# Pinnae and echolocation call differences between *Myotis californicus* and *M. ciliolabrum* (Chiroptera: Vespertilionidae)

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We measured the shape of pinnae from fluid-preserved, museum specimens of 33 *Myotis californicus* and 39
*M. ciliolabrum* and cranial characters from 40 skulls of each species. We also measured 40 specimens of
*Eptesicus fuscus*, which were used as an outgroup. Significant differences were found in aural shape and tragus
height between the two species of *Myotis*. Archived echolocation calls from the two species from across the
range segregated, further suggesting that morphological and call characters are intercorrelated. We tested this
relationship using 17 *M. californicus* and 12 *M. ciliolabrum* captured in the field for external measurements and
echolocation call recordings ($n$ = 1,124 calls in 52 call files, $\bar{x}$ = 2.3 call files per released bat), and found
significant differences (most $P$ < 0.001) in pinnae and call morphology between *M. ciliolabrum* and *M.
californicus* similar to those observed in 'museum' samples. We found that small interspecific differences in
pinna shape and size are correlated with differences in the frequency ranges (larger pinna, lower frequency).

*Key words*: bat calls, Anabat, ear, acoustics, ANOVA, principal component analysis, sexual dimorphism

## INTRODUCTION

Two North American bat species that
have been historically confused morpho-
logically are *Myotis californicus* and *M. ci-
liolabrum* (Bogan, 1974, 1999). *Myotis ca-
lifornicus* is common throughout much of
western North America, especially in the
Colorado Plateau, Great Basin, and higher
elevations of the Sonoran and Chihuahuan
deserts (Hall, 1981; Hoffmeister, 1986). It
occupies arid lowlands but is also common
in piñon-juniper and conifer forests. *Myotis
ciliolabrum* has a similar distribution as *M.
californicus*, however it is most common in

mid- to upper elevations of coniferous for-
est. *Myotis californicus* is an aerial hawking
species that forages over or near water, as
does *M. ciliolabrum*. Food items common-
ly associated with these bats are Lepi-
doptera, Trichoptera, Coleoptera, and
Diptera (Black, 1974; Whitaker *et al*.,
1981; Woodsworth, 1981). Both *M. califor-
nicus* and *M. ciliolabrum* are most active
during the early hours of the evening with
foraging beginning shortly after sunset.
They hunt and feed rapidly and then seek a
night roost to prepare for another foraging
bout (Simpson, 1993). When allopatric,
both species hunt along margins of tree

clumps, edges of tree canopy, over water, and well above ground in open country. In sympatry, their foraging behavior differs. *Myotis californicus* remains aerially hawking over or near the water surface while *M. ciliolabrum* is a gleaner, hunting near rocky bluffs, suggesting spatial resource partitioning (Woodsworth, 1981).

Although difficult to consistently distinguish in the hand, the skull of *M. californicus* is more rounded, the rostrum is narrower, and the coronoid process is lower than in *M. ciliolabrum* (Bogan, 1999). Moreover, other field features that distinguish these two species are: the different pattern of the hair covering the snout, the differences in the thumb length, and the amount that the tail extends from the uropatagial membrane (Constantine, 1998). Nevertheless, the pronounced geographic variation with regards to these characters results in general confusion regarding their taxonomic allocation.

It is generally accepted that bats produce calls that are species-specific (Fenton and Bell, 1981). In fact, new species (phonotypes) have been described initially using only acoustics (e.g., Jones and van Parijs, 1993; Jones *et al.*, 2000). Use of more portable detectors have verified these early discoveries (O'Farrell *et al.*, 1999). O'Farrell and Gannon (1999) showed that the ultrasounds emitted by *M. ciliolabrum* and *M. californicus* were distinguished in New Mexico by characteristic frequency (roughly, 40.0 versus 50.0 kHz), maximum frequency (61.1 and 76.0 kHz), minimum frequency (39.2 and 48.5 kHz), and duration (3.9 ms and 2.0 ms; Fig. 1). Similar specific values were reported from sites in Arizona and Wyoming indicating that these call differences are maintained across their range (O'Farrell *et al.*, 1999). Therefore it has been shown that acoustic data recorded from broad scale divide-by detectors with zero-crossing abilities are reliable as a field technique for differentiating these two

species. Because of these sonic differences, it may be possible to discover additional, reliable morphological characters useful for distinguishing these two species in hand. We propose that a subtle variation in the shape of pinnae may be shown relative to documented call differences. This makes intuitive sense since pinna and tragus shape may improve the directionality and sensitivity of incoming echoes (Obrist *et al.*, 1993; Altringham, 1996).

## MATERIALS AND METHODS

We measured the pinnae of 39 *M. ciliolabrum,* 33 *M. californicus*, and 40 *Eptesicus fuscus* in the collection of the Museum of Southwestern Biology (see Appendix 1). *Eptesicus fuscus* was used in this initial museum collection portion of the study to ensure sensitivity of techniques for detection of differences between the genera (*Eptesicus* versus *Myotis*) by acting as an outgroup.

Also, we initially used fluid-preserved (70% ethyl alcohol) specimens rather than dried skins because the pinnae are more pliable thereby reducing measurement error. Although there is some distortion in the process of fluid preservation (Bininda-Edmonds and Russell, 1992), the distortion was consistent across species. Measurements in the museum portion of the study were not from the same individuals for both calls and pinnae and could only be suggestive of a relationship between call frequency and pinna morphology.

