

Geographic variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*)

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Use of bat detectors to perform inventories, determine activity, and assess differential use of habitats has become a generally accepted method. However, there has been vigorous disagreement as to the level of efficacy, primarily relating to the ability to distinguish certain species and groups of species. The primary explanation suggested for the inability to identify certain species is due to the magnitude of intraspecific variation resulting in overlap among species, presumably compounded by geographic variation. *Lasiurus cinereus* has been identified as exhibiting the greatest degree of geographic variation including recent findings of distinct variation between populations in Hawaii and Manitoba. We find that claims of geographic variation have not been proven because of small sample size and lack of adequate description of method, including the behavior of the bat and the context during which bats were recorded. Previous geographical comparisons of species have relied on standard statistical methods that do not allow a comprehensive examination of the range in variation of diagnostic call parameters. We present data from a broad range of sites throughout mainland United States and Hawaii, and compare a multivariate statistical approach with repertoire plots of characteristic frequency versus call duration. Although we demonstrated a statistical finding of geographic variation in *L. cinereus*, small sample size, context, and behavior could not be discounted as the proximal cause of observed variation. The perceived variation across the geographic range that we sampled did not affect our ability to identify the species by call structure. We suggest methods for future studies of geographic variation.

Key words: acoustic identification, Anabat, echolocation, call structure, geographic variation, *Lasiurus cinereus*

INTRODUCTION

There is a common perception that microchiropteran echolocation calls vary geographically in a way that makes it difficult to use them for species identification (e.g., Brigham *et al.*, 1989; Barclay, 1999). This perception comes from a small number of papers, among which Thomas *et al.*

(1987) is the most often cited. These authors compared call parameters reported by previous studies published for North American vespertilionids, incorporating original observations. Thomas *et al.* (1987) found large discrepancies in call characteristics of several species, yet insignificant differences among other species. They concluded that there must be a thorough under-

standing of intraspecific variation in order to identify bats acoustically. This reasonable caution has given rise to the implication that without local knowledge, identification cannot be achieved from reference calls obtained elsewhere (Barclay, 1999). In spite of this, we have not found any evidence that geographic variation complicates the acoustic identification of North American bats (O'Farrell *et al.*, 1999). Our extensive experience with most of the 50 North American species, and covering a wide range of locations south to Central America ($n = 200$), has not yet revealed a single case where intraspecific differences between widely separated populations are great enough to affect recognition of species.

In this paper, we examine a portion of the basis for the idea that bat calls vary geographically. Thomas *et al.* (1987) identified the hoary bat, *Lasiurus cinereus*, as the species showing the most extreme variation in measured call parameters. More recently, Barclay *et al.* (1999) claimed to demonstrate that hoary bats of the Hawaiian subspecies *L. c. semotus* produced different calls from the mainland subspecies *L. c. cinereus* recorded at Manitoba. They attributed the differences to body size, with the markedly smaller *L. c. semotus* (forearm length, $\bar{x} = 50.89$ and 47.83 mm for 29 females and 12 males, respectively — Museum of Southwestern Biology, University of New Mexico, Albuquerque) producing higher frequency calls than the larger *L. c. cinereus* (forearm length, $\bar{x} = 54.22$ and 52.64 mm for 30 individuals of each sex — Williams and Findley, 1979). We present our own data for this species from many sites throughout the United States, including Hawaii, using two different approaches to analysis. We also discuss the problems inherent in determination of geographic variation and suggest how to deal with it.

MATERIALS AND METHODS

Data Collection

We sampled *Lasiurus cinereus* at various localities from 1994–1999 (number of locations given in parentheses): Arizona (7), California (22), Colorado (1), Massachusetts (1), Michigan (1), Ohio (1), South Dakota (1), Texas (3), Utah (1), and Wyoming (2). In addition, we analyzed calls of *L. c. semotus* that had been recorded to tape by T. Menard at three locations on Hawaii.

We recorded calls using the Anabat II bat detector and zero-crossings analysis interface module (ZCAIM; Titley Electronics, Ballina, NSW, Australia) connected to a laptop computer through a parallel port. Frequency-divided signals from the detector passed directly to the ZCAIM that interfaced with the Anabat software on the computer, allowing real-time display of calls on the computer screen. Calls were saved as hard disk files for later quantitative analyses. Most of the recorded bats were identified as *L. cinereus* by visual observations using spotlights as the bat was in free flight, but some were captured in mist nets or harp traps, and recorded after release in nearby open areas.

Echolocation Call Analyses

We analyzed 2,495 calls from 150 sequence files. It was not possible to be sure how many individual bats contributed to this data set, but it was certain to be less than 150 as some individuals would have contributed more than one file, and it would have been more than 43, which is the number of different localities sampled. We analyzed only calls that we considered to belong to the search phase. In the case of *L. cinereus*, there can be so much variation between adjacent calls that defining search phase is not always easy. However, we avoided calls that were part of an obvious approach sequence or calls that were closer than 100 ms from another call. We considered calls to be part of an approach sequence if they changed progressively towards shorter duration, higher frequencies, and shorter time between calls. We also avoided calls that were recorded so poorly that they contained gaps. Not all calls we analyzed were whole calls. In many cases, the call duration would have been reduced from that emitted by the bat because the lower amplitude parts of the calls were not detected.

Calls were analyzed using Analook version 4.5 software written by C. Corben specifically for viewing and analysis of Anabat recordings. Call sequences were filtered before measurement using an Analook user-defined filter designed to exclude

echoes, unwanted noise, and calls of most other bat species. This filter was also set to exclude any call with duration less than 2 ms.

