# Plasticity in the Echolocation Inventory of *Mormopterus minutus* (Chiroptera, Molossidae)

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We recorded the echolocation behavior of the molossid bat *Mormopterus minutus*, a species that uses a plastic call inventory. During its foraging activity, *M. minutus* searches for insects emitting rather long and narrow-band echolocation calls. Search call design however, can vary noticeably even in a continuous foraging pass. While echolocating in different flying conditions *M. minutus* uses several other call designs such as short CF, QCF, FM/QCF, FM and multi-harmonic FM, with or without harmonic overlap, and QCF/FM. Call plasticity characterizes most echolocation sequences, particularly in bats flying in open spaces. Call variation was also influenced by the presence of conspecifics. In those sequences containing echolocation calls from more than one bat, signals from different individuals were reliably identified. In contrast to other small molossids, the call designs in the echolocation inventory of *M. minutus* show a high level of plasticity. Our results suggest that *M. minutus* has combined the advantages of emitting several call designs, as shown by molossids, with the advantages of manipulating one signal design as shown by vespertilionids within the same sonar inventory.

*Key words*: echolocation, k-means clustering, *Mormopterus minutus*, vocal plasticity

## INTRODUCTION

Microbats make use of echolocation to perceive the environment and this has evolved as an essential adaptation in this order of nocturnal flying mammals (Griffin, 1958; Neuweiler, 2000). For auditory perception, the bat's central nervous system creates an acoustic image that corresponds to the cross-correlation function between the emitted call and the returning echo (Simmons, 1989). Object features are thus encoded in complex spectral and temporal echo patterns that the bat's auditory system extracts by highly elaborate neural computations. Time-windows of enhanced echo-processing, combination-sensitive neurons and corticofugal top-down modulations are mechanisms that may create a specific auditory sensitivity to echoes, resulting in an increased performance of the bat's perceptual system (Neuweiler, 2003). As an evolutionary strategy for better echo-processing, most neural resources in the auditory system of bats focus on the evaluation of the echoes within a limited range of acoustic parameters that characterize a small number of echolocation call designs in each species. As a result, echolocation has become stereotyped.

Many good examples of stereotyped echolocation calls can be found in bats from the family Mormoopidae (e.g., Ibáñez *et al*., 1999; Macías *et al*., 2006). Species in this family often emit one signal design with little quantitative variation except in a few temporal and spectral parameters.

Other bat families like the Vespertilionidae contain species that show a higher degree of call variability in their echolocation inventories (e.g., Surlykke and Moss, 2000). Besides the typical call flexibility associated with capturing maneuvers in insectivorous bats, design variations in these families have been mainly explained as adaptations to the spatial structure of the habitat (Kalko and Schnitzler, 1993).

In the family Molossidae, several small species show a high level of echolocation plasticity. *Tadarida brasiliensis* (Simmons *et al*., 1978), *Molossus molossus* (Mora *et al*., 2004) and *Molossops temminckii* (Guillén-Servent and Ibáñez, 2007) are three

examples of bats that broadcast several call designs that are tailored to perform different perceptual tasks. Vocal plasticity in these small species includes significant spectral shifts of the calls and abrupt changes in their frequency-time structure. These findings make other small molossid species attractive for the study of plasticity in echolocation.

*Mormopterus minutus* is an endemic small molossid species restricted to Central and Eastern Cuba and the only *Mormopterus* species in the Caribbean (Silva, 1979). Within the Cuban bat fauna, *M. minutus* is the slowest flying molossid and shows appropriate aerodynamic characteristics for flight in both open and semi-cluttered spaces where it hunts for insects that represent 100% of its diet (Silva, 1979). In this study, we tested the hypothesis that *M. minutus* adjusts its echolocation calls according to the flying conditions and the presence of conspecifics. We predicted that calls would show different spectral and temporal structures when emitted during foraging, compared with those emitted in the vicinity of the roost, or in enclosed spaces. Furthermore, we expected that, like other molossids, *M. minutus* would change its calls when more than one bat was flying in the same air space. Since there are no acoustic studies of *M. minutus*, we tested these predictions by recording the echolocation calls of this species in different flying scenarios. We then characterized the calls both qualitatively and quantitatively to examine call variation associated with the flying conditions and the presence of conspecifics.