To validate any relationship discovered in the museum-specimen analyses, we also live-captured, measured, and released 17 individuals of *M. californicus* and 12 *M. ciliolabrum*, with successful subsequent recording (1,124 calls in 52 call files; $\bar{x}$ = 17 calls per individual bat; range 5–29 calls in each call file). Captures were made in the vicinity of Portal, Arizona (31°55'N; 109°08'W) with releases performed at a nearby heliport pad (see methods in O'Farrell and Gannon, 1999; Appendix 2). All recordings and analyses were done using Anabat version 6.2d (Titley Electronics, Ballina, NSW, Australia) and Analook version 4.7h, respectively (Corben Scientific, Rohnert Park, CA, USA).

On both museum specimens and live captive bats, aural characters were measured on both right and left body sides to the nearest 0.01 mm with an electronic caliper. These included: height of pinna (from base of tragus at bottom of notch to tip of
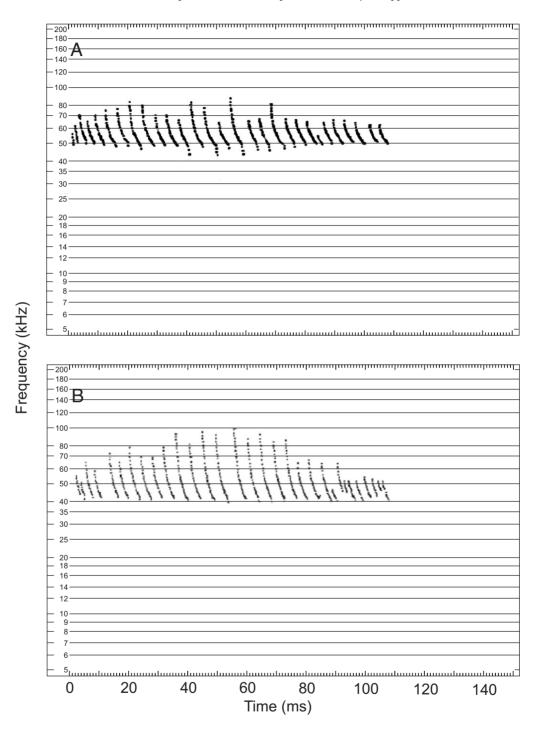
F<sub>IG</sub>. 1. Sound spectrographs produced by Anabat for *Myotis californicus* (A) and *M. ciliolabrum* (B). These are considered species that are difficult to discern when captured in a net or trap, however relatively simple to distinguish by minimum frequency of 50 kHz (A) and 40 kHz (B), respectively. The temporal axis (*x*-axis) is compressed so that duration of each call in the sequence is shown, but intercall duration is absent. Total call sequence duration cannot be calculated from this figure

pinna); width of pinna at middle height (perpendicular to tip of tragus); height of tragus (from base to tip); and width of tragus (measured at base). Additionally, the length of right and left forearms, a measure of body size in bats, was obtained for all individuals (Kunz *et al.*, 1996). Nevertheless, only right-sided characters, except for principal components analyses, are shown in the present study.

Forty skulls were examined in museum specimens of each species (Appendix 1). Cranial features, taken to the nearest 0.01 mm with an electronic caliper, included: width of cochlea; length of cochlea; width between cochleae; width of skull from meatus to meatus; width of skull measured from outermost edges of cochleae; greatest length of skull (from the back to the tip of the rostrum); and greatest height of skull (from base of cochlea to top of the skull). The cochlear traits rather than bullar ones were measured, because cochleae are directly involved in processing sound (Altringham, 1996).

In the initial analysis we looked at calls from the Bat Call Library (http://talpa.unm.edu/batcall/) for the three bat species measured from the MSB collections. These calls had also been recorded previously with an Anabat detector and stored on the web site. For the initial museum analysis we measured 100, 130, and 190 calls of *M. californicus*, *M. ciliolabrum*, and *E. fuscus*, respectively. The search phase, or consistently repetitive portion of the call, was chosen for detailed analyses due to the more uniform nature of the pulses emitted. The field portion of the study included 641 and 837 calls recorded from live-captured *M. californicus* and *M. ciliolabrum*, respective-

ly. Because of missing values these calls were reduced to a total of 1,124 (*M. californicus, n* = 522 and *M. ciliolabrum, n* = 602).

The following call measurements were examined: minimum frequency, maximum frequency, call duration, 'knee' (the break in slope from the initial downward sweep to the flattest portion of the call), and the number of calls per second (Fig. 1; O'Farrell *et al.*, 1999). Although the last measurement is a function of the bats' behavior and activity, rather than of morphology, this variable often is reported in the literature (e.g., Fenton and Bell, 1981; Altringham, 1996). We therefore included it to maintain comparability with other studies. Calls were analyzed individually and their values were untransformed. Although, there is a possibility for pseudoreplication, the outcome will likely be similar whether analyzing individual calls or call sequence means (Jones *et al.*, 2000; Gannon *et al.*, In press). The 'knee' was dropped from the final museum study analysis because of the complexity of shape of the *E. fuscus* call in contrast to the more simple calls belonging to *Myotis*; this character was retained in the field study where only the two species of *Myotis* were compared.

Acoustic and morphometric measurements were analyzed using ANOVA in PROC GLM from SAS (SAS, 1985). Also principal component analyses (PCA) from the SAS package and Ryan-Eynot-Gabriel-Welsch multiple-range test with the Bonferroni correction were applied. Significance in all analyses was determined at $\alpha < 0.05$.