Parameters measured were maximum frequency (F_{\max}), minimum frequency (F_{\min}), mean frequency (F_{mean}), frequency at the knee (F_k), time at the knee (T_k), quality of the knee (Q_k), characteristic frequency (F_c), time at characteristic frequency (T_c), duration (DUR), initial slope (S_i) and characteristic slope (S_c). Frequencies are given in kHz, times given in ms, and slope expressed in octaves per second (octaves/s).

F_{\max} is the highest frequency displayed in a given call, which will tend to slightly underestimate the maximum frequency that would be determined using spectral analysis. F_{\min} is the lowest frequency displayed in a given call. This should correspond roughly to measurement of minimum frequency using spectral analysis, except that determination of F_{\min} using zero-crossings analysis may be complicated by difficulties in determining where the call ends and echoes start. F_{mean} is calculated as $F_{\text{mean}} = (N-1) \times D / (2d)$, where N is the number of dots in the call (e.g., Fig. 3), D is the division ratio, and d is the duration (ms) of the call. It can be thought of as the average frequency of the call, but it is not the average of the frequencies depicted by all the dots in the call, as it is weighted by the time spent between each pair of dots. The flattest portion of the call follows a change in slope referred to as the knee. The change in slope may vary from distinctly bilinear to curvilinear. Q_k is an attempt to quantify the degree of curvilinearity; the lower the number the more curvilinear and less well defined is the knee. F_k is the frequency at the knee and T_k is that time from the start of the call to that point. The characteristic frequency (F_c) is the frequency at the end in time of the flattest part of the call, and T_c is the time from the start of the call to that point. We have found F_c to be the single most important parameter for identification of vespertilionid bats, although it does not correspond closely to any parameter typically derived using spectral analysis. However, for many types of calls, there will be a close correspondence between F_c and F_{\min} . DUR is the time from the beginning to the end of the call. We took great care in excluding echoes from this measure. DUR should correspond closely to the duration measured by spectral analysis. S_i is the steepest slope measured at the beginning of a call between the first dot in the call and one of the following five dots. S_c is the slope of the flattest part of the call (the body of the call between F_k and F_c).

We analyzed our data in two different ways. First, we applied a canonical function analysis (CFA) based on 115 sequences. Calls within a sequence lacked independence, therefore mean values were calculated

for each parameter for a sequence to address pseudoreplication. We used sequences that were separated in time in an attempt to avoid focusing on a single individual for more than one sequence, hence the use of only 115 of the 150 sequences available. After the CFA, we had the opportunity to sample the area in southern Arizona that was studied by Fenton and Bell (1981), where we recorded an additional 563 calls within 30 sequences from 17 individual bats. The distribution of measures did not differ statistically from the existing database (Appendix) so we did not reanalyze our data set to include the recently recorded Arizona calls.

We also examined our data by plotting F_c against DUR, producing a two-dimensional graph hereafter referred to as a repertoire plot. The idea behind this approach is that for most species of bats, the frequencies produced in their echolocation calls vary within an individual depending on their circumstances. One of the key circumstances affecting call frequency is the degree of clutter in which the bat is flying, where clutter can be thought of as the proximity of the bat to echo-producing elements around it. In high clutter, call frequencies tend to increase and call durations decrease compared to low clutter. Ideally, it would be desirable to be able to plot frequency against an independent variable which directly reflects the degree of clutter in which the bat is flying, but in practice, that information is not usually available in a field situation (but see Sherwin *et al.*, 2000). Nevertheless, plotting frequency against duration achieves something of the same effect, because it facilitates visual comparison of calls with similar characteristics.

RESULTS

Repertoire Plots

The repertoire plot for all *L. cinereus* calls provides an envelope of the variation within the species as a whole (Fig. 1). The envelope shows a broad range in both parameters, with F_c ranging from 15 to 34 kHz and DUR from 2 to 23 ms. However, there is a distinct upper boundary to the plot, so that calls with long duration have low frequencies, and calls with high frequencies have short duration. Twelve calls were selected from various points within the repertoire plot (Fig. 1, calls A–L) to illustrate the range in shape of search-phase