## Materials and Methods

### Species Identification and Study Site

*Mormopterus minutus* (Chiroptera, Molossidae) were identified from characters provided by Silva (1979). Animals were recorded from two different colonies in the province of Sancti Spiritus in Central Cuba: a colony sheltered in an old building in the city of Trinidad and a colony occupying the dry dead leaves of a palm *Copernicia vespertilionum* in Caguanes National Park. The palm is known in Cuba by the common name of 'bat's palm' (in Spanish 'palma jata de los murciélagos'). The vegetation in Caguanes National Park is dominated by seasonally flooded grassland savannah combined with widely separated dense patches of palms and seasonally dry bushes resulting in a heterogeneous landscape with marked variation in the height of the vegetation. A total of four and 87 bats were captured from the first and second colony respectively and were all identified as *M. minutus*. Recordings were obtained during several nights in September, 2001, between 18:30 and 21:00 h and between 04:00 and 07:00 h, periods that correspond with the two peaks of maximum nocturnal activity.

### Sound Recordings

The echolocation calls of solitary individuals were recorded under the following flying conditions: 'enclosed space', four bats were allowed to fly in a ($15 \times 5 \times 5$ m) room of the building where their colony was located; 'open space', 24 bats from the palm colony were released from the hand at 200 m from its roosting site; 'vicinity of the roost', 36 bats from the palm colony were recorded as they left their diurnal refuge or returned to it after foraging. Bats in these three flying conditions were followed visually to be sure of the identity of the sender. In addition, 27 passes of echolocation calls were recorded from single bats during their 'foraging' activity. Foraging bats were recorded within 100 m around the palm colony at dusk, night and dawn, and most were followed visually during recordings. Another 10 echolocation passes were analyzed to look for changes in call structure when more than one bat was flying in the same air space.

The bats' calls were recorded using an U30 ultrasonic detector (Ultrasound Advice, London, UK) with a flat response characteristic ($\pm$ 3 dB) between 20 and 120 kHz. During the recording sessions, the heterodyne output was tuned to 40 kHz, to acoustically monitor the individuals. The high frequency output of the bat detector was fed into an analog-digital input port of a digital signal-processing board (model PCM-DAS 16S/330) and controlled with BatSound 2.1 software (Pettersson Elektronik, Uppsala, Sweden). Calls were recorded at a sampling frequency of 312 kHz, and the recordings were commonly made while the bats were flying towards the microphone. Only recorded sequences with at least five pulses with good signal to noise ratio (peak intensity with more than 20 dB above noise level measured in the power spectra) were analyzed. From a total of seven hours of recordings 101 sequences and 1,554 calls were selected for detailed analysis.

### Sound Analysis

For analysis (Avisoft SAS-Lab Pro, Version 4.39), signals were processed through a Fast Fourier Transformation (512 points, Hamming, 100% frame length, 93.75% time overlap), and displayed as sonograms with spectral and temporal resolutions of 376 Hz and 0.17 ms, respectively. Automatic element separation was made by means of a two-threshold algorithm. Every signal was analyzed within (signal's start and end) its 15–20 dB of maximal amplitude. Each call of *M. minutus* was automatically characterized on the fundamental harmonic, which in most calls showed higher intensity. The following acoustic parameters were measured: pulse duration (ms; difference between start and end of call), pulse interval (ms; difference between starting time of two consecutive calls), start frequency (kHz; maximum frequency at -10 dB in the power spectrum calculated at the start of the call), end frequency (kHz; minimum frequency at -10 dB in the power spectrum calculated at the end of the call), bandwidth (kHz; difference between maximum and minimum frequency at -20 dB in the mean spectrum of the entire element), and peak frequency (kHz; frequency at maximum amplitude). From these measurements, we calculated slope (kHz/ms; bandwidth divided by pulse duration), $Q_{10\text{-dB}}$ (peak frequency divided by bandwidth at -10 dB measured in the mean spectrum of the entire element), and duty cycle (%; percentage of time in which signals are emitted, calculated as pulse duration/pulse interval * 100).

