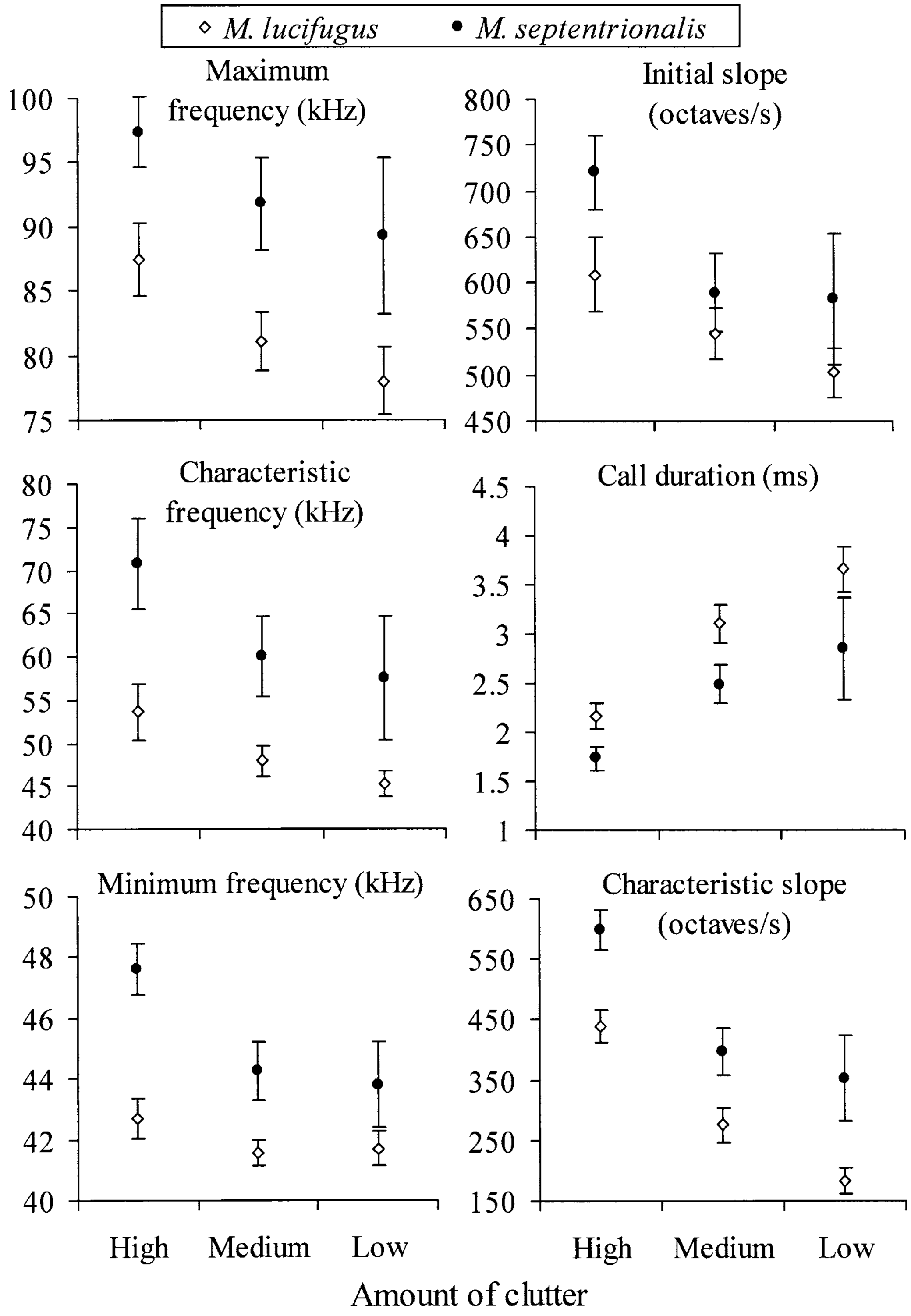

FIG. 2.—Call parameters for search-phase echolocation calls of *M. septentrionalis* and *M. lucifugus* at 3 clutter categories. To prevent pseudoreplication, averages were calculated using Monte Carlo methods. For each of 50,000 trials 1 call was randomly selected from each independent release and the mean was calculated for each call variable. The mean of the 50,000 means was used as an estimate of the true mean. Vertical bars represent 95% confidence intervals.

