

Call Character Lexicon and Analysis of Field Recorded Bat Echolocation Calls

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Introduction

The role of bats as a significant North American natural resource has been emphasized in recent years. Forest management agencies now recognize the need for practical research on bats (Barclay and Brigham 1996). The U.S. Fish and Wildlife Service lists 6 species as endangered or threatened. Species classified as "of concern" number 10 in Arizona, 12 in California, and 13 in New Mexico (Jones and Schmitt 1997).

Bats are difficult to study and generally require multiple techniques simply to determine their presence (Kalko, Handley, and Handley 1996; Kapteyn 1991; Kunz 1988; O'Farrell and Gannon 1999). The use of bat detectors is one approach to determine bat activity (with or without supplemental capture), habitat use, and foraging behavior (Ahlén and Baagøe 1999; Barclay 1985, Barclay and Brigham 1996; Bell 1980; Crome and Richards 1988; Fenton 1982; Fenton, Merriam, and Holroyd 1983; Hayes 1997; MacDonald et al. 1994; Mills et al. 1996; Sherwin, Gannon, and Haymond 2000).

Within the past five years, there has been an increasing number of scientific publications using bat detectors (e.g., 81 abstracts from the annual meetings of the American Society of Mammalogists, North American Bat Research Symposium, and Wildlife Society, 75 citations in nonrefereed reports, and at least 31 peer-reviewed publications). A number of these papers cited the use of an ultrasonic bat detector with varied levels of success. We suggest that some of these studies have not used detector hardware and analytical software to its fullest potential, especially in the choice of characters to measure and the analysis techniques employed (Gannon, Sherwin, and Haymond 2002).

Our purpose is to continue a series of papers on the use and standardization of descriptive (qualitative) to quantitative approaches in identifying free-flying bats with a bat detector, specifically Anabat II (Anabat, Titley Electronics, Ballina, NSW, Australia). Recently, we described qualitative techniques for applying the Anabat detector in research and management arenas (O'Farrell and Gannon 1999; O'Farrell, Miller, and Gannon 1999; O'Farrell, Corben, and Gannon 2000). Here, we specify nomenclature to facilitate the communication of bat-

call characteristics generated by field-portable bat echolocation detectors. A new lexicon is important because detectors like Anabat II allow immediate examination and analysis of the frequency-time structure of large quantities of echolocation data. Moreover, these highly portable devices (and others of this technological generation) quickly generate a large amount of data that is immediately available for analysis. Past terminology relied on the general frequency structure of a call and did not examine structural details necessary for the thorough use and understanding of this system. Previously, terms have been applied to behavioral or physiological contexts for relatively smaller numbers of calls but in greater detail than systems like Anabat provide. The primary purpose of the use of Anabat-like field detectors is to monitor and quickly identify bats free-flying in their natural habitat. Further, characters generated by these systems can be regarded as morphological characters for taxonomic goals.

To date, no paper has provided detailed comparisons among species based on call characters generated by Anabat or among classification techniques used to discriminate groups (but see Gannon et al. 2001; Hayes 1997; Vaughan, Jones, and Harris 1997a). The widespread belief that bats within the genus *Myotis* cannot be separated by call structure prompted tests using five species of *Myotis*. We show that, used in a standardized, repeatable fashion, Anabat-type detectors and analysis software are versatile and accurate for use in detection and analysis of echolocation calls, including the discrimination of *Myotis* species.

Materials and Methods

DEFINITIONS, CALL MORPHOLOGY, AND METHODS

Zero-crossings analysis

There are several ways to process ultrasonic vocalizations as a frequency-time display, one of which is zero-crossings analysis (ZCA). ZCA derives a frequency measurement from the reciprocal of the time period between two like zero-crossings of the signal. Although the ability of ZCA to determine harmonic structure or amplitude envelope is limited, it has the advantage of producing output rapidly in real time. ZCA

differs from other forms of bat-call analyses (e.g., spectral analysis) in shifting emphasis from the complete analysis of a small number of calls to the rapid time-frequency examination of the dominant harmonic for entire sequences of calls.

