# DESCRIPTION OF NOSELEAVES OF PHYLLOSTOMID BATS USING FOURIER ANALYSIS

## HECTOR T. ARITA

*Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, México, D. F. 04510, MEXICO. (Correo electrónico: harita@miranda.ecologia.unam.mx).*

**ABSTRACT**.- The outline shape of noseleaves of Phyllostomid bats is described using Fourier analysis. Line drawings of the noseleaves of nine phyllostomines, seven stenodermatines, and one carolliinae were used to calculate the parameters of a simplified Fourier equation fitted using a multiple-regression model. The outline of noseleaves can be reconstructed by plotting the corresponding Fourier equations. Noseleaves of phyllostomines and stenodermatines were compared using the coefficients of the Fourier equations and no significant difference was detected, although some species such as *Lonchorhina aurita* were clearly outliers.

**RESUMEN**.- Se utilizó el análisis de Fourier para describir la forma de las hojas nasales de los murciélagos filostómidos. Se usaron dibujos del contorno de las hojas nasales de nueve filostominos, siete estenodermatinos y un carolino para calcular los parámetros de una ecuación de Fourier simplificada ajustada por un modelo de regresión múltiple. El contorno de las hojas nasales puede reconstruirse graficando las ecuaciones de Fourier correspondientes. Se compararon las hojas nasales de los filostominos y de los estenodermatinos usando los coeficientes de Fourier y no se detectó ninguna diferencia significativa, a pesar de que algunas especies, como *Lonchorhina aurita*, se salieron totalmente del patrón general.

**Key words:** Chiroptera, Phyllostomidae, Neotropical fauna, noseleaves morphology.

## INTRODUCTION

Fourier analysis is a method of describing the shape of a curve using a mathematical formula that consists of a series of sine and cosine terms. This technique, and the related elliptic Fourier analysis, have been used to describe the outlines of several biological objects, including ostracodes (Kaesler and Waters, 1972), bryozoans (Anstey and Delmet, 1972), hominoid femurs (Lestrel et al., 1977), leaves (Kincaid and Schneider, 1983), protozoans (Roberts et al., 1983), mosquito wings (Rohlf and Archie, 1984), and mussel shells (Ferson et al., 1985). The analysis of biological shape using Fourier series has been criticized on the basis of alleged lack of objectivity (Bookstein et al., 1982), but as discussed by Ehrlich et al. (1983), no method of quantifying shape is infallible, and Fourier series can be valid estimators of shape if the technique is properly used.

In a previous study, I compared the morphology of the noseleaves of phyllostomid bats using multivariate analysis of seven measurements (Arita, 1990). The comparison showed that nectarivorous species (Glossophaginae and Brachyphyllinae) and hematophagous bats (Desmodontinae) possess noseleaves that are distinctively different from those of the frugivores (Stenodermatinae) and the insectivores and omnivores (Phyllostominae). To allow comparisons, herein I use the traditional classification of Phyllostomidae, not the one proposed by Baker et al. (1989). The previous study suggested a correlation between noseleaf morphology and diet among phyllostomines and stenodermatines, but was unable to discriminate the two groups on the basis of the measurements of their noseleaves. In this study, I use Fourier analysis to compare the outline shape of the noseleaves of several phyllostomid bats.

## METHODS

I used the figures of bat faces in Goodwin and Greenhall (1961) to draw the outlines of the noseleaves of nine phyllostomines and seven stenodermatines; I also included one carolliine (*Carollia perspicillata*) as an outside point of comparison. All stenodermatines included are frugivores; among the phyllostomines are strict insectivores, omnivores, and insectivore-carnivores.

The basic data set for a Fourier analysis is a series of radii measured from a constant "center" at equally spaced angles. I used as reference the middle point between the two nostrils. Phyllostomids use their noseleaves to direct the echolocation signals that are emitted from the nostrils (Fenton, 1985; Hartley and Suthers, 1987), so using the nostrils as reference point to measure distances to the margins of the noseleaf seems a reasonable choice. I measured 36 radii at 10-degree intervals (0 to 360 degrees) using as starting radius the sagital line from the reference point to the tip of the noseleaf. Fourier equations are series of sine and cosine elements of the form:

$$r(\theta) = \bar{r} + \sum_{i\,1}^{\infty} (a_i \cos i\theta + b_i \operatorname{sen} i\theta) \qquad \text{Eq.(1)}$$

where $r(\theta)$ is the radius at angle $\theta$, $\bar{r}$ is the mean radius, and $a_i$ and $b_i$ are parameters that fit the equation to the data. For symmetric objects, the sine elements vanish, and the equation simplifies to:

$$r(\theta) = \sum_{i=1}^{\infty} c_i \backslash \cos i\,\theta \qquad \text{Eq. (2)}$$

where the $c_i$ are the parameters of the equation.