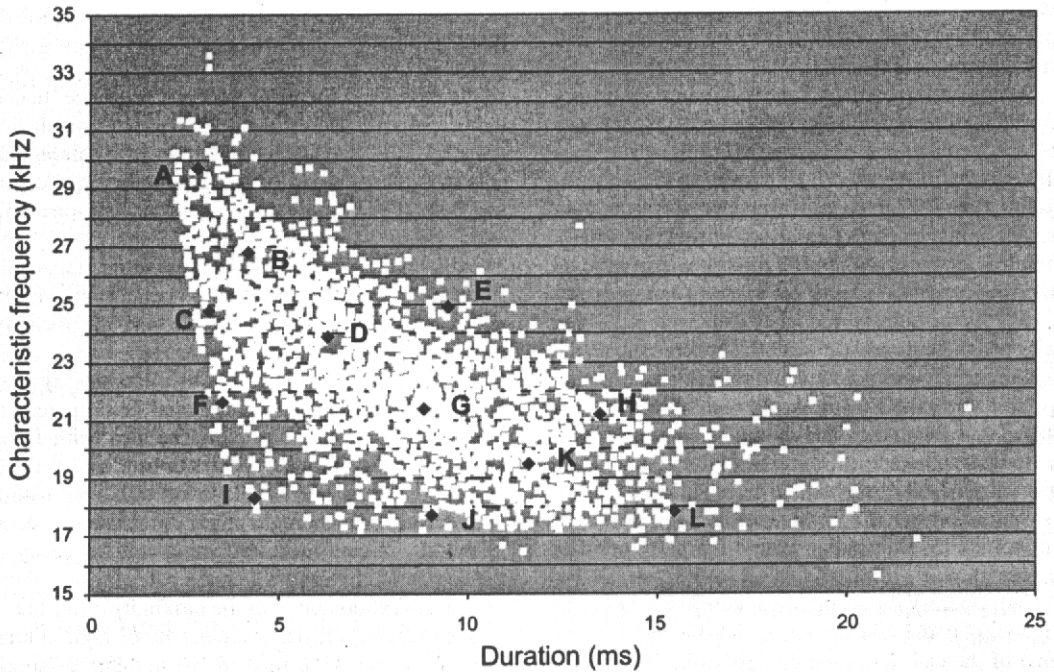


FIG. 1. Repertoire plot of characteristic frequency (F_c) versus duration (DUR) of all echolocation calls obtained for *Lasiurus cinereus*, showing location of example calls (A–L) reproduced in Fig. 2

calls (Fig. 2). The plots for Arizona and California, which had the largest sample sizes, contained data points throughout the envelope for the whole species.

The C, F, and I calls (Fig. 2) all appear at the left edge of the repertoire plot, where calls have shorter duration than most at the same frequency. They are likely to be fragments, where only the loudest part of a call has been detected, perhaps because the bat was too far from the observer. Although it would be preferable to exclude such calls from analysis, there is no objective way to decide that they are fragments. However, when fragments are included in a repertoire plot, their data points will appear to the left of where they would have been had the whole call been detected. This happens because durations are obviously reduced by failing to detect the entire call, but the F_c value is unlikely to be affected because it is measured near the point of maximum intensity. This can easily be seen by looking at

which parts of calls are detected first and last in a sequence, when the bat is too far to be detected completely (C. Corben, personal observation).

Lasiurus cinereus commonly shows two distinctly different kinds of search phase sequences. An individual hunting relatively low to the ground illustrates the distinct frequency fluctuations commonly seen in this species (Fig. 3A), whereas an individual flying in an open situation away from clutter gives much more consistent calls (Fig. 3B). Given that different species in the same genus all show a similar overall pattern (although the range of call frequencies differ for each species), we consider it a reasonable assumption that different subspecies of the same species should also show a similar range of call types. Therefore, a comparison between calls of *L. c. semotus* and *L. c. cinereus* should only be made between calls from similar parts of the species' repertoire. Otherwise, there is a

risk of comparing calls like those in Fig. 3A from one population with calls like those in Fig. 3B from the other.

Measured frequency parameters of the steeper calls will be higher than those of the flatter calls, so a simple comparison of means of call frequency parameters will be vulnerable to different mixes of call types in the samples being compared. If the *L. c. semotus* sample was dominated by steeper calls and the *L. c. cinereus* sample was dominated by flatter calls, the means of call parameters would appear different, without any underlying difference in echolocation strategy between the subspecies. Therefore, a simple comparison of frequencies between populations could be misleading, unless it was demonstrated that similar types of calls were being compared from each population. The importance of the repertoire plot is that calls of different types will be spread out in two-dimensional space while calls showing similar features will cluster together. Our assumption is that dif-

ferent populations should ultimately produce similar clouds of points when adequately sampled, though shifted in frequency if those populations differ. Clouds of points differing in shape would suggest inadequate sampling or the presence of cryptic taxa.

The states that differed most conspicuously from the others were Hawaii and the block of Massachusetts, Michigan, and Wyoming. For further discussion, we separated the data set into three groups: Hawaii, northern USA (Massachusetts, Michigan, and Wyoming), and southern USA (remaining states). Northern USA data points lie mostly along the lower edge of the entire cloud of points (squares, Fig. 4), indicating that these bats were producing calls at the lower end of the overall frequency range. These calls generally look like those in the sequence shown in Fig. 3B, which was recorded in Michigan. Although data for northern USA would have a different mean compared to those from elsewhere, we sug-