TABLE 1. Descriptive statistics ($\bar{x} \pm$ SD) for morphological variables measured from museum specimens of *E. fuscus* (*n* = 40)*, M. californicus* (*n* = 39), and *M. ciliolabrum* (*n* = 33). *F*-values and *P*-levels derived from ANOVA for intergeneric comparisons between *Eptesicus* and grouped *Myotis* are also shown (see Appendix1 for specimens examined)

| Character | Taxa | | *F*-statistics for intergeneric differences |
|---|---|---|---|
| | *Eptesicus fuscus* | *Myotis* spp. | |
| Pinna height | 13.89 ± 0.87 | 11.48 ± 0.75 | 11.7** |
| Pinna width | 9.27 ± 0.73 | 6.69 ± 0.55 | 2.3 |
| Tragus height | 5.80 ± 0.34 | 6.23 ± 0.58 | 1.5 |
| Tragus width | 2.26 ± 0.18 | 1.77 ± 0.22 | 1.5 |
| Forearm length | 47.18 ± 1.56 | 32.54 ± 1.20 | 25.3*** |
| Cochlea length | 2.45 ± 0.19 | 2.20 ± 0.13 | 34.4*** |
| Cochlea width | 2.06 ± 0.11 | 1.64 ± 0.09 | 208.8*** |
| Greatest length between cochleae | 7.11 ± 0.48 | 5.40 ± 0.32 | 302.6*** |
| Greatest length between meati | 8.47 ± 0.37 | 6.27 ± 0.30 | 516.0*** |
| Greatest length of skull | 18.59 ± 0.01 | 13.53 ± 0.36 | 1,713.2*** |

\* = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001

RESULTS

*Museum Specimens*

Coarse separation between the museum specimens of *Eptesicus* and *Myotis* was achieved easily for characters of the skull, pinna, and calls. The univariate analysis of external and cranial measurements using all taxa showed a distinct separation of *Eptesicus fuscus* and *Myotis* spp. in body size (as expressed by forearm length and greatest length of skull), skull width, and cochlear lengths and widths (Table 1). Scaled for body size (using forearm length), pinnae of *E. fuscus* were also larger and wider than those of either *M. ciliolabrum* or

*M. californicus*, although only differences in their pinnae heights were statistically significant. Separately, we examined characters of the two *Myotis* species represented by museum specimens and found that pinnae dimensions and tragus height were significantly different between them (Table 2). In addition, the GLM model of SAS revealed significant differences between *M. californicus* and *M. ciliolabrum* for call duration, and for maximum and minimum frequencies, and frequency at the call's knee (Table 2). Moreover, the principal component analysis (PCA) showed that the height and width of pinnae were the most important features on PC1 (32% variation explained — Table 3), which more or less

TABLE 2. General linear model analysis of variance examining species variation ($\bar{x}$ ± SD) of *M. californicus* and *M. ciliolabrum*. In the top table 72 fluid-preserved museum specimens were measured and 300 archived calls downloaded from http://talpa.unm.edu/batcall. In the bottom table, 29 individuals were hand-captured, measured, and released for call recording ($n = 1,124$ calls)

| Character | *M. californicus* | *M. ciliolabrum* | Interspecific *F*-statistics |
|---|---|---|---|
| | Museum | | |
| Forearm length | 31.83 ± 1.06 | 33.26 ± 1.33 | 4.11 |
| Pinna height | 11.17 ± 0.74 | 11.79 ± 0.78 | 102.33*** |
| Pinna width | 6.30 ± 0.52 | 7.08 ± 0.61 | 6.78* |
| Tragus height | 6.14 ± 0.60 | 6.32 ± 0.68 | 32.55*** |
| Tragus width | 1.69 ± 0.25 | 1.81 ± 0.32 | 2.24 |
| Call duration | 2.56 ± 0.82 | 2.86 ± 0.54 | 32.33*** |
| Maximum frequency | 71.89 ± 8.20 | 65.67 ± 9.18 | 21.28*** |
| Minimum frequency | 48.16 ± 2.40 | 41.51 ± 1.60 | 11.09** |
| Mean frequency | 58.24 ± 1.39 | 47.33 ± 2.77 | 1.33 |
| Frequency at knee | 60.00 ± 2.40 | 53.83 ± 1.57 | 24.10*** |
| Characteristic frequency | 49.89 ± 4.21 | 40.15 ± 2.12 | 5.71 |
| | Field | | |
| Forearm length | 30.17 ± 1.12 | 32.90 ± 1.41 | 74.89*** |
| Pinna height | 12.19 ± 0.09 | 12.73 ± 0.28 | 64.39*** |
| Pinna width | 6.21 ± 0.51 | 7.18 ± 0.77 | 5.87** |
| Tragus height | 6.92 ± 0.70 | 5.95 ± 0.37 | 67.80*** |
| Tragus width | 1.74 ± 0.17 | 1.88 ± 0.51 | 0.96 |
| Call duration | 2.01 ± 0.50 | 3.91 ± 1.05 | 49.28*** |
| Maximum frequency | 76.00 ± 10.89 | 61.10 ± 10.28 | 39.77*** |
| Minimum frequency | 48.55 ± 2.53 | 39.20 ± 2.11 | 5.77** |
| Mean frequency | 65.81 ± 3.04 | 46.87 ± 3.14 | 0.69 |
| Frequency at knee | 54.33 ± 5.23 | 49.10 ± 3.02 | 1.42 |
| Characteristic frequency | 51.22 ± 3.62 | 41.26 ± 1.99 | 2.39* |

\* = $P < 0.05$, \*\* = $P < 0.01$, \*\*\* = $P < 0.001$

separated *M. californicus* from *M. ciliolabrum* in the morphospace examined (Fig. 2). The next principal component (16%) indicated asymmetry between the external ear structures (Table 3) and did not shown any clear species-based groups. These results allowed us to continue with the field portion of this study (below), which was to sample live individuals and examine those significant characters resolved thus far more closely.