Chris Corben designed an implementation of ZCA that produced output on the screen of an IBM-compatible computer from a countdown-type bat detector. Once developed, Titley Electronics provided Anabat as a commercial product. The Anabat II frequency-time output is displayed in real time and can be saved to a computer disk in files that average 3 KB. Part of the software evolution is the ongoing development of an auxiliary program (Analook) for managing data, viewing saved calls, and editing and measuring characteristics of a call or sequences of calls.

Clarification of traditional call terminology

Existing terminology generally does not apply to the output of all detection equipment and in many cases reflects inferences on target discrimination and habitat use, rather than specific structural features of call morphology. Anabat and other ZCA-type equipment provide information mostly for the harmonic with greatest strength (this could include the fundamental or any subsequent harmonic). Additionally, calls that are received—particularly at the higher frequencies of a given harmonic—due to attenuation, orientation, or distance of the bat to the microphone may be truncated (constant frequency [CF] and quasi-CF calls may also be affected; Kalko and Schnitzler 1993; Schnitzler, chapter 44, this volume). We designate a *call* as a single, continuous vocalization separated from all other calls by a period of silence. Bats produce a variety of other vocalizations unrelated to echolocation; these are generally referred to as social calls. A related string of calls contained within a single file makes up a *sequence*. A *pass* comprises a continuous sequence of calls, given by a single bat, from the time it was first detected until the bat travels beyond the range of the detector. A pass may be made up of one or more call sequence files.

The discovery that echolocation calls were not simply a single frequency, but rather incorporated a broad range of frequencies, gave rise to the concept of frequency-modulated calls (FM; Griffin 1958). Some bats, primarily of the family Rhinolophidae, use calls now referred to as FM-CF-FM in recognition of their profound frequency sweeps. Griffin further distinguished certain call characters that differ among species—mainly duration, intensity, and the presence or absence of harmonics—and recognized that call duration and repetition rate changed according to bat behavior (Griffin, Webster, and Michael 1960). These changes are described in three phases: *commuting calls* (similar to search-phase calls in low clutter), when calls are of greatest duration and low repetition rate; *approach phase*, when call duration de-

creases and repetition rate increases progressively; and *terminal phase*, when call duration is minimal and repetition rate has increased to the point that produces a burst of calls. Since these early studies, echolocation calls are described in terms of CF, FM, or a combination of these frequency characteristics and the implied behavior incorporated in duration and call rate (Simmons, Fenton, and O'Farrell 1979). Fenton (1999) asserted that terms such as FM and CF are inadequate for describing echolocation behavior of bats, since a free-flying bat can produce a wide range of call morphology in a single call sequence. A detailed description of characters and types of echolocation sounds was presented by Simmons and Stein (1980) and Obrist (1995): duration, harmonics, constant frequency, frequency modulation, sequence of frequency components, amplitude, and adaptive variations of the preceding six dimensions. The variety of sonar sounds includes multiple-harmonic short-CF, multiple-harmonic low-amplitude FM, short-CF/FM, FM/short-CF, short-CF or FM, and long-CF/FM. Further examination of echolocation patterns under natural conditions reveals a wider range of sound types representing more complex combinations and gradations of the basic types (Kalko and Schnitzler 1993; O'Farrell and Miller 1997).

Descriptions of call structure and variability commonly use characters measured along both frequency and temporal scales (Faure and Barclay 1994; Kalko and Schnitzler 1993; Simmons, Howell, and Suga 1975; Simmons, Fenton, and O'Farrell 1979). Variability in these characteristics are commonly reported with respect to the activity of one species or the interactions between species (Obrist 1995). Frequency, duration, and the pattern of frequency change over time were used to separate species by echolocation calls (Ahlén 1990; Fenton and Bell 1981). We propose a call character lexicon that simply describes the structural aspects of a call processed with any ZCA, without incorporating implications as to physiology or behavior of the bat, but allowing increased understanding and clarity of how these variables should be used among researchers.