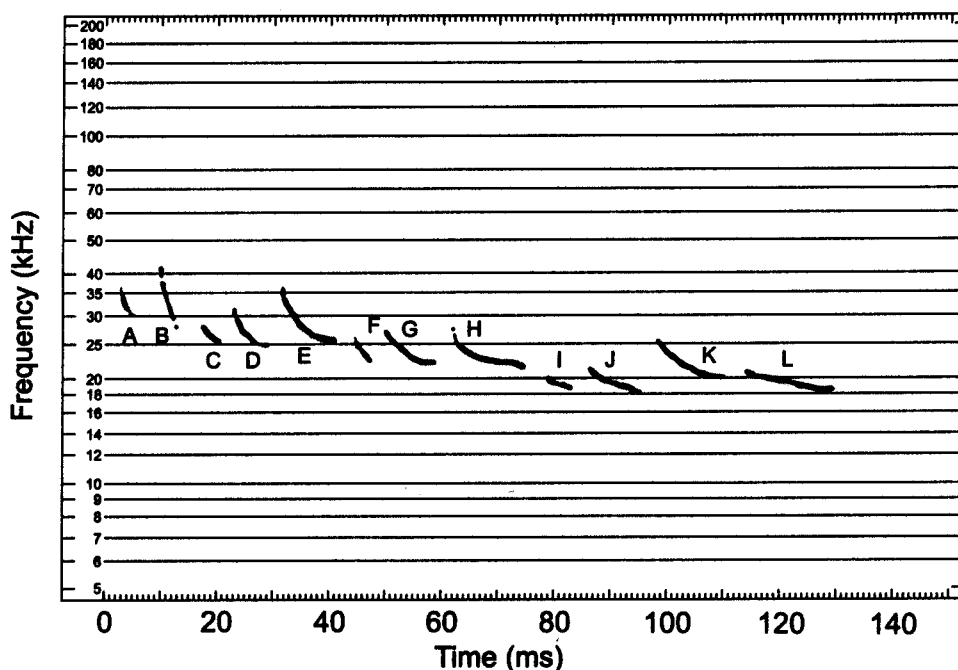


FIG. 2. Examples of *Lasiurus cinereus* calls from different parts of the repertoire plot depicted in Fig. 1

gest that the differences probably are a result of sampling bias instead of geographic differences. The cloud of points from northern USA forms a subset of the cloud for southern USA.

The Hawaiian data show calls occupying the upper portion of the total range of frequencies, generally lacking calls of longer duration (triangles, Fig. 4). Hawaii appears to represent a subset of the calls from southern USA rather than a separate cloud of data points shifted along the frequency axis. We acknowledge that a larger sample size might extend the Hawaiian cloud upwards as well as downwards, in

which case the repertoire for Hawaiian bats would clearly extend above that for mainland bats. However, it is equally plausible that the upper range of frequencies has been effectively sampled and only the lower part of the Hawaiian cloud is missing.

Canonical Function Analysis

There was variation among states for the call parameters measured from *L. cinereus* (Appendix), and CFA revealed significant differences among geographic localities (Table 1). The first four canonical axes accounted for 90.8% of the variance observed. Frequency parameters (F_{\min} ,

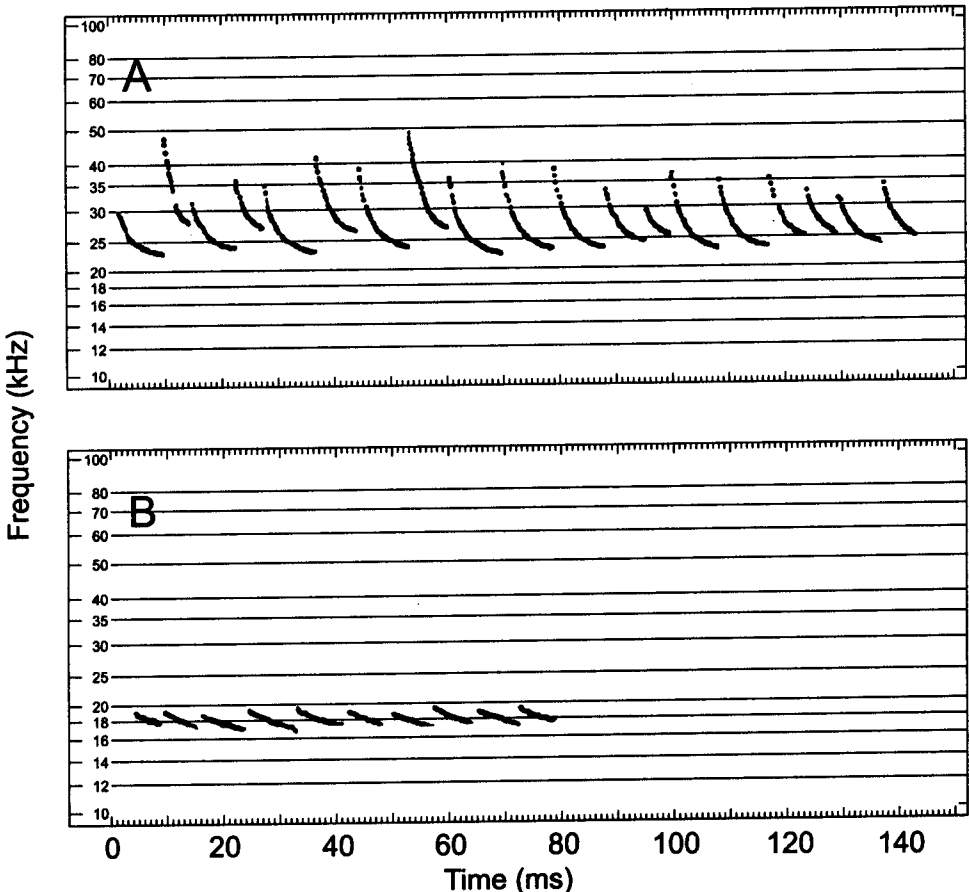


FIG. 3. Two different types of search-phase call sequences produced by *L. cinereus*. (A) Sequence with fluctuating frequencies seen in moderate clutter. (B) Lower frequency sequence with uniform frequencies as seen in zero clutter