### Field Study

Finer resolution of the hypothesis proceeded on wild-caught and recorded specimens within the genus *Myotis* as suggested by the results of museum specimen analysis (above). Since there was a significant difference within species by sex (ANOVA, $F = 13.35$, $d.f. = 16$, $P < 0.01$ for *M. californicus* and $F = 8.99$, $d.f. = 11$, $P < 0.01$ for *M. ciliolabrum*) males and females were analyzed separately (Table 4). Multiple range tests showed that male *M. californicus* differed from the three other categories (females of both *Myotis* spp. and male *M. ciliolabrum*) in call duration, and minimum and maximum call frequencies (Table 4). Calls plotted for both *Myotis* species for duration versus characteristic frequency showed typical *M. ciliolabrum* clustering in the vicinity of 40 kHz with the calls recorded from Portal, AZ dominating the center of that cluster (Fig. 3). Likewise, *M. californicus* from Arizona occupied the cloud of points between 46 and 60 kHz being in agreement with findings from other locations (Fig. 3). The GLM model of SAS revealed significant differences between *M. californicus* and *M. ciliolabrum* for call duration, and for maximum, minimum, and characteristic frequencies, as well as for all body measurements (Table 2). A PCA with call and ear variables measured from wild-captured animals showed that these variables constituted 69.3% of the total variation for PC1, with call duration and mean call frequency dominating, although in opposite directions (Table 3). Call duration was interrelated with pinna height, whereas mean, minimum, and maximum call frequencies, as well as tragus height worked synergistically. PC2 described ca. 20% of total variation and was dominated by pinna height (Table 3). In general both components resulted either in complete (PC1) or at least partial separation (PC2; see Fig. 4)

TABLE 3. Eigenvector scores, eigenvalues, and variance explained resulting from the principal component (PC) analyses of selected aural and echolocation call characters from museum (top) and wild-captured (bottom) *M. californicus* and *M. ciliolabrum*. The highest values are marked in bold

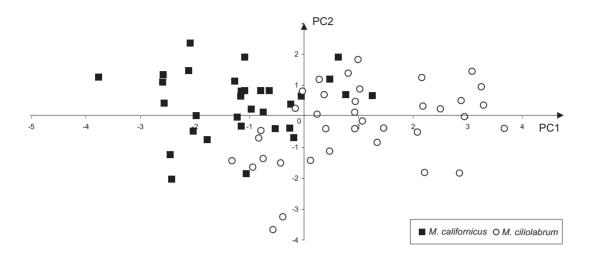| Character | PC1 | PC2 |
|---|---|---|
| Museum | | |
| Right pinna height | 0.399 | -0.152 |
| Left pinna height | 0.408 | **0.531** |
| Right pinna width | **0.432** | -0.172 |
| Left pinna width | **0.467** | -0.270 |
| Right tragus height | 0.305 | -0.018 |
| Left tragus height | 0.223 | **0.604** |
| Right tragus width | 0.213 | 0.010 |
| Left tragus width | 0.181 | 0.014 |
| Eigenvalue | 2.85 | 1.48 |
| Proportion (%) | 31.6 | 16.4 |
| Cumulative (%) | 31.6 | 48.0 |
| Field | | |
| Right pinna height | 0.250 | **0.598** |
| Left pinna height | 0.240 | **0.625** |
| Right tragus height | -0.377 | 0.352 |
| Left tragus height | -0.350 | 0.320 |
| Call duration | **0.414** | 0.002 |
| Minimum call frequency | -0.365 | 0.001 |
| Maximum call frequency | -0.365 | 0.158 |
| Mean call frequency | **-0.421** | -0.005 |
| Eigenvalue | 5.55 | 1.57 |
| Proportion (%) | 69.3 | 19.6 |
| Cumulative (%) | 69.3 | 88.9 |

FIG. 2. The relationship between the first two principal components (PC) derived from four pinna characters and four tragus measurements obtained from fluid-preserved specimens of *M. californicus* and *M. ciliolabrum* (see also Table 3)

## DISCUSSION

*Eptesicus fuscus* separated from the species of *Myotis* in all respects: cranial morphology, external morphology, and echolocation call 'morphology.' A quick glance at the bat in hand easily distinguishes it from either *Myotis*. It is intriguing that the two species of *Myotis*, which are both cryptic in the hand (Bogan, 1974), exhibit significant differences in many variables measured in our analyses.

The question of how morphologically similar species can coexist and how mor-

phological character patterns can be used for better understanding the processes of selection is one of the foremost questions in evolutionary ecology (e.g., Bogdanowicz, 1990; Findley, 1993; Arlettaz, 1995). To this end, the multivariate results for both museum and field-based studies reveal that the external ear morphology is distinctive between *M. californicus* and *M. ciliolabrum*. *Myotis ciliolabrum* has larger pinnae than *M. californicus*. The former also has a significantly longer and wider skull than the latter, however, the cranial differences are not as dramatic as that of size of

TABLE 4. Ryan-Einot-Gabriel-Welsch multiple range tests (compare A, B, and C along rows) for four pinna and four call characters from wild-caught *M. californicus* (nine males and eight females), and of *M. ciliolabrum* (eight males and four females). In all cases α < 0.05. Bold indicates the values where male *M. californicus* does not conform to one group or another

