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METHODS TO DISCRIMINATE ECHOLOCATION CALLS BETWEEN MALE AND FEMALE BIG BROWN BATS (*EPTESICUS FUSCUS*)

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ABSTRACT

Methods to discriminate echolocation calls of male and female big brown bats (*Eptesicus fuscus*) during the non-mating season were investigated. A total of 4,018 calls from 23 bats (12 males and 11 females) were analyzed. The bat calls were recorded in natural settings in Georgia (13 bats) and Ohio (10 bats). Both hand-held and flying calls were analyzed. Calls were further divided into multiple classes based on duration. A discriminant function analysis (DFA) detected sexual differences between the calls in some situations. In particular, when calls of similar durations were compared, the results indicated that short calls may be especially useful in differentiating the sexes.

Keywords: big brown bats, echolocation, *Eptesicus fuscus*, sex differences

INTRODUCTION

Bats use echolocation for many purposes, such as targeting and capturing prey, communicating between individual bats, and navigating through cluttered environments (1). There are many ways to characterize the variation in bat echolocation calls as calls can differ in their duration, their harmonic structure, their frequency pattern, and their amplitude (1). An echolocation call is classified as a constant-frequency (CF) call when the entire call is made at the same frequency (1). Conversely, an echolocation call classified as a frequency-modulated (FM) call sweeps downward through a range of frequencies (1). This variation in echolocation calls is associated with differences in hunting behavior as well as correlating with the species of bat (2). For example, bats living in cluttered environments tend to use more FM calls, as these types of calls can provide better multidimensional acoustic images (1). There can also be variation in a bat's repertoire as calls change in response to environmental and social factors (3). There is also debate on the importance of geographic variation, where calls of a given species change throughout its geographic range, because such variation may complicate attempts to classify calls (4-7).

Acoustical differences between males and females have been shown in other mammalian species (8). Because bats fly at night when visual acuity is impaired, and male and female bats are generally monomorphic in their physical appearance, they have limited ability to tell the sexes apart by sight (9). Bats are also not likely to use olfactory signals alone, as chemicals have a slow speed of transmission through the air, and would not be very accurate for locating a bat in flight (9). Differences between the echolocation calls of male and female bats have been identified in some species (10-13), but these have typically been species that use CF calls (14). Big brown bats use FM calls, and there is evidence that females of the species are able to discriminate between male and female bat sonar calls (9). Kazial and Masters (2004) performed playback experiments in which a female *E. fuscus* was presented with playback of echolocation calls from unfamiliar conspecifics. Their results showed that the subject animals responded differently to calls of the two sexes, which further reinforces the hypothesis that bats can determine sex difference through echolocation calls alone (9). Although this behavioral study has shown that female big brown bats can indeed recognize members of the opposite sex, researchers thus far have been unable to identify reliable differences in the echolocation calls of males versus females (14,15). Current research has identified some variables that distinguish male and female *E. fuscus* calls, such as duration and frequency-related variables, but they have proven useful only during the mating season (16).

The purpose of our project was to statistically examine the differences between echolocation calls of male and female big brown bats, extending the results of previous work. The study done by Masters et al. (1995) looked only at the differences between juvenile males and females of *E. fuscus* born in captivity. Kazial et al. (2001) looked at the differences between adult male and female E. fuscus, all from Ohio. Research at Auburn University by M. Grilliot (16) has looked at bats from Georgia and Alabama in a captive colony during mating season. All of these studies used calls recorded from bats in enclosed spaces, which may result in calls that differ from those produced by a bat in open areas (17). Additionally, the calls were used from bats that came from a fairly localized region. Our study examined bat echolocation calls from a wider geographical range using calls recorded in the open, rather than using recordings from enclosed spaces. Analysis of these calls may allow more reliable differentiation of male and female echolocation calls.

MATERIALS AND METHODS

Capture of the bats. – We captured bats in Ohio and Georgia. The ten Ohio bats were captured in separate locations on the campus of the Ohio State University between 1990 and 1995 (14). Georgia bats were captured in two different locations in the summer of 2004. Eleven bats were captured as they were leaving a roost in the Eatonton Church of Christ in Eatonton, Georgia. Two additional bats were captured in Hampton, Georgia, in the basement of a private home. We caught the bats either by hand or by using mist nets over the opening of roosts.