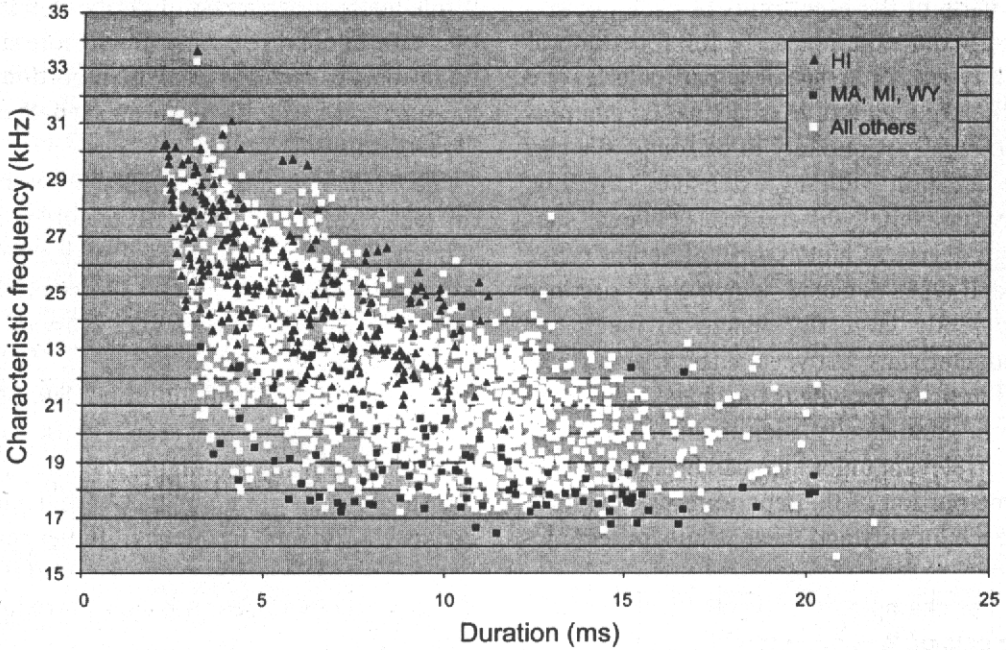


FIG. 4. Repertoire plot of characteristic frequency (F_c) versus duration (DUR) for *L. cinereus* from three different regions. Abbreviations: HI = Hawaii; MA = Massachusetts; MI = Michigan; WY = Wyoming

F_{mean} , F_k , and F_c) were most important in the first axis, and time-related parameters (T_k , and DUR and T_c , respectively) were important in the second and third axes (Fig. 5). The quality of the knee (Q_k) also significantly accounted for the variation in the second axis. Variables within each set of parameters were redundant. Overall variability was least for F_c but virtually identical with F_{min} (coefficient of variation, CV = 8.41 and 8.42%, respectively) and DUR approximated that of T_c (CV = 25.97 and 25.15%, respectively). Initial slope (S_i) and degree of curvilinearity (Q_k) loaded most heavily in the fourth axis. Hawaii was at the extreme for high frequency and low duration parameters. Wyoming and Massachusetts were at the opposite extreme. CFA depicted statistically significant differences between some locations, suggesting geographic variation in the structure of echolocation calls we examined (Fig. 5).

DISCUSSION

Documenting the Call Envelope

Barclay *et al.* (1999) used comparisons of means to justify their findings that calls of *L. c. semotus* differed from those by *L. c. cinereus*. This approach shares a common element with ours in that they compare sets of calls and conclude that there are differences based on statistical tests. Our repertoire plot (Fig. 4) shows calls from Hawaii occupying a different part of the call envelope (where species call characters fall in bivariate plot space) as compared to those from northern USA. We would expect to find statistically significant differences between these populations based on widely divergent means and marginal overlap of data points. However, such a comparison can only be meaningful if we assume that the samples drawn from these different localities are truly random samples of simi-

lar parts of the repertoires of each population. In our experience, the full repertoire of call types for a species, particularly one with large variation, such as *L. cinereus* (see Fig. 1) is unlikely to be found at a single location without extensive sampling. Environmental differences between sites (e.g., degree of clutter) will affect the range of call types detected, which could produce apparently large differences in mean call characteristics between sites without real differences between the bats inhabiting them. Statistically significant differences are irrelevant unless we can be sure that the same portion of the repertoire was sampled at each locality and these results reflect biological reality.

For example, in a hypothetical scenario, the bats of Wyoming might tend to feed on moths that fly in the open, well away from vegetation, while those in Hawaii might feed on moths flying closer to the ground. Such a difference could come about because of factors entirely exogenous to the bats, but strongly correlated with locality.

While such a difference might be detected by a careful observer, other much more subtle influences could affect which portion of the repertoire was likely to be seen at any given locality.

Lasiurus cinereus commonly shows two distinctly different kinds of search phase sequences. All other species of *Lasiurus* examined to date (*L. ega* — O'Farrell and Miller, 1999; *L. blossevillii*, *L. borealis*, *L. xanthinus*, and *L. intermedius* — C. Corben and M. J. O'Farrell, unpublished data) also show a similar variety of search phase calls, including both fluctuating, higher frequency, steeper calls (e.g., Fig. 3A) and more consistent, lower frequency, flatter calls (e.g., Fig. 3B). However, the different species occupy different bands of frequencies.