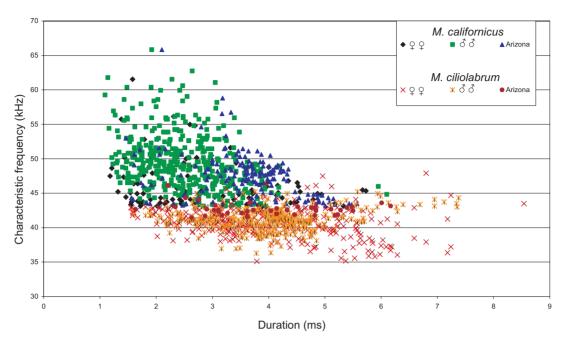| Character | M. californicus | | M. ciliolabrum | |
| --- | --- | --- | --- | --- |
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| Pinna height | 12.33 ± 0.21 (A) | 12.17 ± 0.11 (A) | 12.79 ± 0.30 (B) | 13.01 ± 0.29 (B) |
| Tragus height | 6.90 ± 0.02 (B) | 7.12 ± 0.07 (B) | 5.87 ± 0.22 (A) | 6.08 ± 0.09 (A) |
| Call duration (ms) | **2.99 ± 0.33** (B) | 2.08 ± 0.43 (A) | 4.02 ± 0.89 (C) | 3.99 ± 0.63 (C) |
| Minimum frequency | **45.66 ± 3.11** (B) | 51.02 ± 2.03 (C) | 40.55 ± 1.97 (A) | 38.32 ± 2.31 (A) |
| Maximum frequency | **68.30 ± 8.32** (B) | 77.00 ± 5.22 (C) | 62.91 ± 9.23 (A) | 60.91 ± 6.11 (A) |
| Mean frequency | 65.21 ± 2.87 (B) | 60.54 ± 3.44 (B) | 50.44 ± 3.64 (A) | 45.50 ± 3.75 (A) |

Fɪɢ. 3. Bivariate plot of call duration and characteristic frequency of *M. californicus* and *M. ciliolabrum*. Calls are plotted for both sexes of both species from samples across their ranges. Samples recorded from hand-released individuals of both species captured in Portal, Arizona are also shown

pinnae. The frequency range of calls and the number of calls per second of both species are also significantly different. The variation in call duration could be attributable to the echolocating phase of the call (behavior of the bat) and may not be a reliable character to distinguish between the two species; a more conservative sampling approach may tease this out in future analyses.

The frequency range of calls from all three species correlates with the height of the pinnae: the longer the pinna, the lower the call frequency. Increasingly, it has been shown that bats of larger size have a lower call frequency (e.g., Altringham, 1996; Bogdanowicz *et al.*, 1999; Jones *et al.*, 2000). Francis and Habersetzer (1998) also found a strong negative relationship in cochlear size and echolocation frequency among chiropteran families Hipposideridae and Rhinolophidae: the wider the cochlea the lower the call frequency. Although we did

measure cochlear width and length, differences were not significant. However, this is the first time that it has been shown that pinna shape and echolocation call characters are statistically linked. The implication of this study is that each species operates under a synergistic set of call characters to produce a unique call, possibly independent of body mass, even with the constraints imposed on bats as an Order to use echolocation for perception (Griffin, 1958).

Empirical data on diet and habitat use will be required to address ecological relationships between *M. californicus* and *M. ciliolabrum* (as, for example, done for Neotropical emballonurids by Kalko, 1985). The larger size of pinnae in *M. ciliolabrum* could be related to the fact that this species is mostly a gleaner in certain (sympatric) circumstances, hence foraging on a different suite of insect prey. Call frequency differences between *M. californicus* and *M. ciliolabrum* are consistent throughout their
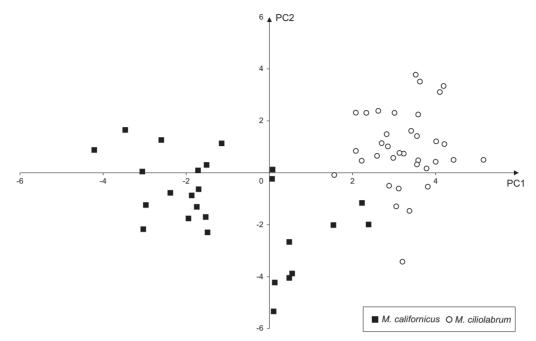
FIG. 4. The relationship between the first two principal components (PC) derived from four aural and four call characters (as in Table 3) obtained from hand-released individuals of *M. californicus* and *M. ciliolabrum*

ranges, both in sympatry and allopatry. But perhaps these differences are maintained to reduce competition due to species recognition or character compression (Gannon, 1997). Analysis of morphological patterns alone may not be sufficient to infer underlying processes. Behavioral considerations in roost selection, the use of habitats, and social structure are factors that are not reflected in morphology necessarily, but can affect outcomes in species interactions (e.g., Fenton, 1985; Aldridge and Rautenbach, 1987). Even 10 kHz difference in minimum frequency of the echolocation call may be sufficient for bats to separate 'auditory space,' thereby reducing interspecific competition or enforcing prey selection processes (also see Schnitzler and Kalko, 1998). Although we may not be able to conclude that this one difference in a call that sweeps 50 kHz is enough to define a species' niche, combined with other morphological and non-morphological features, it may define the species. Other studies

have shown that similar sized bats (e.g., *Pipistrellus* spp.) in sympatry have different call frequency values in a single or just a few characters (Jones and van Parijs, 1993; Barlow *et al*., 1997; see also Novick, 1977 and O'Farrell *et al*., 1999). We propose that an investigation of correlations between ecological relationships of bat species morphology and behavior could further elucidate this sort of species interaction or community-level questions.