call structure. *Myotis septentrionalis* is predominantly a forest interior species and rarely forages in open areas (Broders 2003a; Broders et al. 2003; Jung et al. 1999; LaVal et al. 1977). Therefore, the range of distances over which they perceive with echolocation are shorter than for *M. lucifugus*, which resulted in greater estimates of theta for *M. septentrionalis* than for *M. lucifugus*, as the model predicted. This difference in maximum perceptual distance reflects interspecific differences in foraging

TABLE 2.—Estimate of theta (see Fig. 1b) for 7 echolocation call variables for *M. septentrionalis* and *M. lucifugus*.

	M. septentrionalis	*M. lucifugus*
Duration (ms)	2.09	1.68
Maximum frequency (kHz)	2.25	2.06
Minimum frequency (kHz)	7.22	−9.30
Characteristic frequency (kHz)	4.28	2.07
Time to characteristic frequency (ms)	1.53	1.45
Initial slope (octaves/s)	19.62	1.47
Characteristic slope (octaves/s)	4.71	1.78

strategies and is further supported by the lower wing loading and aspect ratios of *M. septentrionalis* relative to *M. lucifugus* (Farney and Fleharty 1969), indicating that *M. septentrionalis* is more morphologically adapted to flying in cluttered habitats than is *M. lucifugus* (Arita and Fenton 1997). Our model might be more rigorously tested in a flight cage where the flying environment could be precisely manipulated and calls recorded and analyzed over a continuous range of clutter conditions. The most important variables in such an analysis would likely be frequency bandwidth, duration, and intensity (Boonman and Jones 2002; Schnitzler and Kalko 2001; Siemers et al. 2001).

The high and statistically significant levels of interspecific and intraspecific variation in echolocation call structure due to clutter suggests that quantitatively including a clutter variable in species identification protocols should improve classification results. Therefore, echolocation call libraries should be built for researcher-defined clutter categories (based on a priori knowledge of the study species and the study objectives). Then, researchers interested in using ultrasonic detection as a tool to study habitat associations should survey sites that correspond to these categories.

Our rates of misclassification of echolocation calls were lowest in high clutter. In this clutter category using a binary classification scheme, only 5% of calls were incorrectly classified. For most research questions, this level of confidence is probably sufficient, and it is probably not necessary to include an unclassified category. In medium and low clutter, the proportion of calls misclassified was similar but greater than that in high clutter and may not be sufficient for many research questions. Therefore, to identify *M. septentrionalis* and *M. lucifugus* in these clutter categories with the methods outlined here, it would be necessary to include an unclassified category. This would, of course, decrease misclassification rate at the expense of leaving calls unclassified (Fig. 3). Alternatively, a different suite of call variables with greater interspecific variability may be more appropriate in these clutter categories. These variables may include frequency-time variables or other variables not obtainable using frequency division systems such that used by Anabat (e.g., harmonic and intensity information).

Ultrasonic survey considerations.—There are a wide variety of commercially available ultrasonic detectors. These instruments vary in cost and in quantity and quality of recorded data (Fenton 2000; Parsons et al. 2000). For ecologists, the most appropriate recording device for a particular situation depends on the predictions being tested and the similarity of the echolocation calls of the species of interest relative to all other local species. Researchers should only attempt to test predictions that involve methods that can control for the biases (Hayes 2000; Sherwin et al. 2000) and limitations of the particular tool during data collection or statistical analysis.