## *Statistical Procedures*

The echolocation call inventory of *M. minutus* contained several call types, similar to those that have been described previously for other molossid bats (*Tadarida brasiliensis*: Simmons *et al.*, 1978; *Molossus molossus*: Mora *et al.*, 2004; *Molossops temminckii*: Guillén-Servent and Ibáñez, 2007). However, in contrast with the situation reported for *T. brasiliensis*, *M. molossus* and *M. temminckii*, in *M. minutus* the large quantitative variation within each call type made it difficult to classify calls of intermediate characteristics. Thus, following a careful visual inspection of the entire recorded inventory, calls were placed side-by-side based on variations in each of the acoustic parameters of interest: duration, start and end frequency, slope and harmonic distribution of the energy. Approach and final phase calls were excluded from the analysis. We identified seven qualitatively different call types, and used k-means clustering analysis to group the calls. We specified seven groups and used the parameters: duration, start frequency, end frequency, slope, peak frequency, bandwidth and $Q_{10\text{-}dB}$. To minimize possible pseudo-replication, calls of the same type were averaged within each sequence and treated as a single measurement before further analysis. All values of the acoustic parameters are given as $\bar{x} \pm 1SD$. Since the data sets were not normally distributed (Kolmogorov-Smirnov test), we used nonparametric statistics (Kruskal-Wallis ANOVA) to test among flying conditions and call types. Statistical differences among mean values were analyzed with a nonparametric Student Newman-Keuls post-hoc test. A multivariate analysis of variance (MANOVA) was performed to compare echolocation calls recorded in those sequences in which several bats were flying together. Differences in calls emitted by several bats flying together were visualized using Principal Component Analysis. All analyses were made with a level of significance of $\alpha = 0.05$. Statistical analysis was carried out using STATISTICA for Windows version 6.0 (Stat-Soft, Inc., 2001).

## Results

### *Echolocation Behavior at Foraging*

During foraging, *M. minutus* showed the three phases of echolocation for hunting insectivorous bats (Fig. 1). While searching for insects, the species emitted rather long ($\approx$ 10 ms) and narrow-band (< 4 kHz bandwidth) echolocation calls (Fig. 1, search I). Call design in the spectrograms followed a slightly concave shape. However, search call design did vary noticeably even in a continuous foraging pass. In the example shown in Fig. 1, short (< 5 ms) and wide-band (> 25 kHz bandwidth) downward frequency-modulated sweeps were emitted in the phase labeled search II, which was emitted after the silent gap following the final phase of capture corresponding to search I. Other variations during the search phase consisted of calls with two harmonics and a variable range of frequency overlaps, frequency modulation rates and bandwidths. It is noteworthy that call design alternation was found in 40%

of the echolocation passes (Fig. 2). Search call interval averaged $125.4 \pm 54.5$ ms.

During the approach phase, *M. minutus* emitted relatively long ($9.4 \pm 1.6$ ms; $n = 7$ passes, 14 calls) downward frequency modulated calls of higher spectral content. The end frequency of the approach calls ($38.2 \pm 2.1$ kHz) was higher than the start frequency of the previous search call by $1.2 \pm 0.9$ kHz. A monotonous decrease of call duration along the approach phase was also found. Average duration however, decreased only in 3.3% with respect to previous search calls. Since call interval showed a larger decrease ($75.2 \pm 18.7$ ms; $n = 7$ passes) duty cycle increased from $7.03 \pm 2.9\%$ to $12.9 \pm 2.7\%$. Approach calls occasionally interrupted the sequence of search calls (Fig. 1).

The final phase of capture consisted of a fast train (call interval: $7.3 \pm 1.4$ ms) of short ($1.4 \pm 0.1$ ms; $n = 12$ calls) and steep downward frequency-modulated pulses emitted with lower frequency content (start frequency: $41.7 \pm 1.6$ kHz; end frequency: $20.9 \pm 1.7$ kHz). The final phase of capture was not divided into the usual buzz I and buzz II sections that are observed in other species.