Revised bat detector call character lexicon and call morphology

Bat calls exhibit a wide range of shapes over time. Figs. 63.1 and 63.2 illustrate the general variety of call shape encountered in Western Hemisphere vespertilionid and molossid bat species. However, portrayal of bat species by one call (e.g., Fenton and Bell 1981) is oversimplified, because it ignores the variation present from calls in free-flying bats. Regardless of the shape, a call comprises three useful frequency characters: maximum frequency (F_{\max}), minimum frequency (F_{\min}), and characteristic frequency (F_c ; fig. 63.1). A call can possess three elements: initial sweep, body, and terminal sweep (fig. 63.1). Although the body is defined as the flattest

portion of a call, one that is a simple down sweep of short duration is composed entirely of the body (fig. 63.1C). At times, parameter values can be redundant (e.g., when F_{\min} and F_c are equal or highly correlated). In general, F_c is a more consistent measure, because F_{\min} is more affected by intensity, distance, orientation to the detector, and intensity of echoes than is F_c .

Call Variables Measured by Analook

The remaining parts of call structure are best defined in relation to a standard reference point at which the char-

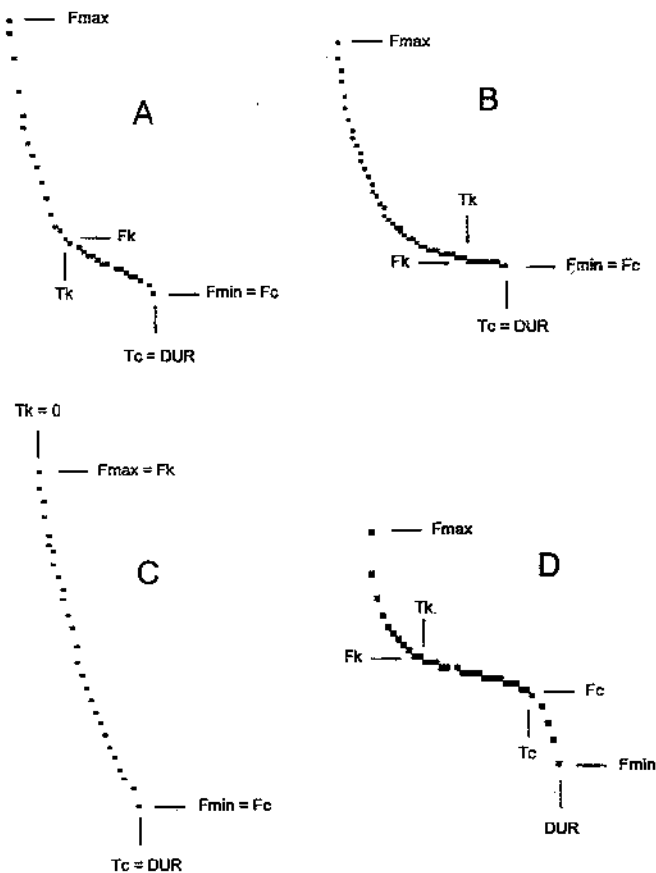


Fig. 63.1. Commonly encountered shapes of echolocation calls from North American bats. The number of calls per call sequence was recorded as N . The following variables were measured from each bat call: DUR = duration of a call (ms); F_{\max} = maximum frequency, the highest frequency of the call; F_{\min} = minimum frequency, the lowest frequency of a call; F_{mean} = mean frequency, the area under the curve divided by the duration; F_c = characteristic frequency given in kHz; T_k = time (ms) from the start of the call to the point at which F_k is measured (i.e., to the start of the body); F_k = frequency of the knee (kHz), the point at which the slope abruptly changes from the steep, initial down sweep to the flatter portion (body) of the call. T_c = time from the start of the call to the point at which F_c is measured (i.e., to the end of the body); S_1 = initial slope (decades/s; DPS), the first five points in a call; S_c = characteristic slope (decades/s; DPS), the slope of the flattest (most horizontal) part of the call.