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## APPENDIX 1

Fluid-preserved specimens and skulls of *M. californicus* (*n* = 33 and 40, respectively) and *M. ciliolabrum* (*n* = 39 and 40, respectively) housed in the Museum of Southwestern Biology, Albuquerque, and examined in the present study:

| No. | Sex | Country | State | County | Specific Locality |
|---|---|---|---|---|---|
| | | | *M. californicus* (fluid) | | |
| 35161 | ♂ | Mexico | Sonora | Not applicable | 17.7 km E (by Road) Imuris, Highway 2 |
| 82371 | ♀ | Mexico | Baja California | N/A | 4.5 km up Arroyo Dominquito |
| 82372 | ♂ | Mexico | Baja California | N/A | 4.5 km up Arroyo Dominquito |
| 82373 | ♂ | Mexico | Baja California | N/A | 4.5 km up Arroyo Dominquito |
| 34150 | ♀ | Mexico | Sonora | N/A | 6.4 km S El Novillo Dam, Yaqui River |
| 32146 | ♂ | Mexico | Sonora | N/A | Approx. 8 km W San Carlos Bay |
| 34175 | ♀ | Mexico | Sonora | N/A | Tunnel 15 km E Imuris (by Road) Highway 2 |
| 34174 | ♂ | Mexico | Sonora | N/A | Tunnel 15 km E Imuris (by Road) Highway 2 |
| 34176 | ♀ | Mexico | Sonora | N/A | Tunnel 15 km E Imuris (by Road) Highway 2 |
| 45898 | ♀ | USA | New Mexico | Hidalgo | Animas Mts, Gibson Tank |
| 29267 | ♂ | USA | New Mexico | Hidalgo | Granite Gap, 30 km NNE Rodeo |
| 32524 | ♀ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32514 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32515 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32516 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32527 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32528 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32529 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |

Appendix 1. Continued

| No. | Sex | Country | State | County | Specific Locality |
|---|---|---|---|---|---|
| 32530 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32531 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32078 | ♀ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 29397 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 26717 | ♂ | USA | New Mexico | Hidalgo | Sycamore Wells, T33S, R14W |
| 40679 | ♀ | USA | California | Humboldt | 12.8 km N, 2.4 km E Arcata |
| 40680 | ♀ | USA | California | Humboldt | 12.8 km N, 2.4 km E Arcata |
| 37819 | ♀ | USA | New Mexico | San Juan | 1,795 m above sea level |
| 37768 | ♀ | USA | Arizona | Yuma | Buckhorn Tank, 560 m a.s.l. |
| 37769 | ♀ | USA | Arizona | Yuma | Buckhorn Tank, 560 m a.s.l. |
| 37766 | ♂ | USA | Arizona | Yuma | Buckhorn Tank, 560 m a.s.l. |
| 37767 | ♂ | USA | Arizona | Yuma | Buckhorn Tank, 560 m a.s.l. |
| 48090 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Refuge, 357 m a.s.l. |
| 48089 | ♂ | USA | Arizona | Yuma | Cabeza Prieta Game Refuge, 357 m. a.s.l. |
| 37992 | ♂ | USA | Arizona | Yuma | Tule Tank, Cabeza Prieta Game Range |
| | | | *M. ciliolabrum* (fluid) | | |
| 42841 | ♀ | Mexico | Baja California | N/A | Mission de San Borja |
| 35275 | ♀ | Mexico | Chihuahua | N/A | 2.4 km SE El Bosque |
| 27221 | ♂ | USA | Colorado | Las Animas | Near Wootton, 2,275 m a.s.l. |
| 24105 | ♂ | USA | New Mexico | Bernalillo | Cedar Crest |
| 24099 | ♂ | USA | New Mexico | Bernalillo | Manzano Mts, Cedro Canyon |
| 29110 | ♀ ♀ | USA | New Mexico | Bernalillo | San Pedro Wash, 3.4 km E and 3.7 km N San Antonito |
| 29112 | ♀ | USA | New Mexico | Bernalillo | San Pedro Wash, 3.4 km E and 3.7 km N San Antonito |
| 32191 | ♂ | USA | New Mexico | Bernalillo | UNM Campus (Mesa Vista Dormitory), Albuquerque |
| 45899 | ♂ | USA | New Mexico | Hidalgo | Animas Mts, New Well, Double Adobe Canyon |
| 32532 | ♀ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32068 | ♀ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 32069 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo, Hueco Mts |
| 24087 | ♀ | USA | New Mexico | Lincoln | Fort Stanton Cave |
| 29079 | ♂ | USA | New Mexico | Lincoln | Fort Stanton Cave |
| 20623 | ♀ | USA | New Mexico | Lincoln | Gypsum Sink |
| 24106 | ♀ | USA | New Mexico | Rio Arriba | Coyote, 72 km NE Cuba |
| 28166 | ♂ | USA | New Mexico | San Miguel | 32 km N Las Vegas |
| 29067 | ♂ | USA | New Mexico | San Miguel | Camp Luna, ca. 4.8 km N Las Vegas |
| 28159 | ♂ | USA | New Mexico | Sandoval | 17.4 km S, 7.7 km W Los Alamos, Cochiti Canyon |
| 28156 | ♂ | USA | New Mexico | Sandoval | 17.4 km S, 7.7 km W Los Alamos, Cochiti Canyon |
| 29115 | ♀ | USA | New Mexico | Sandoval | Above Cochiti Canyon |
| 29119 | ♀ | USA | New Mexico | Sandoval | East Fork Jemez River Section 2 |
| 30674 | ♀ | USA | New Mexico | Santa Fe | 1.7 km S, 1 km W Golden |
| 24775 | ♂ | USA | New Mexico | Santa Fe | 1.7 km S, 1 km W Golden |
| 27453 | ♂ | USA | New Mexico | Santa Fe | 1.7 km S, 1 km W Golden |
| 33328 | ♀ | USA | New Mexico | Santa Fe | Cerrillos Hills |
| 22254 | ♂ | USA | New Mexico | Socorro | 10.5 km S, 3.2 km W Socorro |
| 22255 | ♂ | USA | New Mexico | Socorro | 10.5 km S, 3.2 km W Socorro |
| 43497 | ♀ | USA | New Mexico | Socorro | 14.5 km E San Antonio |
| 43496 | ♂ | USA | New Mexico | Socorro | 14.5 km E San Antonio |