In real situations, the summation can go from zero to the number of radii measured, and the parameters of the equation can be fitted using a least-square multiple regression model with radius as dependent variable and the terms as independent variables (Neff and Marcus, 1980). I used PROC GLM of the Statistical Analysis System (SAS Institute, 1985) to estimate the first 18 parameters of the equation for each of the 17 species. I wrote a BASIC program to analyze visually the mathematical reconstructions of the contours of the noseleaves.

## RESULTS AND DISCUSSION

The elements of the Fourier series are orthogonal (independent) of each other, so it is possible to analyze the relative contribution of each component by choosing arbitrary combinations of the elements of the series. The reconstruction of the noseleaf of
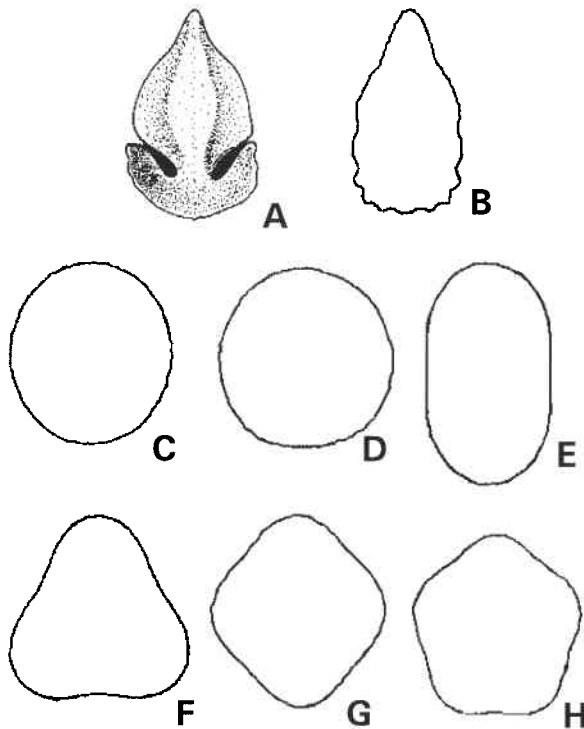


Figure 1.-A. Noseleaf of a phyllostomid bat, *Phyllostomus hastatus* (from Goodwin and Greenhall, 1961). B. Reconstruction of the noseleaf of *P. hastatus* using 18 Fourier parameters. C-H. Reconstruction of the noseleaf using the zeroth parameter (C), zeroth and first parameters (D), zeroth and second (E), second and third (F), zeroth and fourth (G), and zeroth and fifth (H).
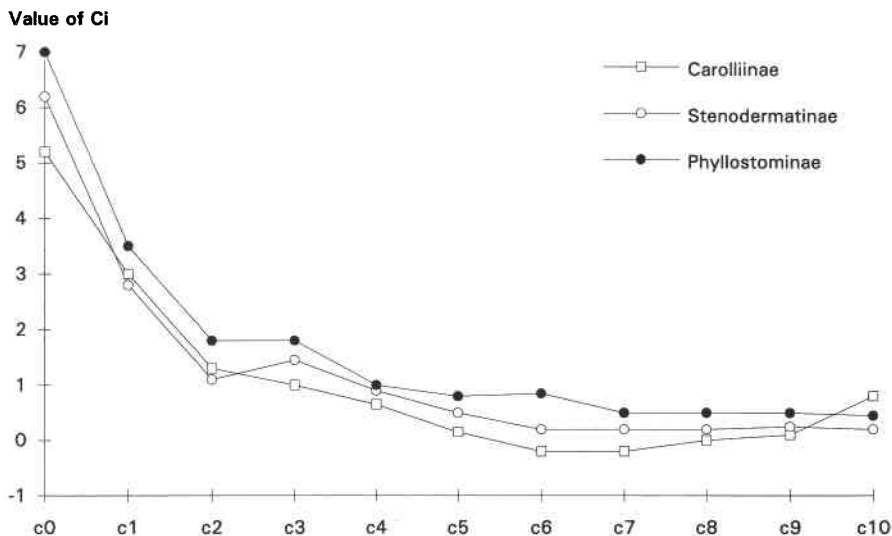
**Value of Ci**



Figure 2.--Profiles of the Fourier parameters of *Carollia perspicillata*, the mean of the Phyllostominae ($n = 9$), and the mean of the Stenodermatinae ($n = 7$).