acteristic frequency (F_c) is measured (figs. 63.1, 63.2). The body occurs prior to the F_c reference point, and the terminal sweep follows this point. If the terminal sweep forms a pronounced downward sweep, F_{\min} will be measured at the end of the sweep rather than corresponding with F_c . If the slope is negative (i.e., frequency rising), F_{\min} could be at the start of the call. The body is the flattest portion of the call ending at F_c . This change in slope is the *knee*, which marks the beginning of the body. Not all calls have a recognizable knee. The body is the flattest portion of the call (could be a very short segment). The knee is at the start of the body. A straight call has the knee at the very start and the body is the rest of that straight call. In a J-shaped call, the body is the flat part of the call at the bottom of the J, in which case the knee and characteristic frequency will be the same value.

In addition to the basic parameters describing a call (such as F_{\max} , F_{\min} , and F_c above), other measurements are generated by Analook software that may be of value in identifying species. For instance, F_k is the frequency (kHz) of the knee and T_k is the time (ms) from the start of the call to the knee (figs. 63.1, 63.2). Further, T_c is the time from the start of the call to F_c . The slope (octave/s) over the first five points of the call is the initial slope (S_1); and the slope of the body, between T_k and T_c , is the characteristic slope (S_c).

The mean frequency (F_{mean} ; kHz) is calculated as $F_{\text{mean}} = (N - 1)D/2d$, where N is the number of points in the call counted from the call display, D is the division ratio, and d is the duration (ms) of the call. This is a weighted mean—not just the average of the frequency of points—that takes into account the fact that points constituting a call are more widely spaced at lower frequencies. The total time (ms) that a call lasts is the duration (DUR). The time between calls (TBC) is the time (ms) measured from the beginning of one call to the beginning of the next. Additional analytical features are being developed in updated versions of Analook software. For more details on analyses, additional features, and free software updates contact, Chris Corben (www.hoarybat.com).

QUANTITATIVE CALL ANALYSIS

Measurements

To demonstrate the structural characters obtained with Analook, we divided North American vespertilionids into functional groups based upon their call structure (Fenton and Bell 1981; Gannon, Sherwin, and Haymond 2002). One such group included five *Myotis* species—*M. ciliolabrum*, *M. volans*, *M. lucifugus*, *M. californicus*, and *M. yumanensis*. We measured commuting calls because they are the least variable type of call within a species and are less likely to be significantly influenced by proximity to clutter or foraging behavior. We collected commute-phase calls in the field from free-flying or recently captured and released bats using Anabat. Calls were edited to exclude fragmentary calls,

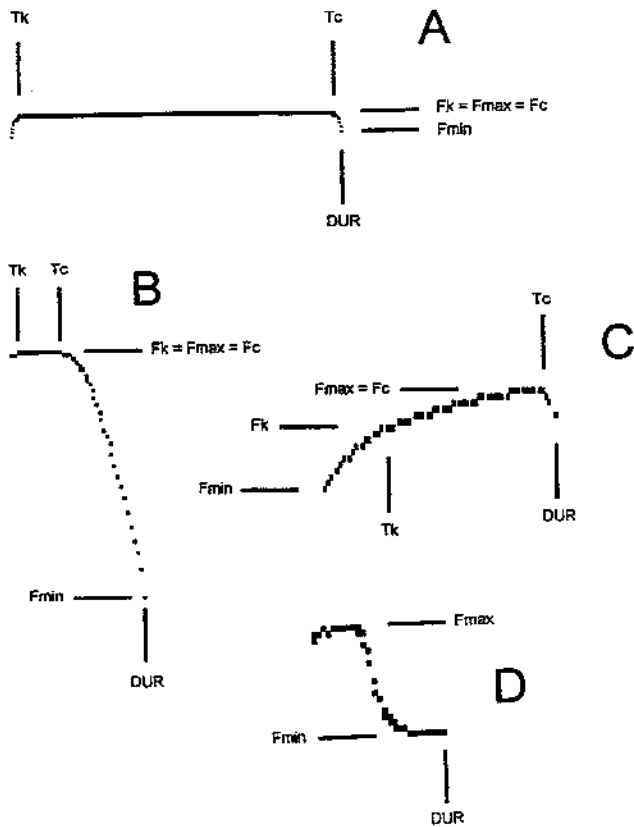


Fig. 63.2. More shapes of echolocation calls from North American bats (see fig. 63.1).