Although concerns have been raised regarding using Anabat recordings to describe the echolocation calls of bats (Fenton 2000; Fenton et al. 2001), the patterns present in our data were real, although they might not be comparable to those recorded using other types of recording systems. Concerns regarding the Anabat system raised by Fenton et al. (2001) include that there are potentially important call variables that are not recorded (e.g., the different harmonics), that the parameters of the variables recorded with the Anabat might not be comparable to that of other models, and finally, that Anabat is less sensitive than more expensive models at lower frequencies (but more sensitive at higher frequencies). Concerns such as these should be considered in the design phase of all studies using ultrasonic detectors. However, if the question(s) of interest include spatial and temporal distribution patterns of species, if enough sound information is recorded to identify the species of interest, the specifics of the device are clearly documented, and the sensitivities of the system(s) are standardized, then any ultrasonic recording system is valid. In northeastern North America, Krusic and Neefus (1996; http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp23.htm, accessed November 2003) demonstrated that many bat species can be reliably identified using frequency division ultrasonic recording systems. As a result, in northeastern North America there are several species available for which it will be possible to test species-specific ecological predictions using ultrasonic detectors. However, further study might be needed on how calls of these species can vary with clutter. In areas with many species that have similar call structures, a time expansion recording instrument might be required to collect higher resolution sound data (i.e., intensity and harmonic information) to confidently identify species of interest.

For many research questions it is not necessary to be able to identify all species in a study area. However, it is vital that the species (1 or more) of interest can be distinguished from all other local species. Research questions that involve interspecific comparisons are more problematic than single species questions. Echolocation call intensity might differ among species (Faure et al. 1993; Fenton 1991; Miller and Treat 1993; Schnitzler and Kalko 1998), therefore even if the abundance of each species is equal in an area, recorded activity levels of each species will be different. It might be possible to derive a correction factor for this by determining call intensity of each species; however, intraspecific variation might occur among habitats (different amounts of clutter—Boonman and Jones 2002; Miller and Treat 1993), and perhaps foraging situations (i.e., whether the bat is foraging alone or with others of the same or a different species in close proximity—Obrist 1995). Even if call intensity is the same or controlled for, not all species forage at the same height above ground (Hickey and Fenton 1990; Saunders and Barclay 1992), and a species might