Recording calls. – Prior to release, we weighed the bats, determined their sex, and measured their forearm length. A total of ninety seconds of calls were recorded for each bat. For the first minute, one experimenter held the bat approximately two meters away from the microphone. Then, we released the bat, and additional calls were recorded for as long as the bat was in range of the microphone. We recorded calls using CBDISK software (Engineering Design, Belmont MA) and portable recording equipment (18). This system is a broadband digital recording system that records ultrasonic frequencies in real time. This means that our recording system is not hampered by the limitations that affect recording systems that use time-expansion or zero-crossing analysis (19,20). In particular, we can record without the need to wait for the time-expansion system to export its data. Additionally, our recordings allow us to examine amplitude and harmonic structure, something that is not possible with a zero-crossing system (19,20). The bats captured in Ohio were recorded in an open field near the Olentangy River on the Ohio State University campus. The bats captured in Eatonton, Georgia were recorded upon release in a field adjacent to the building containing the roost. The bats captured in Hampton, Georgia were recorded when released in an area surrounding another private residence in Stockbridge, Georgia. Because each bat's ninety second recording was written to one data file, the individual echolocation calls were later extracted using a specially designed program written by Burnett and Masters for Matlab (Version 7.0.4, Mathworks, Inc.).

Echolocation call analysis. – After extracting the calls, there were a total of 8,137 individual calls from 11 female and 12 male big brown bats. We analyzed the calls using another custom program in Matlab. We visually verified the analysis of each file by the Matlab program and calls were discarded if they were not echolocation calls (e.g. audible sounds produced by the bat, wind noise, or other background noise or static). We also excluded calls if they were not analyzed correctly, such as misidentification of the call start or the call end, misidentification of the frequency tracing of the call, or misapplication of a best-fit curve to the call (Figure 1a). After we screened the calls, there remained 4,018 usable calls (2,341 female calls and 1,677 male calls) (Figure 1b). The Matlab program analyzed each of the calls and recorded 36 variables describing each call (Appendix 1). These variables can be divided into a number of categories: 1) variables that describe the timing of various events in the call, 2) variables that describe the frequencies present in the call, 3) variables that describe the amplitude of the call, 4) variables that use mathematical models that attempt to fit the structure of the time and frequency of the calls, and 5) variables that describe how well these mathematical models fit the individual call.