echoes, and extraneous noise prior to extraction of parameter measurements automatically calculated using Analook (figs. 63.1, 63.2).

Statistical analysis

Discriminant function analysis (DFA) is the most commonly used statistical technique for classifying calls into predetermined, a priori groupings (Sherwin, Gannon, and Haymond 2000). Logistic regression, neural networks, and classification trees are alternative statistical methods that can be used to classify bat calls (Cheng and Titterton 1994). Here, we consider the commonly applied discriminant function analysis and classification trees. A classification tree is a nonparametric classification technique (Brieman et al. 1993), in which the tree is grown using a sequential binary partitioning of the predictor variables. The algorithm is similar in spirit to forward selection of variables in multiple regression. Statistical techniques, such as pruning and shrinking, are used with cross-validation to eliminate tree branches that do not improve prediction. Unlike DFA, which is ideally suited for normally distributed data, predictor variables for a classification tree can be categorical, interval, or ordinal data. Another advantage of classification trees is that the output is easy to understand and interpret. In addition, transformations of the predictors are handled automatically, as are interactions

among variables: variables that define a “split” can be used repeatedly and split at different points in different branches of the tree. Trees can be grown using many standard statistical software packages—for example, SPSS, Splus, CART, and SYSTAT. We used Splus in this analysis.

Ten variables were measured from each bat call (figs. 63.1, 63.2): F_{\max} , F_{\min} , F_{mean} , F_c , F_k , T_c , S_1 , S_c , DUR, and TBC. Measurements were taken on 2737 calls from *E. fuscus* (648 calls; 23 individuals), *M. californicus* (1068 calls; 21 individuals), *M. ciliolabrum* (49 calls; 2 individuals), *M. lucifugus* (655 calls; 30 individuals), *M. volans* (73 calls; 5 individuals), and *M. yumanensis* (244 calls; 9 individuals). Data were randomly partitioned into a training set of 1369 bat calls and a test set of 1368 calls. The training set was used to construct the classification rule, which was then used to predict the species corresponding to the calls in the test set. Stepwise- and backward-discriminant analyses on the training set showed that all 10 features were important for distinguishing species. Hence, the classification rule for DFA was constructed using all variables.

Results

Almost all *E. fuscus* calls were correctly identified using DFA. Of the remaining five species, *M. lucifugus*, *M. ciliolabrum*, and *M. yumanensis* proved easiest to classify, with misclassification rates of only 6%, 8%, and 9%, respectively. The misclassification rates for *M. californicus* and *M. volans* were somewhat higher, 20% and 25%, respectively. Not surprisingly, most of the misclassified *M. californicus* calls were identified as *M. yumanensis*, and vice versa. The overall misclassification rate, which is the average of the species-specific error rates (assuming equal prior probabilities for all six species), was 11.6%. The raw misclassification rate, or the observed percentage of test cases misclassified, was 11.3% (155 of 1368).