### *Call Variability*

When call characteristics emitted by bats in different flying conditions ('open space', 'enclosed space', 'vicinity of roost', and 'foraging') were compared, acoustic differences were found in every parameter. Calls emitted during foraging exhibited the longest duration, the smallest bandwidth and the largest $Q_{10\text{-}dB}$ (Table 1).

To verify whether the extent of echolocation plasticity found for search calls was also present in other flying conditions, we recorded echolocation passes from *M. minutus* released from the hand. Animals emitted different call designs within the same call sequence and the emitted calls showed monotonic changes in their acoustic parameters (Fig. 3). Overall, calls emitted by *M. minutus* in different flying conditions showed variations in each of the acoustic parameters of interest, i.e. call: duration, start and end frequency, slope and harmonic distribution of the energy (Fig. 4A). However, only seven different call types were qualitatively identified: short constant frequency (CF), quasi-constant frequency (QCF), frequency modulated/QCF (FM/QCF), FM, multi-harmonic FM with no harmonic overlap, multi-harmonic FM with harmonic overlap, and QCF/FM (Fig. 4B). It was difficult however, to assign intermediate
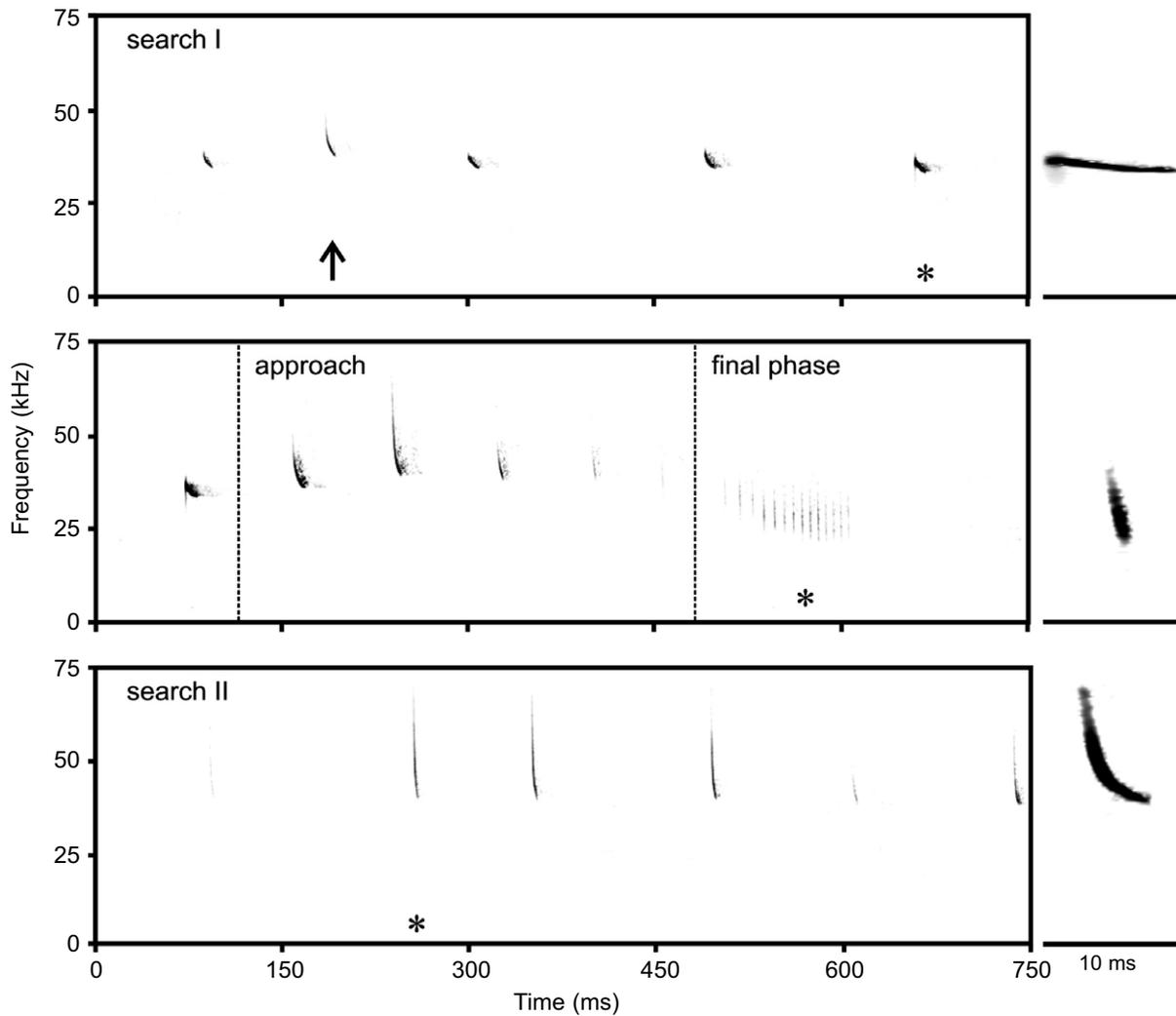
FIG. 1. Left: spectrograms of a continuous echolocation sequence emitted by an individual *M. minutus* during its foraging activity in the wild. The foraging phases are identified. The arrow shows an approach call emitted between search calls. Search calls emitted after the final phase (search II) are different in design to calls in search phase I. Right: expanded spectrograms of calls indicated with asterisks in the foraging pass