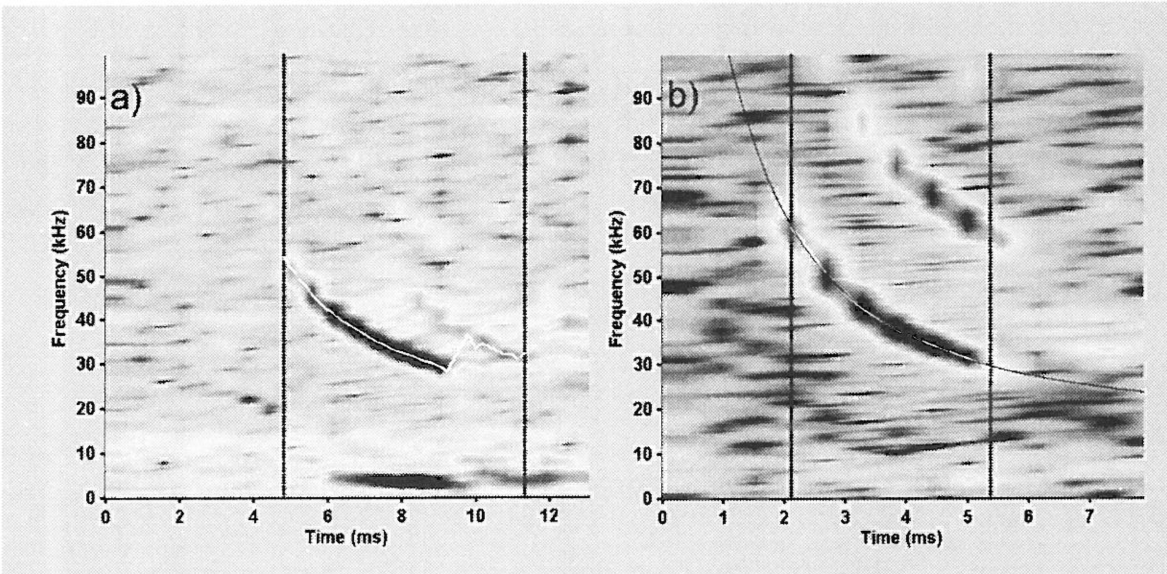

Figure 1. (a) Example of a bad call analysis by the Matlab program. The program has incorrectly identified the call end, causing the contour tracing to follow an echo. (b) Example of a good call analysis by the Matlab program. The program has correctly identified the call start and call end, has correctly traced the frequency contour of the call, and has correctly applied a best-fit curve to the call.

Even though there was a large number of calls from each bat, it was necessary to reduce our sample size and statistically examine only one call from each bat. This was necessary because discriminant function analysis (DFA) is susceptible to errors if given a large sample of data that are not independent (17). Although this resulted in a small number of calls to analyze, error in the analysis that might show differences in calls arising from the individuality of the bats rather than their sex needed to be reduced. Using more than one call from each bat would have weighted the results in favor of that bat's individuality rather than the sex of the bat. The call that was included for a particular bat was randomly selected by the statistical software. Each time we selected a smaller set of calls (e.g., calls less than four milliseconds in duration) we had the software choose a new random call.

Statistical analysis. – Even with only one call per bat, the number of variables for each call was large. When conducting discriminant function analyses, a large number of variables can produce misleading results, even if cross-validation of results is performed (21,22). There is no clear agreement on the number of variables that is acceptable, but the problem is greatest when there is a small number of categories, as in this experiment (21). Therefore, we reduced the number of variables by performing a principal component analysis (PCA) in SPSS (Version 13.0, SPSS, Inc.). For every PCA, we used varimax rotation to ensure each principal component was independent. We ran a PCA on the entire set of male calls to determine the variables that capture the variation present in those calls. A second PCA was run on the female calls. The total number of variables was reduced to the two by comparing the correlations of the variables with the principal components. PCA calculates a series of mathematical components that describe the variation present in a data set, with each component describing the variation in a different "dimension" so that each component is independent from the others. The components are constructed so that the first component describes the majority of the variation in the data, while each subsequent component describes smaller amounts of variation. Individual variables can be related to particular components by examining a correlation coefficient between that variable and each component. Because the components are uncorrelated, a variable that has a strong correlation with one component will have relatively low correlations with other components. For these reasons, we selected the variable with the highest absolute correlation with the first principal component, and then we repeated the process using the second principal component, giving us two uncorrelated variables that described a large amount of variation in the data set. We performed this process for all of the calls from each sex, producing four potential variables for use in our analyses. When selecting which variables to use based on the results from the principal component analysis, we did not consider variables that used various mathematical functions to describe the data, because these equations did not adequately describe every call (Appendix 1). For example, one call may be well described by a linear frequency function, but another call may be well described by an inverse time curve.

There was no single mathematical function that fit all of the calls; therefore, these variables were not ideal for trying to find a method to discriminate among all of the possible calls. Also, we did not include the variable duration, because as part of the experiment, we divided calls into categories based on their duration. For these subcategorized calls, the duration variable would no longer be applicable in discriminating among different calls.

Prior to running a discriminant function analysis (DFA), we separated the calls into hand-held calls and flying calls. Then, we ran a DFA on each set of calls using the selected variables. To determine how well these variables can identify the sex of the calling bat, we used the DFA with cross-validation, which builds a function using most of the calls, then uses that function to classify the unused calls. This avoids the possibility that the function would appear to be successful because it was being tested against the data that were used to build it.

Since M. Grilliot had previously identified variables that helped to differentiate the sexes during the mating season (16), we ran a DFA on our calls (which came from the non-mating season) using these variables as well.