At the subspecific level Barclay *et al.* (1999) concluded that the calls of *L. c. semotus* differ from those of *L. c. cinereus* based on a simple comparison of the means of frequency and duration parameters. They argued that the statistically significant dif-

TABLE 1. Total canonical structure for canonical function analysis of echolocation calls of *Lasiurus cinereus* by site. Abbreviations: DUR = duration (ms), F_{\max} = maximum frequency (kHz), F_{\min} = minimum frequency (kHz), F_{mean} = mean frequency (kHz), T_k = time at the knee (ms), F_k = frequency at the knee (kHz), Q_k = quality of the knee, T_c = time at the characteristic frequency (ms), F_c = characteristic frequency (kHz), S_i = initial slope (octaves/s), S_c = characteristic slope (octaves/s) (see Materials and Methods for definitions). Variables with the highest 'loadings' are in bold

Call variable	Canonical axis			
	1st	2nd	3rd	4th
DUR	-0.713	0.197	0.334	0.065
F_{\max}	0.780	0.336	0.062	-0.322
F_{\min}	0.920	-0.058	0.081	-0.202
F_{mean}	0.902	0.067	0.086	-0.240
T_k	0.389	0.842	-0.044	0.099
F_k	0.927	-0.041	0.144	-0.136
Q_k	0.490	0.711	0.048	-0.359
T_c	-0.717	0.243	0.357	0.039
F_c	0.927	-0.069	0.084	-0.209
S_i	0.613	0.379	0.011	-0.404
S_c	0.810	-0.186	-0.034	-0.118
Cumulative Variance	0.436	0.718	0.832	0.908
Significance	< 0.001	< 0.001	< 0.001	< 0.05

ferences found between Manitoba and Hawaii supported their prediction that the smaller *L. c. semotus* would have higher frequency calls than the larger *L. c. cinereus*. Therefore, they attributed differences between means to factors endogenous to the bats, and did not consider the possibility that they might be due to environmental factors. However, they described calls from Manitoba as having shallower frequency sweeps, indicating they were comparing different kinds of calls between Manitoba and Hawaii. Therefore, their conclusions would require the assumption that Hawaiian bats differed from those of Manitoba by lacking shallow frequency sweep calls in their vocal repertoire. If true, this would suggest that *L. c. semotus* differs more from *L. c. cinereus* than *L. c. cinereus* does from other congener *Lasiurus*. Barclay *et al.* (1999) further stated that Hawaiian *L. cinereus* flew in more cluttered habitats than do North American individuals. This could explain why they encountered different call types between Hawaii and Manitoba, and it would suggest that the differences they found could have been exogenous, without any inherent differences between the subspecies. In our opinion the differences that they report could be entirely due to the relative amounts of clutter where bats were recorded.

In another situation, Barclay *et al.* (1999) invoked exogenous factors to explain certain findings that contradicted their expectations. When bats at open sites produced shorter duration, higher frequency calls than those at closed sites, they argued against genetic differences between sites, attributing the differences to some unknown, exogenous factors. Yet they argued that call differences between different islands in Hawaii could have been due to genetic differences. If unknown exogenous factors could cause the differences

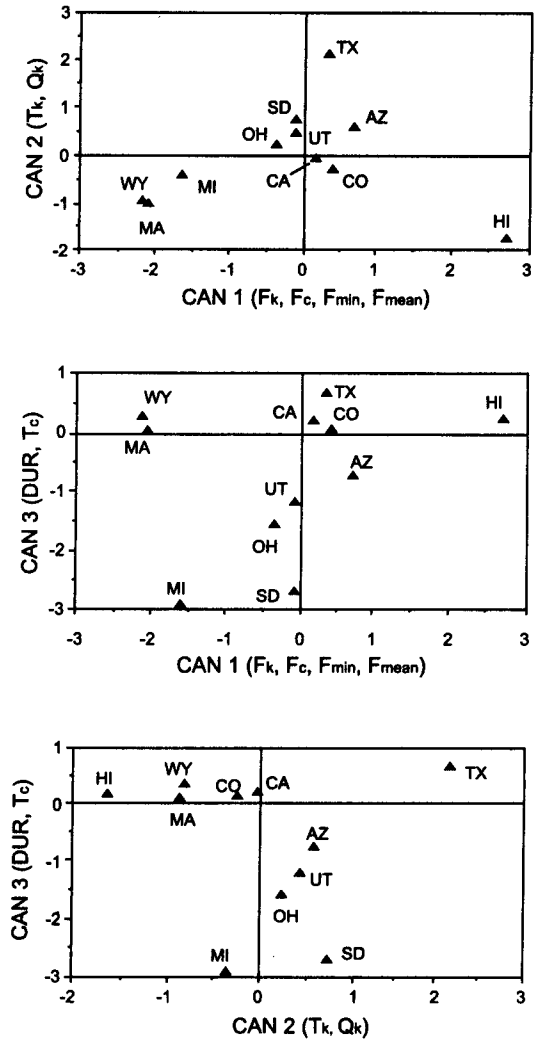


FIG. 5. Distribution of bat calls by state (AZ = Arizona; CA = California; CO = Colorado; HI = Hawaii; MA = Massachusetts; MI = Michigan; OH = Ohio; SD = South Dakota; TX = Texas; WY = Wyoming), within the discriminant space formed by (A) Canonical Axis 1 (CAN 1) and Canonical Axis 2 (CAN 2), (B) Canonical Axis 1 and Canonical Axis 3 (CAN 3), and (C) Canonical Axis 2 and Canonical Axis 3. Abbreviations: DUR = duration (ms); F_{min} = minimum frequency (kHz); F_{mean} = mean frequency (kHz); T_k = time at the knee (ms); F_k = frequency at the knee (kHz); Q_k = quality of the knee; T_c = time at the characteristic frequency (ms); F_c = characteristic frequency (kHz)

between open and closed sites, they could also explain the small differences between

different islands, or the larger differences between Manitoba and Hawaii.