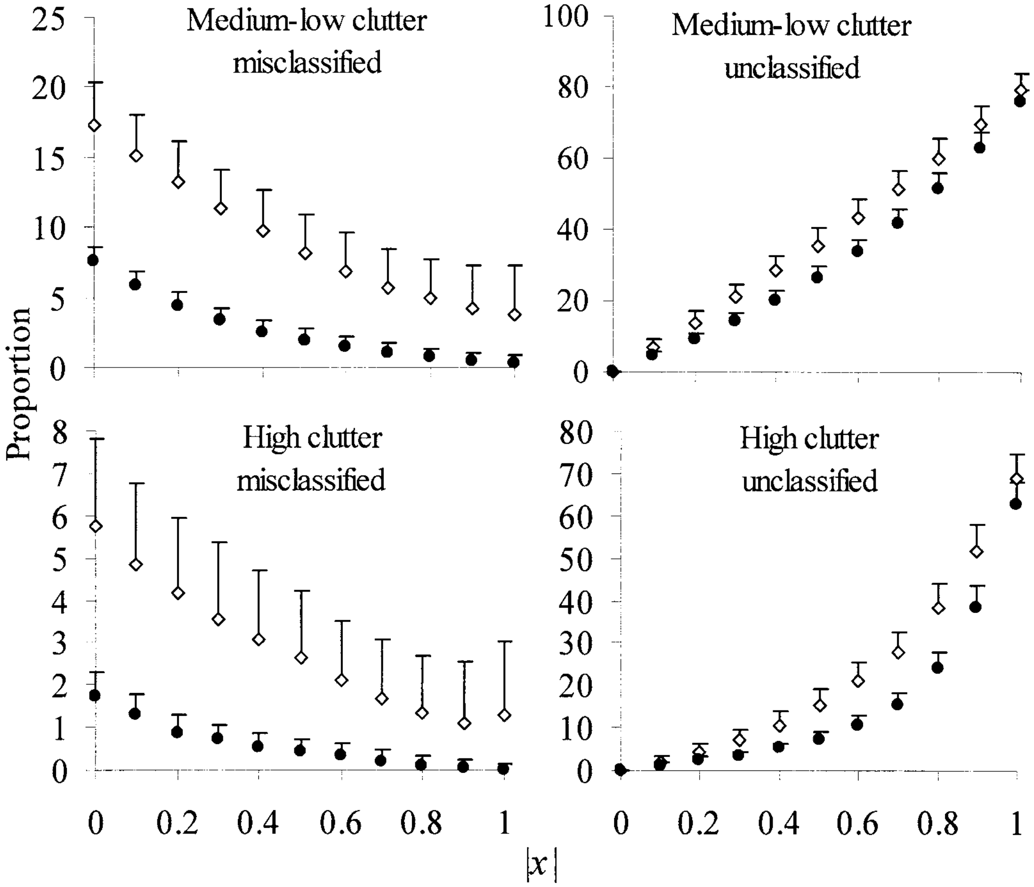

Fig. 3.—Proportion of calls (+1 *SD*) misclassified and unclassified for the training (closed circles) and testing (open diamonds) datasets for different values of $|x|$ (i.e., varying sizes of the unclassified category).

forage at different heights in different habitats (Racey and Swift 1985). Therefore, higher flying species or individuals will be less likely to be recorded than species that fly closer to the ground using ground based detection systems. If the prediction(s) involve single species, researchers should either sample only in 1 clutter category or derive correction factors to control for the effects of clutter on the size of the reception area (Jung et al. 1999). By choosing the most cost-efficient bat detector that can provide appropriate data, acquisition of multiple units might be possible. This can permit simultaneous sampling to minimize the effects of temporal and spatial variability in activity patterns (Broders 2003b; Hayes 1997). However, use of multiple systems necessitates standardization of the size of the reception area among detectors (Hayes 2000; Krusic and Neefus 1996, http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp23.htm, accessed November 2003).

Recognizing the biases of sound detection systems and implementing proper research design will lead to powerful studies. In our study area, *M. septentrionalis* and *M. lucifugus* can be identified using these methods. As a result, frequency division systems such as Anabat should be an appropriate tool for research on bats in the Greater Fundy National Park Ecosystem. The fact that *M. septentrionalis* uses low intensity echolocation calls is evident from the fact that in our study area capture rates along forested trails for the 2 species were approximately equal, yet during passive ground based echolocation surveys, <20% of the recorded sequences were attributable to *M. septentrionalis* (Broders 2003a). Therefore, researchers considering using echolocation surveys for *M. septentrionalis* should experiment with using the highest standardized sensitivity possible without recording too much extraneous noise, and experiment with placing detectors off the ground. The fact that our approach is based on echolocation calls, and not sequences, will allow researchers to identify short sequences or those with only one or a few unfragmented calls.

ACKNOWLEDGEMENTS

This project was funded by an NSERC PGS–B grant to HGB, Fundy National Park, Sir James Dunn Wildlife Research unit at the University of New Brunswick, the New Brunswick Wildlife Trust Fund, and Parks Canada Headquarters. Field assistants included R. Blackler, J. Connors, K. Gosse, M. Healy, J. Higdon, G. Holloway, D. Mitchell, G. Quinn, and C. Stratton. We are indebted to G. Forbes for providing logistical support and constructive criticisms of this manuscript. The manuscript was improved by reviews of earlier drafts by R. Barclay, S. Parsons, D. Sleep, I. Thompson and 3 anonymous reviewers.

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Submitted 30 June 2002. Accepted 20 March 2003.

Associate Editor was William L. Gannon.