We also ran a DFA on the averaged calls from each of the 23 bats. The numerous calls from each bat contained a large amount of variation, so averaging the calls might account for some of the variability that is lost by selecting a single call. The averaged calls contained both hand-held and flying calls.

We questioned the validity of comparing all bat calls to one another independently of other factors such as duration. It is well-known that bats change their calls as they approach targets during flight (23) and so the information content of those calls might change as well. So we decided to determine if there were differences between male and female echolocation calls of certain duration. We separated the calls based on duration, and then analyzed the calls within each duration class. Hand-held calls were analyzed separately from flying calls. We classified the 4,018 usable calls into the following categories: calls less than 4.00 ms, calls less than 4.50 ms, calls less than 5.00 ms, calls greater than 4.00 ms, calls greater than 4.50 ms, and calls greater than 5.00 ms. No calls greater than 10.00 ms were used. We then ran a DFA on each duration category of call.

RESULTS

Table I shows the loadings produced by the principal component analysis on each subset of calls. We used the results from the PCA to narrow the number of variables. The two variables with the highest correlation coefficients for the male calls as determined by the principal component analysis, excluding those mentioned previously, were the starting frequency of the fundamental (h1start; correlation coefficient 0.954) and the time to reach the middle frequency of the fundamental (t50; correlation coefficient 0.882). The two variables with the highest correlation coefficients for the female calls were the starting frequency of the fundamental (h1start; correlation coefficient 0.873) and the time to reach the middle frequency of the fundamental (t50;

correlation coefficient 0.919). Since the two most highly correlated variables for each sex were the same, these two variables were the only two selected for the DFA.

Table I. Principal Component Analysis Component Matrix showing the loadings produced by the PCA analysis on each subset of calls. Variables with the highest correlation coefficients are the ones that best describe that subset of calls. This table only shows the variables that were considered for use in the DFA.

	h1start	h1mid	h1end	t50	curvatur	h1maxa	h1maxf	th1maxf	l3fh1	u3fh1	l10fh1	u10fh1
Male Calls:												
Component 1	.954	.612	.363	-.130	-.031	.152	.557	-.266	.619	.459	.812	.429
Component 2	-.041	-.357	-.011	.882	.665	-.225	-.496	.756	-.455	-.517	-.286	-.247
Female Calls:												
Component 1	.873	.662	.278	.215	.083	.480	.460	-.021	.639	.373	.866	.328
Component 2	.291	-.025	.227	.919	.677	-.230	-.391	.820	-.362	-.276	-.085	.049

We ran a DFA on one random hand-held call from each of 23 bats. DFA was able to classify male bats with a 55.6% success rate and female bats with a 81.8% success rate (Table I). We also ran a DFA on one random flying call from each of the 23 bats. Using these parameters, DFA was able to classify male bats with a 66.7% success rate and female bats with a 70.0% success rate (Table II).

Table II. DFA results for discriminating sex, using 1 hand-held and 1 flying call per bat. Percentage is based on cross-validation. Two sets of variables were used: the first set were derived from a principal component analysis (PCA), and the second set had previously been shown to be helpful in sex determination during the mating season (16).

Test	Cross-Validated % Correct (Males)	Cross-Validated % Correct (Female)
HAND-HELD CALLS:		
h1start, t50	55.6	81.8
duration, h1maxa, th1maxf	66.7	81.8
FLYING CALLS:		
h1start, t50	66.7	70.0
duration, h1maxa, th1maxf	33.3	60.0

The variables previously found useful for differentiating calls during the mating season were the call duration (duration), the frequency of the maximum amplitude (h1maxa), and the time to reach the maximum frequency (th1maxf) (16). Using these variables on hand-held calls, DFA was able to classify male bats with a 66.7% success rate and female bats with a 81.8% success rate (Table I). Using these variables on flying calls, DFA was able to classify male bats with a 33.3% success rate and female bats with a 60.0% success rate (Table II).

When we ran DFA on the averaged call using the h1start and t50 variables, DFA was able to classify male bats with a 66.7% success rate, and female bats with a 72.7% success rate (Table III). Using the second set of variables, DFA was able to classify male bats with a 50.0% success rate and female bats with a 63.6% success rate (Table III).