Fig. 63.3 shows the classification tree grown in Splus from the 1369 bat calls in the training set. The pruned classification tree used 7 of the 10 measurements to classify calls: DUR, F_{\min} , F_c , F_k , T_c , T_k , and S_1 . The tree contained 12 terminal nodes that define the branches or distinct partitions of the predictor space. Each branch of the tree gives a prediction or classification for a call. For example, the terminal node labeled “mylu” corresponds to calls with $F_c < 44.02$ kHz (initial split), $F_{\min} > 34.005$ kHz at the next split, and $F_c < 39.07$ kHz at the final split. The condition $F_c < 44.02$ kHz is redundant, given $F_c < 39.07$ kHz, so an equivalent characterization of this branch is $F_{\min} > 34.005$ kHz and $F_c < 39.07$ kHz. Each call with these parameters was predicted to be from *M. lucifugus*. The fraction $1/333$ below this terminal node was the observed misclassification rate for this branch—that is, the proportion of the 333 calls in the training data with $F_{\min} > 34.005$ kHz and $F_c < 39.07$ kHz that are incorrectly classified as *M. lucifugus* in this case is 1.

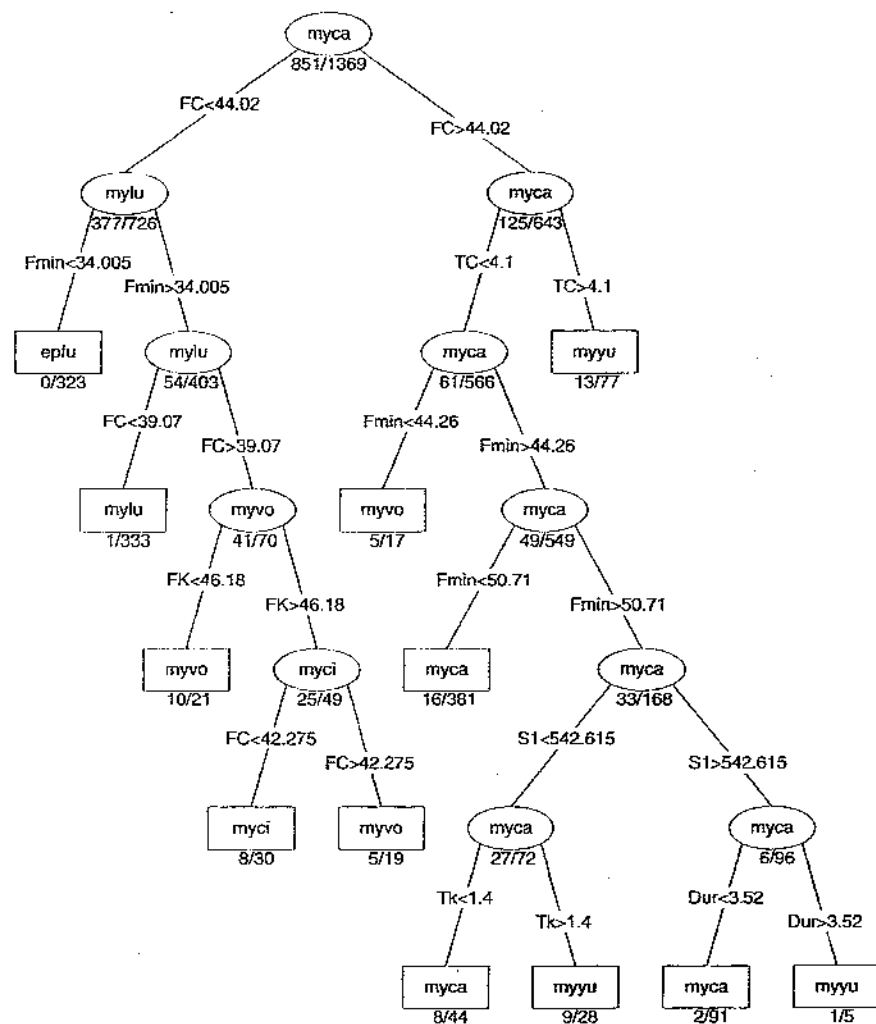


Fig. 63.3. Classification tree grown in Splus from the 1369 bat calls in call data training set. The pruned classification tree used 7 of 10 measurements to classify calls: Dur, F_{min} , F_c , F_k , T_c , T_k , and S_1 . The tree contained 12 terminal nodes that define the branches or distinct partitions of the predictor space. Each branch gives a prediction or classification for a call.