designs to one or another call type by means of visual inspection.

We used k-means clustering to distribute *M. minutus* calls into seven clusters. Acoustic differences were found for every parameter, which also differed among most call types. Long duration calls exhibited the smallest bandwidth (type I), and short calls exhibit the largest bandwidth (type V–VII — Table 2).

*Variability Sources*

One source of the variability found in the echolocation inventory of *M. minutus* is at the individual or sequence level. Most echolocation sequences (80/91) contain more than one type of call design.

It was noticeable that in around 30% of the sequences four or more call types were combined. A second source of variability resulted from the flying condition. The maximum amount of variation was found for sequences recorded from bats in 'open space' where every call type was recorded. Type I calls were not emitted in 'enclosed space' and in the 'vicinity of the roost', while 'foraging' bats did not emit call types V, VI and VII. In addition, a source of call variation was found in the presence of conspecifics. In those sequences in which echolocation calls from more than one bat were recorded, individual signals were reliably identified (Fig. 5). In 10 sequences analyzed, call designs from different bats differed significantly (MANOVA, $P < 0.01$).

TABLE 1. Mean values (and SD) of acoustic parameters characterizing calls of each condition recorded in *M. minutus*. All *H*-values statistically significant, confirming significant differences among examined call types. Lowercase letters represent the results of a Student-Newman-Keuls post-hoc test applied to each parameter (identical letters mean no statistically significant difference between the means). *n* = the number of call sequences; freq = frequency

| Parameter | Flying condition | | | | Kruskal-Wallis $H$ (3, $n$ = 91), $P < 0.001$ |
|---|---|---|---|---|---|
| | Enclosed space $n$ = 23 | Open space $n$ = 22 | Vicinity of the roost $n$ = 22 | Foraging $n$ = 24 | |
| Duration (ms) | 5.47[b] (0.91) | 5.88[b] (2.49) | 4.25[c] (1.02) | 8.04[a] (2.05) | 33.67 |
| Start freq (kHz) | 78.61[a] (9.29) | 59.68[c] (14.14) | 75.43[b] (11.99) | 55.66[d] (14.58) | 49.16 |
| End freq (kHz) | 32.72[b] (6.19) | 31.10[c] (8.02) | 33.39[b] (8.76) | 39.56[a] (3.05) | 22.41 |
| Slope (kHz/ms) | 8.59[b] (2.00) | 6.58[c] (4.83) | 10.31[a] (3.05) | 2.57[d] (2.80) | 40.22 |
| Peak freq (kHz) | 42.17[b] (3.89) | 39.71[c] (4.97) | 44.77[a] (6.67) | 43.04[b] (4.84) | 25.65 |
| Bandwidth (kHz) | 30.74[a] (10.41) | 20.26[b] (13.75) | 31.83[a] (10.62) | 10.95[c] (9.24) | 43.86 |
| $Q_{10\text{-dB}}$ | 2.86[c] (1.57) | 7.42[b] (3.66) | 2.72[c] (1.47) | 10.93[a] (7.05) | 38.26 |