Table III. DFA results for discriminating sex, using averaged calls. Percentage is based on cross-validation. Two sets of variables were used: the first set were derived from a principal component analysis (PCA), and the second set had previously been shown to be helpful in sex determination during the mating season (16).

Test	Cross-Validated % Correct (Males)	Cross-Validated % Correct (Female)
h1start, t50	66.7	72.7
duration, h1maxa, th1maxf	50.0	63.6

After placing the calls in all the duration categories for which they were eligible, we had between 181 and 2,077 hand-held calls to select from and between 150 and 499 flying calls to select from for each category. We ran a DFA on each duration category, using the two sets of variables on the separated hand-held and flying call sets (Table IV). We obtained the most notable results when comparing shorter calls. Using the variables h1start and t50 on hand-held calls, the DFA was able to correctly identify male calls 83.3% of the time and female calls 72.7% of the time. Using the same two variables on the flying calls, the DFA was able to correctly identify male calls 80.0% of the time and female calls 62.5% of the time. With flying calls less than 4.50 ms, male calls could be correctly classified 90.0% of the time and female calls could be correctly classified 62.5% of the time. With flying calls less than 5.00 ms, male calls were correctly identified 70.0% of the time, and female calls were correctly identified 90.9% of the time. The second set of variables did not show promising results for either hand-held calls or flying calls.

Table IV. DFA results for discriminating sex, using 1 hand-held and 1 flying call per bat with calls divided into duration categories. Percentage is based on cross-validation. Two sets of variables were used: the first set were derived from a principal component analysis (PCA), and the second set had previously been shown to be helpful in sex determination during the mating season (16).

Test	**Variables Used: h1start, t50 (% Correct)**		**Variables Used: duration, h1maxa, th1maxf (% Correct)**	
	Hand-Held Calls	**Flying Calls**	**Hand-Held Calls**	**Flying Calls**
Calls less than 4.00 ms:				
Males	83.3	80.0	41.7	60.0
Females	72.7	62.5	63.6	37.5
Calls less than 4.50 ms:				
Males	58.3	90.0	41.7	60.0
Females	72.7	62.5	72.7	62.5
Calls less than 5.00 ms:				
Males	58.3	70.0	41.7	50.0
Females	45.5	90.9	81.8	81.8
Calls greater than 4.00 ms:				
Males	50.0	55.6	50.0	33.3
Females	25.0	55.6	50.0	55.6
Calls greater than 4.50 ms:				
Males	40.0	0	40.0	62.5
Females	33.3	55.6	0	44.4
Calls greater than 5.00 ms:				
Males	25.0	14.3	75.0	42.9
Females	66.7	22.2	33.3	44.4

DISCUSSION

The comparison of a random sample of hand-held and flying echolocation calls between male and female big brown bats did not lead to any substantial conclusions about statistical differences between the sexes. Although the DFA showed a high success rate (81.8%) for identifying female hand-held calls using both sets of variables, the success rates for male determination were not much better than those that could be predicted by chance alone (~50%). Averaging the calls also did not lead to any substantial conclusions about statistical differences between the sexes.

After comparing calls of similar durations, some promising results were discovered with short calls using the variables h1start and t50. When calls were less than 4.00 ms in duration, the DFA was reasonably successful in identifying male calls from female calls. Furthermore, for flying calls less than 5.00 ms, there were high identification success rates. The second set of variables, however, showed no significant results for differentiating short calls.

When comparing the descriptive statistics for the calls less than 4.00 ms, an interesting characteristic was noticed. When the calls are short (i.e. less than 4.00 ms), the males tended to begin their calls at a higher frequency than the females. The average beginning frequency for short hand-held male calls was 57.21 KHz (±6.52 KHz), whereas the average beginning frequency for short hand-held female calls was 49.94 KHz (±6.91 KHz). The average beginning frequency for short flying male calls was 57.26 KHz (±5.66KHz), whereas the average beginning frequency for short flying female calls was 54.63 KHz (±7.16 KHz). Interestingly, the frequency difference seemed to be most noticeable in the hand-held calls, and the females are the ones who seemed to be changing the starting frequency of their call depending on the situation.