*Does Geographic Variation Occur in *Lasiurus cinereus*?*

Statistically significant call differences were found between bats recorded in different places (Barclay *et al.*, 1999; this study), but there is no evidence to determine whether these discrepancies resulted from genetic variation or from environmental factors. It is important to make this distinction if possible. If the observed differences between the bats of Hawaii and the mainland are a consequence of environmental factors, then this is less biologically significant than if they were due to genetic variation between the populations. In addition, it would mean that the observed differences would be less likely to persist in time, and that long-term observation probably would show the entire repertoire in both regions. We stress here that whatever variation exists between geographic areas, the ability to identify *L. cinereus* acoustically is not affected by it.

We suggest that one of the following three scenarios would explain data currently available on geographic variation in *L. cinereus*:

(1) there might be no endogenous differences among populations of *L. cinereus* throughout its range. Those between Hawaiian and mainland forms could be a result of environmental variability and may disappear with further sampling. In this case, additional sampling will result in repertoire plots that are similar for all populations;

(2) mainland forms all have the same range of calls, but *L. c. semotus* differs by producing calls with consistently higher frequencies. In this case, further data collection in Hawaii would extend the repertoire plot until it had a similar shape to that for main-

land animals, but to be shifted upwards along the frequency axis;

(3) differences may exist between populations on the mainland as well as between the mainland and Hawaii. The samples we have for California and Arizona might be composite, containing representation of more than one mainland call type. In this case, our repertoire plot for southern USA will have been extended in range by including data from more than one distinct population.

Recommendations for Determining Geographic Variation in Echolocation Calls

Any attempt to examine geographic variation should begin with a comprehensive understanding of the total repertoire of each population of interest. At a minimum, this will require sampling in a variety of habitats and in a broad range of clutter conditions. Seasonal changes in foraging and other behavior may also be critical to document. In the absence of such knowledge, the best compromise would be to assume that different populations will show similar vocal repertoires, and to compare calls only from the same part of the repertoire. This could be accomplished by comparing only calls of similar shape or calls that are part of similar sequences. In the case of *Lasiurus*, for example, it might be reasonable to compare only calls like those in Fig. 3B, or calls in sequences showing the similar degree of frequency fluctuation and time between calls. Also, we believe that the use of concordant data sets (e.g., Gannon *et al.*, In press) will help to answer questions of geographic variation.

We acknowledge that it might be possible for closely related populations to differ fundamentally in the range of call types they produce. However, this should not be the default assumption, especially if it can be shown that populations more removed

taxonomically share similar repertoires. We argue that examination of the range of call types seen in similar species could be helpful to interpreting variation within a species.

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LITERATURE CITED

- BARCLAY, R. M. R. 1986. The echolocation calls of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats as adaptations for long- versus short-range foraging strategies and the consequences for prey selection. *Canadian Journal of Zoology*, 64: 2700–2705.
- BARCLAY, R. M. R. 1999. Bats are not birds: a cautionary note on using echolocation calls to identify bats. *Journal of Mammalogy*, 80: 290–296.
- BARCLAY, R. M. R., J. H. FULLARD, and D. S. JACOBS. 1999. Variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*): influence of body size, habitat structure, and geographic location. *Canadian Journal of Zoology*, 77: 530–534.
- BELWOOD, J. J., and J. H. FULLARD. 1984. Echolocation and foraging behaviour in the Hawaiian hoary bat, *Lasiurus cinereus semotus*. *Canadian Journal of Zoology*, 62: 2113–2120.
- BRIGHAM, R. M., J. E. CEBEK, and M. C. HICKEY. 1989. Intraspecific variation in the echolocation calls of two species of insectivorous bats. *Journal of Mammalogy*, 70: 426–428.
- FENTON, M. B., and G. P. BELL. 1981. Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy*, 62: 233–243.
- FENTON, M. B., H. G. MERRIAM, and G. L. HOLROYD. 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. *Canadian Journal of Zoology*, 61: 2503–2508.
- GANNON, W. L., R. E. SHERWIN, T. N. DECARVALHO, and M. J. O'FARRELL. In press. Pinnae and echolocation call differences between *Myotis californicus* and *M. ciliolabrum* (Chiroptera: Vespertilionidae). *Acta Chiropterologica*.
- MCCRACKEN, G. F., J. P. HAYES, J. CEVALLOS, S. Z. GUFFEY, and F. C. ROMERO. 1997. Observations on the distribution, ecology, and behaviour of bats on the Galapagos Islands. *Journal of Zoology (London)*, 243: 757–770.
- OBRIST, M. K. 1995. Flexible bat echolocation: the influence of individual, habitat, and conspecifics on sonar signal design. *Behavioral Ecology and Sociobiology*, 36: 207–219.
- O'FARRELL, M. J., and B. W. MILLER. 1999. Use of vocal signatures for the inventory of free-flying Neotropical bats. *Biotropica*, 31: 507–516.
- O'FARRELL, M. J., B. W. MILLER, and W. L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, 80: 11–23.
- SHERWIN, R. E., W. L. GANNON, and S. HAYMOND. 2000. The efficacy of acoustic techniques to infer differential use of habitat by bats. In *Contributions to the study of bats: field use of acoustic detectors* (W. L. GANNON and W. BOGDANOWICZ, eds.). *Acta Chiropterologica*, 2: 145–153.
- THOMAS, D. W., G. P. BELL, and M. B. FENTON. 1987. Variation in echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. *Journal of Mammalogy*, 68: 842–847.
- WILLIAMS, D. F., and J. S. FINDLEY. 1979. Sexual size dimorphism in vespertilionid bats. *The American Midland Naturalist*, 102: 113–126.