*Phyllostomus hastatus* is very close to the original shape when using 18 elements of the series (Fig. 1 B). The equation including only the zeroth element generates a circle with radius equal to the mean radius of the noseleaf (Fig. 1 C). Combinations of this element with the first, second, third, fourth, and fifth components produce figures with circular, oval, triangular, quadrangular, and pentagonal shape, respectively (Fig. 1 C to G).

    Noseleaves are basically triangular objects, and the profile plots of the values of the parameters of the Fourier equation show a distinctive peak for the third parameter (Fig. 2). To contrast the contribution of the second and third components, I plotted the species on a graph of values of and divided by (Fig. 3). There is no clear separation of the clusters of Stenodermatinae and Phyllostominae. Most species have robust noseleaves with little size difference between the horseshoe and the spear and are concentrated on the lower left part of the graph. A few species have larger spears and lie on the center of the graph. One species (*Lonchorhina aurita*) is clearly an outlier and shows a very long spear and a comparatively smaller horseshoe. There are some shapes
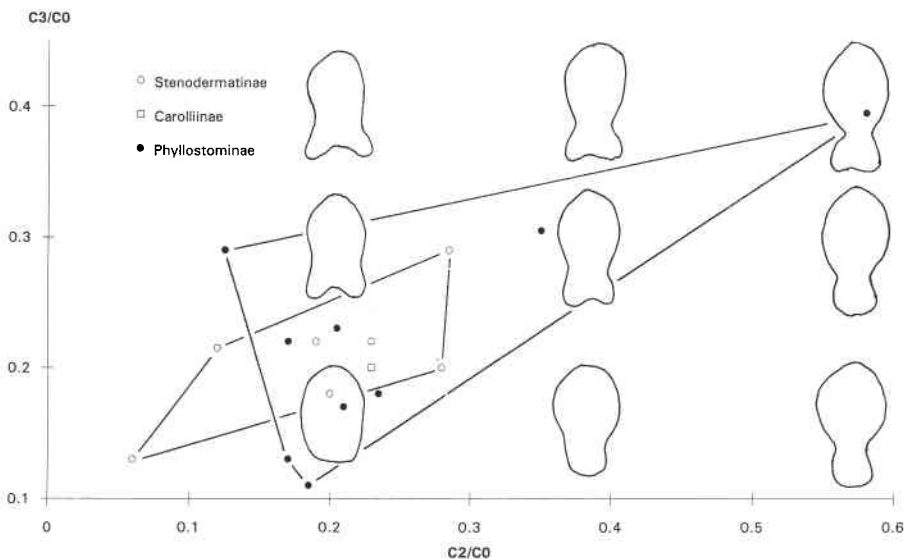
Figure 3.--Plot of $c_3/c0$ vs. $c_2/c_0$ showing the position of phyllostomines and stenodermatines. Silhouettes are reconstructions of noseleaves using the zeroth, first, second, and third Fourier parameters for different values of $c_2$ and $c_3$.

that apparently do not exist among phyllostomids: noseleaves with large and robust spears and small horseshoes (Fig. 3, lower right), or noseleaves with a divided horseshoe (Fig. 3, upper left).

It is apparent that the noseleaves of stenodermatines and phyllostomines are very similar (Figs. 2 and 3). One way of testing the differences between the two groups is to use profile analysis (Johnson and Wichern, 1988). The idea is to separate the comparison into two different hypotheses; $H_0 1$: the profiles of stenodermatines and phyllostomines in Fig. 2 are parallel, $H_0 2$: if $H_0 1$ is true, then the lines are coincident. The first hypothesis tests shape similitudes, because isometric objects should show parallel profiles when using their Fourier parameters; the second hypothesis tests the equivalence of size once the similitude of shape has been shown. The hypothesis of parallelism can be tested using the equivalent hypothesis:

$$H_o{:}C\mu_1{=}C\mu_2 \qquad\qquad \text{Eq. (3)}$$

where $\mu_1$ and $\mu_2$ are the vectors of mean Fourier parameters for the two populations and $C$ is a contrast matrix of the form:

$$\begin{bmatrix} 1 & -1 & 0 & 0 & \ldots & 0 & \ldots & 0 \\ 0 & 1 & -1 & 0 & \ldots & 0 & \ldots & 0 \\ . & . & . & . & \ldots & . & \ldots & . \\ 0 & 0 & 0 & 0 & \ldots & 1 & \ldots & -1 \end{bmatrix} \qquad \text{Eq. (4)}$$

The hypothesis of line coincidence can be tested using the equivalent hypothesis:

$$H_o{:}1'\mu_1{=}1'\mu_2 \qquad\qquad \text{Eq. (5)}$$

where 1 is the unit vector (Johnson and Wichern, 1988).