The tree was far better than DFA for correctly classifying *M. californicus* calls, but it was less successful than DFA for classifying calls from *M. ciliolabrum* and *M. yumanensis* (tables 63.1, 63.2). The overall misclassification rate from the classification tree analysis was higher than DFA (20.2% versus 11.6%), in part because the tree does not work as well on species with the smallest sample sizes. However, the raw misclassification rate is lower than DFA (9.3% versus 11.3%), which suggests that classification trees might perform as well, or better, than DFA in data sets where the sample sizes for *M. ciliolabrum*, *M. volans*, and *M. yumanensis* are larger than our sample sizes. In general, our results suggest that classification trees provide a useful alternative to DFA for classifying bat calls.

Discussion

CLASSIFICATION TREES

The traditional use of discriminant function analysis may be warranted with Anabat echolocation calls to classify two species with multivariate data sets (Gannon

et al. 2001; Lance et al. 1996). However, other methods, such as classification trees, may be most appropriate with suites of species using hundreds of calls for each. A recommendation of greater sample size is not surprising, but we found that at least 300 calls are required to provide significant separation between the five *Myotis* species examined. Some authors (e.g., Barclay and Brigham 1996; Grindal 1999; Krusic et al. 1996) either cite low sample sizes or simply do not report the number of calls examined. It is imperative to state not only the number of calls measured, the number of individual bats used in the study, and the characters that were measured and analyzed, but also to list the assumptions that the investigators made in following their study design (Gannon, Sherwin, and Haymond 2002).

Although our intent was to examine classification procedures and exercise a revised call lexicon, we discovered here that we did not have adequate sample sizes for all species. Further, we note that our analyses use multiple calls from individual bats; therefore, all observations are not independent. The intraclass correlation between responses on a bat varies from 0.29 on S_1 to 0.62

TABLE 63.1. Discriminant function analysis test data (number of observations and percentage classified into species).

Species	<i>E. fu</i>	<i>M. ca</i>	<i>M. ci</i>	<i>M. lu</i>	<i>M. vo</i>	<i>M. yu</i>	Total
<i>Eptesicus fuscus</i>	318 98.15	0	0	6 1.85	0	0	324 100.00
<i>Myotis californicus</i>	0	442 80.36	4 0.73	0	7 1.27	97 17.64	550 100.00
<i>Myotis ciliolabrum</i>	0	0	23 92.00	2 8.00	0	0	25 100.00
<i>Myotis lucifugus</i>	1 0.33	1 0.33	16 5.23	287 93.79	1 0.33	0	306 100.00
<i>Myotis volans</i>	0	0	5 15.63	3 9.38	24 75.00	0	32 100.00
<i>Myotis yumanensis</i>	0	12 9.16	0	0	0	119 90.84	131 100.00
Error count estimate	0.0185	0.1964	0.0800	0.0621	0.2500	0.0916	0.1164

TABLE 63.2. Classification trees test data (number of observations and percentage classified into species).

Species	<i>E. fu</i>	<i>M. ca</i>	<i>M. ci</i>	<i>M. lu</i>	<i>M. vo</i>	<i>M. yu</i>	Total
<i>Eptesicus fuscus</i>	322 99.38	0	0	2 0.62	0	0	324 100.00
<i>Myotis californicus</i>	0	515 93.64	0	0	6 1.09	29 5.27	550 100.00
<i>Myotis ciliolabrum</i>	0	0	16 64.00	3 12.00	6 24.00	0	25 100.00
<i>Myotis lucifugus</i>	0	2 0.65	7 2.29	284 92.81	13 4.25	0	306 100.00
<i>Myotis volans</i>	0	0	11 34.38	0	21 65.62	0	32 100.00
<i>Myotis yumanensis</i>	0	48 36.64	0	0	0	83 63.36	131 100.00
Error count estimate	0.0062	0.0636	0.3600	0.0719	0.3428	0.3664	0.2020