Appendix 1. Continued

| No. | Sex | Country | State | County | Specific Locality |
|---|---|---|---|---|---|
| 32213 | ♀ | USA | New Mexico | Socorro | Beartrap Canyon |
| 35204 | ♂ | USA | New Mexico | Socorro | Beartrap Canyon, San Mateo Mts |
| 32210 | ♂ | USA | New Mexico | Socorro | Springtime Campground |
| 32211 | ♂ | USA | New Mexico | Socorro | Springtime Campground |
| 29281 | ♀ | USA | New Mexico | Socorro | Weir Tank, 2.4 km E by Road from Springtime Campground |
| 29283 | ♀ | USA | New Mexico | Socorro | Weir Tank, 2.4 km E by Road from Springtime Campground |
| 28113 | ♂ | USA | New Mexico | Valencia | 30.5 km S Grants, Cave in Lava Field |
| 28135 | ♂ | USA | New Mexico | Valencia | 30.5 km S Grants, Cave in Lava Field |
| 36058 | ♀ | USA | New Mexico | Valencia | Las Lunas |
| | | | *Myotis californicus* (museum) | | |
| 52954 | ♀ | USA | Arizona | Pima | Cabeza Prieta Game Range, Papago Well |
| 52955 | ♀ | USA | Arizona | Pima | Cabeza Prieta Game Range, Papago Well |
| 52956 | ♀ | USA | Arizona | Pima | Cabeza Prieta Game Range, Papago Well |
| 52958 | ♂ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52959 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52960 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52961 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52962 | ♂ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52963 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52964 | ♀ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 52965 | ♂ | USA | Arizona | Yuma | Cabeza Prieta Game Range, Tule Well, 360 m |
| 40654 | ♀ | USA | California | El Dorado | 10 km E Somerset |
| 40655 | ♀ | USA | California | El Dorado | 10 km E Somerset |
| 40656 | ♀ | USA | California | El Dorado | 10 km E Somerset |
| 40676 | ♀ | USA | California | Humboldt | 12.8 km N, 2.4 km E Arcata |
| 40677 | ♀ | USA | California | Humboldt | 12.8 km N, 2.4 km E Arcata |
| 40678 | ♀ | USA | California | Humboldt | 12.8 km N, 2.4 km E Arcata |
| 37379 | ♂ | USA | California | Mariposa | North Fork, Merced River, near Bower Cave |
| 37380 | ♂ | USA | California | Mariposa | North Fork, Merced River, near Bower Cave |
| 37381 | ♂ | USA | California | Mariposa | North Fork, Merced River, near Bower Cave |
| 37363 | ♂ | USA | California | Stanislaus | 3.2 km S La Grange |
| 32743 | ♂ | USA | California | Stanislaus | Del Puerto Cr., 24 km W Patterson |
| 7349 | ♂ | USA | Colorado | La Plata | Allison |
| 14523 | ♂ | USA | New Mexico | Catron | Black Range, 3.2 km NE Wall Lake, Taylor Creek |
| 13008 | ♀ | USA | New Mexico | Catron | Taylor Creek, 3.2 km NE Wall Lake |
| 56526 | ♀ | USA | New Mexico | Grant | Big Burro Mts, Junction Saddle Rock and Black Hawk |
| 56527 | ♀ | USA | New Mexico | Grant | Big Burro Mts, Junction Saddle Rock and Black Hawk |
| 89160 | ♂ | USA | New Mexico | Grant | Burro Mountains |
| 56532 | ♂ | USA | New Mexico | Grant | Red Rock, W Side Gila River, 1,230 m a.s.l. |
| 19217 | ♀ | USA | New Mexico | Hidalgo | Dirt Tank North of New Mexico Highway 79 |
| 19007 | ♂ | USA | New Mexico | Hidalgo | Guadalupe Canyon, Guadalupe Mts |
| 32591 | ♂ | USA | New Mexico | Hidalgo | Sycamore Well, Alamo Hueco Mts |
| 31312 | ♀ | USA | New Mexico | Hidalgo | Sycamore Wells Alamo Hueco Mts |
| 17292 | ♀ | USA | New Mexico | Hidalgo | Tank at East Entrance of Clanton Canyon |
| 17921 | ♀ | USA | New Mexico | Hidalgo | Temporary Pond in Canyon Bottom |
| 12869 | ♂ | USA | New Mexico | Luna | Mine Shaft, E Side South Peak, Tres Hermanos Mts |