I used PROC GLM (SAS Institute, 1985), option MANOVA to test these hypotheses using the parameters to comparing phyllostomines and stenodermatines. The small sample size would have invalidated the use of more components because the degrees of freedom of the MANOVA decrease as the number of variables increases. The first test was unable to reject the null hypothesis (Wilk's $\lambda = 0.833$, $P = 0.52$), so I assumed that the profiles for the two groups are parallel, meaning no difference in overall shape between the noseleaves of the two groups. The test for the second hypothesis was not significant (Wilk's $\lambda = 0.901$, $P = 0.24$). No difference can be claimed between phyllostomines and stenodermatines on the basis of their noseleaf outline.

In the previous study (Arita, 1990), I suggested an association between noseleaf morphology and feeding habits because nectarivorous and hematophagous bats separated clearly from frugivores and insectivores. Herein, I could not include nectarivores and vampire bats because Goodwin and Greenhall (1961) did not present illustrations of these bats, and I was unable to find good pictures with reliable scales elsewhere. Noseleaves of phyllostomines and stenodermatines are very similar, although subtle differences can be shown using canonical discriminant analysis (Arita, 1990).

One possible explanation for the inability of the MANOVA to show a difference between the two groups is the great variability that exists among phyllostomines. As discussed by Arita (1990), it is probable that this variation reflects the differences in trophic ecology, foraging behavior and habitat selection among the phyllostomines. A

problem associated with the use of Fourier analysis is that the technique provides information on the outline of the objects only, ignoring the structural features that may be inside the contours. In the case of the noseleaves, the relative size and shape of the horseshoe and the spear are important characteristics in separating the different groups (Arita, 1990). Fourier analysis allows the description of horseshoe and spear morphology only in a very vague way (Fig. 3). By the same token, this method provides no information on the position and size of the medial rib or on the separation between the nostrils.

A final limitation, in common with other comparative studies, is the possible effect of phylogenetic constraints (Brooks and McLennan, 1991; Harvey and Pagel, 1991). The Phyllostominae are a paraphyletic group (Honeycutt and Sarich, 1987), but there is disagreement on the correct phylogeny of the group (Baker, 1967; Baker et al., 1989; Patton and Baker, 1978; Smith, 1976). The subfamily Stenodermatinae seems to be monophyletic (Owen, 1987), but its relationship with the Phyllostominae is unclear (Smith, 1976). Consequently, when comparing morphological features of the two groups, I am neglecting the possible influence of phylogenetic inertia on size and shape.

Fourier analysis is a convenient way of describing the outline shape of simple objects, and can be used both in descriptive and analytical studies. However, the technique has some limitations, especially in the case where the objects possess some important morphological feature not associated with the margin. Fourier analysis is no substitute for other morphometric techniques, and it should be used in combination with other methods to fully exploit its analytical power.

## ACKNOWLEDGMENTS

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## APPENDIX I

BASIC program for the reconstruction of noseleaves using Fourier analysis

```
10 C0=27.3333
20 C1=11.6681
30 C2=6.474
40 C3=4.9056
50 C4=2.1053
60 C5=1.7254
70 C6=1.5555
80 C7=.9362
90 C8=1.0101
100 C9=1
131 SCREEN 1: COLOR 9,0
132 VIEW (30,20)-(308,172),0,2
133 WINDOW (-60,-38)-(60,38)
140 FOR T=0 TO 6.28 STEP .01
150 RAD=C0+C1*COS(T)+C2*COS(2*T)+C3*COS(3*T)+C4*COS(4*T)+C5*COS(
5*T)+C6*COS(6*T)+C7*COS(7*T)+C8*COS(8*T)+C9*COS(9*T) ...
160 X=RAD*COS(T) : Y=RAD*SIN(T)
170 LINE-(X,Y)
180 NEXT T
190 END
```

## APPENDIX II

SAS program for profile analysis

```
DATA TEST;
  INFILE '    ';
  INPUT SPECIES $ SUBFAM $ C0 C1 C2 C3 C4 C5 C6 C7 C8 C9 C10;
  CARDS;
PROC SORT;
  BY SUBFAM;
PROC GLM;
  CLASS SUBFAM;
  MODEL C0 C1 C2 C3=SUBFAM;
  MANOVA H=SUBFAM M=(1 -1 0 0, 0 1 -1 0, 0 0 1 -1)
/ PRINTE PRINTH;
  RUN;
PROC GLM;
  CLASS SUBFAM;
  MODEL C0 C1 C2 C3=SUBFAM;
  MANOVA H=SUBFAM M=(1 1 1 1) / PRINTE PRINTH;
RUN;
```