on F_{mean} , with an average of 0.52. This indicates that the effective sample size is much smaller than 2737, and that the misclassification rates are less reliable than would have been obtained with independent samples. There are a variety of ways to deal with the dependence, of which we mention two possible approaches. We are developing a discriminant function model with a random effect for bats within species. This model provides for arbitrary numbers of correlated responses within a bat. A simple alternative method is to average the responses on each variable within bats, and then to analyze the averages. In our data, averaging the responses within bats reduces the data set from 2737 calls to 136 call averages. A discriminant function analysis on the averages, using the data both to create the classification rule and then to assess its accuracy, gives a misclassification rate of 2.3%. Although this result is promising, the sample sizes for several species were too small to unequivocally recommend this approach. We are examining these issues more carefully; nonetheless, it appears that those species with 300 calls or 20 individuals were more easily classified than those with less data.

We were able to show that, based on calls, DFA and classification trees can distinguish among species of *Myotis*. The outgroup, *Eptesicus*, separated from *Myotis* species early and consistently in the analysis because these calls are quite different morphologically. Among *Myotis*, species were grouped into 50 kHz and 40 kHz species, similar to the initial qualitative separation used by O'Farrell, Miller, and Gannon (1999). Within these two groupings, bats could be separated further to species. Some classification error (25% in one case) could have been due to our technician's inexperience in using Analook to measure call characters, which likely contributed to the overall error rate. As with many techniques used in biology (for instance, DNA extraction and sequencing), increased experience in using the Analook system and understanding the biological and natural history differences among species could increase species discrimination and classification processes. These results are important for several reasons. Critics (e.g., Barclay 1999; Corben and Fellers 2001; Fenton 2000; O'Farrell et al. 1999; Thomas and LaVal 1988) have cited the impossibility of distinguishing certain species

acoustically, particularly among *Myotis*. O'Farrell, Miller, and Gannon (1999) have shown that it is possible to show qualitatively that there are distinguishable differences between species, even within the genus *Myotis*. Here, we have shown that repeatable, quantitative differences exist among six bat species based on defined structural characters of commute-phase echolocation calls.

FIELD RECORDING OF CALLS

Because calls were recorded in a field setting, and not all conditions affecting sound propagation and bat behavior were controlled, analysis and interpretation of call characters should not be assumed to be simple or straightforward. For instance, the transmission and reception of sound can be affected by Doppler shifts, echo, or environmental factors (e.g., temperature, humidity, vegetation structure of background). Given the high number of calls we examined, Doppler shift affected all species equally and was not likely a reason for differences found in the analysis. Some species such as *M. yumanensis* (and to some extent, *M. lucifugus*) were recorded directly over water where recordings contained strong echoes.

Although both DFA and classification trees were equivocal in discriminating groups, classification trees

may work well or better with programs such as Analoop to predict group or species membership through program-controlled filters bundled with analysis packages such as Splus. Lastly, programs such as Analoop, and those of other systems, are being improved regularly with greater utility and analysis capability. It is the duty of the practitioner to keep up with these changes and to use the equipment in an informed manner.

Acknowledgments

We gratefully acknowledge all those students who have worked diligently to master the new generation of echolocation call detectors and have applied the methods described herein (and elsewhere) to scientific questions that produce repeatable results. We especially thank Lisa T. Arciniega and Natalie M. Gannon for allowing William L. Gannon the time to thoroughly learn Anabat and its application. The authors thank M. Scott Burt, Luis A. Ruedas, Richard E. Sherwin, and two anonymous reviewers for greatly improving the clarity of this paper. Support from agencies such as the U.S. Bureau of Land Management, the U.S. Forest Service, and the New Mexico Department of Game and Fish (Share with Wildlife program) is immensely appreciated.

Part Five / Literature Cited

(Note: Book format contained lit. cit. for multiple chapters in Part Five – below are those citations relevant only to Chapter 63 – wlg)

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ECHOLOCATION

in Bats and Dolphins