APPENDIX

Grand means (\bar{x}) and standard deviations (SD) of measurement variables from echolocation calls of *Lasiorus cinereus* from various locations in the United States. Variables measured: DUR = duration (ms), F_{\max} = maximum frequency (kHz); F_{\min} = minimum frequency (kHz); F_{mean} = mean frequency (kHz); T_k = time at the knee (ms); F_k = frequency at the knee (kHz); Q_k = quality of the knee; T_c = time at the characteristic frequency (ms); F_c = characteristic frequency (kHz); S_i = initial slope (octaves/s); S_c = characteristic slope (octaves/s) (see text for definitions). State acronyms: AZ = Arizona; SE AZ = southeast Arizona — same locality as in Fenton and Bell (1981); CA = California; CO = Colorado; HI = Hawaii; MA = Massachusetts; MI = Michigan; OH = Ohio; SD = South Dakota; TX = Texas; UT = Utah; WY = Wyoming

Variable	AZ	SE AZ	CA	CO	HI	MA	MI	OH	SD	TX	UT	WY
DUR ^a												
\bar{x}	7.11	9.67	8.48	8.37	5.32	13.72	6.78	9.15	8.52	10.46	8.42	11.54
SD	1.62	2.80	2.51	1.80	1.42	4.19	—	2.74	1.23	1.52	3.31	3.18
F_{\max}												
\bar{x}	33.71	27.44	28.18	27.21	34.81	20.23	19.42	25.19	25.09	33.22	30.24	20.83
SD	6.06	7.35	4.74	7.82	6.06	1.42	—	5.76	1.18	5.85	7.76	3.14
F_{\min} ^b												
\bar{x}	22.76	21.11	21.64	21.22	25.41	18.26	17.71	19.86	20.40	21.66	21.44	18.70
SD	1.69	2.42	1.93	4.01	1.53	0.71	—	2.05	0.92	0.75	1.91	1.65
F_{mean}												
\bar{x}	25.19	22.62	23.29	22.89	27.95	18.96	18.27	21.19	21.50	24.16	23.40	19.37
SD	2.58	3.41	2.43	4.65	2.52	0.87	—	2.80	0.90	1.73	2.94	1.98
T_k												
\bar{x}	3.40	2.85	2.86	2.84	2.47	1.90	1.94	3.41	4.16	4.80	3.17	1.50
SD	0.67	1.25	1.22	0.66	0.52	1.27	—	1.14	0.69	0.78	1.12	1.12
F_k												
\bar{x}	24.36	22.60	23.39	23.12	27.60	19.54	18.76	21.23	21.27	23.49	22.73	19.79
SD	1.82	2.94	2.19	4.02	1.81	0.75	—	2.49	1.00	1.11	2.26	1.98
Q_k												
\bar{x}	10.19	5.73	5.67	4.70	6.30	1.09	1.33	4.76	4.73	12.12	8.47	1.72
SD	3.69	4.54	3.65	3.21	3.34	1.04	—	3.51	0.39	5.37	6.20	1.70
T_c												
\bar{x}	6.76	9.02	7.88	7.98	4.92	12.28	6.36	8.64	7.81	10.05	7.67	10.82
SD	1.45	2.61	2.35	1.75	1.24	3.14	—	2.68	1.21	1.39	2.85	2.86
F_c												
\bar{x}	22.88	21.22	21.73	21.45	25.70	18.34	17.78	19.94	20.46	21.78	21.59	18.78
SD	1.75	2.42	1.97	4.00	1.51	0.74	—	2.08	0.93	0.79	1.91	1.61
S_i												
\bar{x}	230.27	138.61	135.83	100.99	198.31	23.36	42.60	85.77	80.32	208.48	183.93	45.33
SD	99.79	102.88	72.50	52.07	149.67	33.62	—	71.67	23.57	87.01	124.01	39.96
S_c												
\bar{x}	32.90	22.04	26.52	24.99	48.23	10.75	16.71	21.79	15.55	22.20	23.65	10.90
SD	12.69	17.15	10.30	8.43	21.13	5.19	—	13.94	3.90	6.51	14.05	8.42
n (sequence files)	15	30	33	3	13	3	1	4	2	16	4	21
n (calls)	536	563	918	38	284	13	11	50	50	390	124	81

^a — Arizona, 15 ms (Fenton and Bell, 1981); British Columbia, Canada, > 5 ms (Fenton *et al.*, 1983), and 10.2 ms alone and 9.6 ms with conspecifics (Obrist, 1995); Hawaii, 8.0 ms (Belwood and Fullard, 1984); Manitoba, 10.3 ms (Barclay, 1986); Galapagos, Ecuador, 7.3, 7.4, 11.7 ms (McCracken *et al.*, 1997)

^b — Arizona, 26 kHz (Fenton and Bell, 1981); British Columbia, Canada, 20 kHz (Fenton *et al.*, 1983), and 17.1 kHz alone and 18.0 kHz with conspecifics (Obrist, 1995); Hawaii, 25.4 kHz (Belwood and Fullard, 1984); Manitoba, 16.9 kHz (Barclay, 1986); Galapagos, Ecuador, 22.6, 22.5, 24.2 kHz (McCracken *et al.*, 1997)