The results indicate that short duration calls, either flying or hand-held, may provide a means of statistically discriminating between male and female bats. Currently, recording is used for species identification (20), but our results suggest that recordings of echolocation calls have the potential to provide additional information. Our analyses suggest potential applications for study of wild bat populations, particularly if our results are found to hold for more species. Because recording is non-invasive, it would be possible to learn about the structure of a population by examining the calls that the bats are producing, without requiring capture of the animals. The results are based on a large number of calls for a relatively small number of bats of a single species. Therefore, it is our goal to gather more recordings from a wider variety of bats and use these recordings to further investigate the differences in calls between males and females.

One possible explanation for the finding that short calls could be used to differentiate between the sexes could be that the bats have adapted short calls to use as a means of communication. Short calls would require less energy than long calls, and so would be the ideal type of echolocation call to use for communication purposes. Short echolocation calls are also the type of call that a bat would hear from conspecifics when in a confined space, such as a roost, when social interactions (e.g., mating) are likely to occur. It has also been hypothesized that echolocation calls have evolved from communication calls (2), so perhaps short calls could be considered as being the ancestral type of call. Long calls could then have evolved to produce better targeting capabilities when flying and searching for prey.

Furthermore, it would be beneficial to look at the ways in which male and female bats sequence their calls. In what order are the long calls mixed with the short calls and how far apart are the various calls spaced? It is possible that a statistical difference could be found in the bat's repertoire of calls, and this approach may serve to yield more results than just looking at random calls individually.

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APPENDIX 1
The 36 variables recorded by Matlab for each bat call

Code used by Matlab	Description of Variable
Variables Related to Time:	
duration	Call duration in milliseconds (ms)
t50	Time to reach the middle frequency of the call (ms)
th1maxf	Time to reach the maximum frequency (ms)
Variables Related to Frequency:	
h1start	Starting frequency of the fundamental harmonic (KHz)
h1mid	Middle frequency of the fundamental harmonic (KHz)
h1end	Ending frequency of the fundamental harmonic (KHz)
curvatur	Shape of call - based on Boonman and Schnitzler (2005) (24)
h1maxf	Frequency of the maximum amplitude (KHz)
13fh1	Frequency of first harmonic 3 dB below max, after maximum frequency
u3fh1	Frequency of first harmonic 3 dB below max, before maximum frequency
l10fh1	Frequency of first harmonic 10 dB below max, after maximum frequency
u10fh1	Frequency of first harmonic 10 dB below max, before maximum frequency
Variables Related to Amplitude:	
h1maxa	Amplitude of maximum frequency (V)
Variables Related to a Model Fit:	
efmse	Mean squared error of the exponential frequency decay equation
etmse	Mean squared error of the exponential time decay equation
lpmse	Mean squared error of the straight line fit to the period of the signal
lfmse	Mean squared error of the linear frequency function
itmse	Mean squared error of the inverse time curve equation
p3mse	Mean squared error of the power-3 sweep equation

Variables Describing Mathematical Models:	
efhi	Starting frequency of the call (KHz)
efasym	Asymptotic frequency of the call (KHz)
efdcay	Decay constant for the exponential frequency decay equation (ms)
etlow	Ending frequency of the call (KHz)
etasym	Time asymptote
etdcay	Decay constant for the exponential time decay equation (KHz)
lpslope	Slope of the line resulting from the straight line fit to the period of the signal (_s/ms)
lpinter	Starting period of the call (_s)
lfslope	Slope of the line from the linear frequency function (KHz/ms)
lfinter	y-intercept of the line from the linear frequency function (KHz)
itslope	Slope of the line from the inverse time curve (KHz/ms)
itinter	y-intercept of the line from the inverse time curve (KHz)
itoffset	Constant from the inverse time curve (ms)
pow3Fo	Starting frequency (KHz)
pow3F1	Ending frequency (KHz)
pow3Fa	Decay constant 1 for the power-3 sweep equation
pow3Fc	Decay constant 2 for the power-3 sweep equation