Appendix 1. Continued

| No. | Sex | Country | State | County | Specific Locality |
|---|---|---|---|---|---|
| 75619 | ♂ | USA | New Mexico | Otero | 32º54'N, 106º08'W, Holloman AFB. Malone Draw |
| 75664 | ♀ | USA | New Mexico | Otero | Lincoln National Forest, Guadalupe District |
| 55451 | ♂ | USA | New Mexico | Socorro | 61 km S, 14 km W Magdalena |
| 55452 | ♂ | USA | New Mexico | Socorro | 61 km S, 14 km W Magdalena |
| | | | *Myotis ciliolabrum* (museum) | | |
| 42777 | ♀ | Mexico | Baja California Sur | N/A | 3.2 km NE Rosarito |
| 43107 | ♂ | Mexico | Baja California Sur | N/A | La Grulla, Sierra De San Pedro Martir |
| 70879 | ♀ | Mexico | Baja California Sur | N/A | 23º30'N, 110º04'W, 424 m a.s.l. La Burrera Ranch |
| 26867 | ♂ | USA | Arizona | Cochise | 4.3 km S, 3.9 km W Portal, S Fork Cave Creek |
| 6754 | ♀ | USA | Colorado | La Plata | Allison |
| 12618 | ♀ | USA | New Mexico | Bernalillo | Sandia Mts, Embudo Cave |
| 21256 | ♀ | USA | New Mexico | Bernalillo | Cedro Canyon, Manzano Mts |
| 12986 | ♂ | USA | New Mexico | Bernalillo | Embudo Cave, Sandia Mts |
| 13220 | ♂ | USA | New Mexico | Bernalillo | Sandia Mts, Embudo Cave |
| 12912 | ♀ | USA | New Mexico | Catron | Taylor Creek, 3.2 km NE Wall Lake, Black Range |
| 18018 | ♀ | USA | New Mexico | Chaves | Cleve Residence |
| 18036 | ♂ | USA | New Mexico | Chaves | Old Church on New Mexico Highway 83, Reeves Ranch |
| 69420 | ♀ | USA | New Mexico | Cibola | El Malpais National Monument, T7N, R12W South 1/2 Section |
| 69422 | ♂ | USA | New Mexico | Cibola | El Malpais National Monument, T7N, R12W South 1/2 Section |
| 75667 | ♀ | USA | New Mexico | Eddy | Lincoln National Forest, Guadalupe District 32º15'N, |
| 24998 | ♀ | USA | New Mexico | Grant | Bar Six Canyon |
| 17372 | ♂ | USA | New Mexico | Hidalgo | Pond on Godfrey Ranch |
| 21811 | ♂ | USA | New Mexico | Lincoln | Gypsum Sink |
| 11801 | ♀ | USA | New Mexico | Mckinley | 12.9 km N, 24 km E Crownpoint |
| 75620 | ♀ | USA | New Mexico | Otero | 32º54'N, 106º08'W; Holloman Air Force Base, Malone Draw |
| 18944 | ♂ | USA | New Mexico | Otero | Alamo Mountain |
| 40081 | ♀ | USA | New Mexico | Rio Arriba | Cebolla |
| 17252 | ♀ | USA | New Mexico | San Juan | 13 km W, 1.6 km S Sheep Springs, Chuska |
| 10295 | ♂ | USA | New Mexico | San Juan | Approx 3.2 km S, 3.2 km W Bloomfield |
| 6635 | ♀ | USA | New Mexico | Sandoval | Bluebird Mesa, Jemez Mts |
| 6636 | ♂ | USA | New Mexico | Sandoval | Bluebird Mesa, Jemez Mts |
| 37455 | ♂ | USA | New Mexico | Sandoval | 8 km E, 5 km S Bernalillo, Tunnel Springs |
| 18882 | ♀ | USA | New Mexico | Santa Fe | Golden |
| 22230 | ♂ | USA | New Mexico | Santa Fe | State Capitol, Santa Fe |
| 24990 | ♀ | USA | New Mexico | Sierra | Macho Canyon Spring |
| 43495 | ♀ | USA | New Mexico | Socorro | 14.5 km E San Antonio |
| 31384 | ♂ | USA | New Mexico | Socorro | Weir Tank, Springtime Campground, San Mateo Mts |
| 17871 | ♀ | USA | New Mexico | Taos | 10.5 km N, 2.4 km E Questa, Rito Del Medio 2,438 m a.s.l. |
| 14312 | ♂ | USA | New Mexico | Taos | 8 km S, 2.4 km El Ranchos De Taos |

Appendix 1. Continued

| No. | Sex | Country | State | County | Specific Locality |
|-----|-----|---------|-------|--------|-------------------|
| 17870 | ♂ | USA | New Mexico | Taos | 10.5 km N, 2.4 km E Questa, Rito Del Medio 2,438 m a.s.l. |
| 19359 | ♀ | USA | New Mexico | Union | 5 km W Kenton, Oklahoma |
| 23679 | ♀ | USA | New Mexico | Valencia | 47 km (by New Mexico Highway 6) W Los Lunas |
| 27582 | ♀ | USA | Washington | Douglas | Douglas Creek, 2.4 km NW of Moses Coulee |
| 27583 | ♂ | USA | Washington | Douglas | Douglas Creek, 2.4 km NW of Moses Coulee |
| 27867 | ♀ | USA | Washington | Grant | 10 km W Quincy on Babcock Ridge |

APPENDIX 2

Echolocation Field Samples: Arizona: Cochise Co., 8 km west Portal — 52 call voucher files recorded from 29 hand released *M. californicus* and *M. ciliolabrum*. Calls are available for download on http://talpa.unm.edu/batcall:

*Myotis californicus* (*n* = 9 ♂♂ and 8 ♀♀):
95252323.02#, 95252326.29#, 95252327.35#, 95252329.48#, 95262122.28#, 95262122.43#, 95262150.04#, 95262152.34#, 95262152.49#, 95262154.05#, 95262244.01#, 95262256.34#, 95262257.57#, 95262302.17#, 95272239.01#, 95272241.12#, 95272242.59#, 95272243.24#, 95272245.04#, 95272332.48#, 95272335.25#, 95272337.11#, 95272339.01#, 95272338.29#, 95272340.30#, 95272341.48#, 95262250.23#;

*Myotis ciliolabrum* (*n* = 8 ♂♂ and 4 ♀♀):
95252328.35#, 95252328.51#, 95262148.58#, 95262151.32#, 95262152.59#, 95262155.24#, 95262155.37#, 95262232.14#, 95262246.09#, 95262247.14#, 95262249.00#, 95262251.57#, 95262252.08#, 95262252.15#, 95262252.22#, 95262255.16#, 95262259.20#, 95262300.44#, 95262303.48#, 95272246.45#, 95272250.01#, 95272330.59#, 95272344.29#, 95272347.44#, 95272347.59#.