## DISCUSSION

### *Foraging Echolocation Behavior in* M. minutus

While foraging, the small molossid bat, *M. minutus*, shows an echolocation behavior that can be clearly distinguished from other bat species studied so far in their use of different call designs to deal with similar perceptual tasks, e.g., searching and tracking flying prey. Most species in other families (e.g., Vespertilionidae, Mormoopidae) search for their prey by broadcasting one type of call design that frequently works as a species specific signature and therefore allowing its acoustic identification

(Kalko and Schnitzler, 1993; Mora *et al.*, 2005; Macías *et al.*, 2006). There are many factors affecting the acoustic parameters that characterize a species 'distinctive' design. These include habitat structure, foraging mode, body mass, individual sex and age, geographic distribution and the presence of conspecifics (Denzinger *et al.*, 2004). The majority of the changes within the species inventory however, can be considered quantitative and include more minor than substantial adjustments in the duration and spectral content of the calls.

In our study, we recorded and analyzed call sequences from a colony of *M. minutus* foraging over
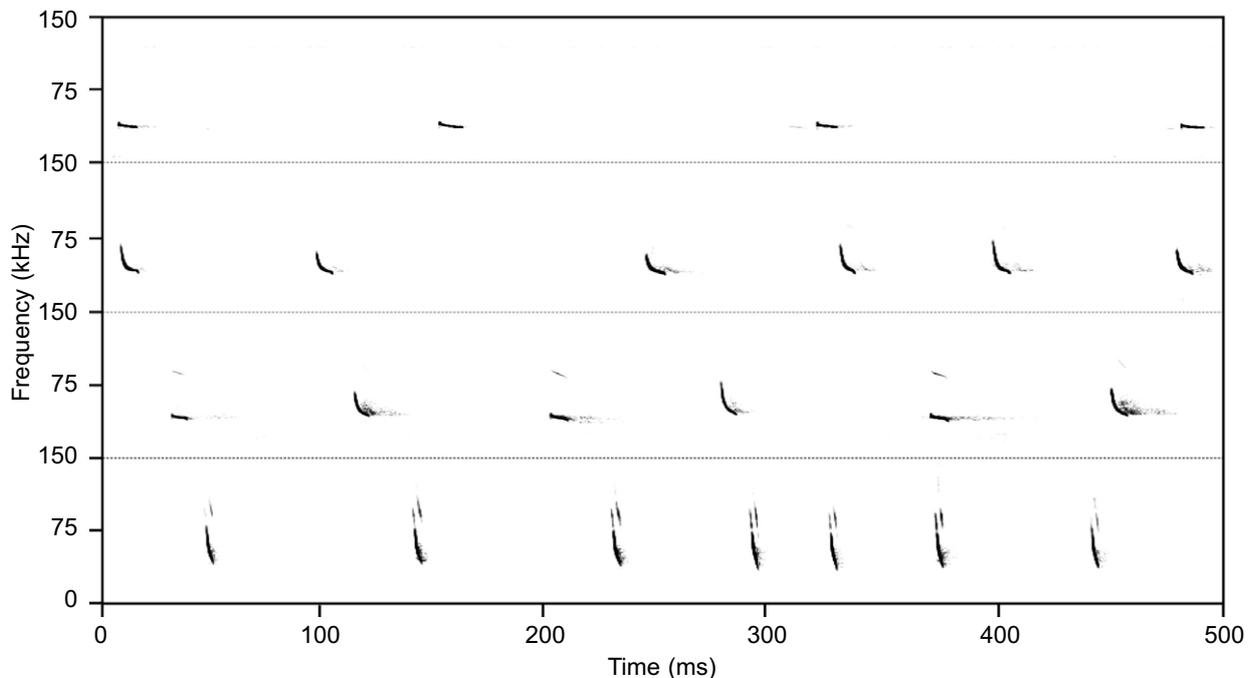


FIG. 2. Spectrograms of four echolocation sequences including different call designs used by *M. minutus* while searching for its prey. Differences can be found in duration, bandwidth, slope of frequency modulation and harmonic composition. In sequence 3, two call designs are alternated
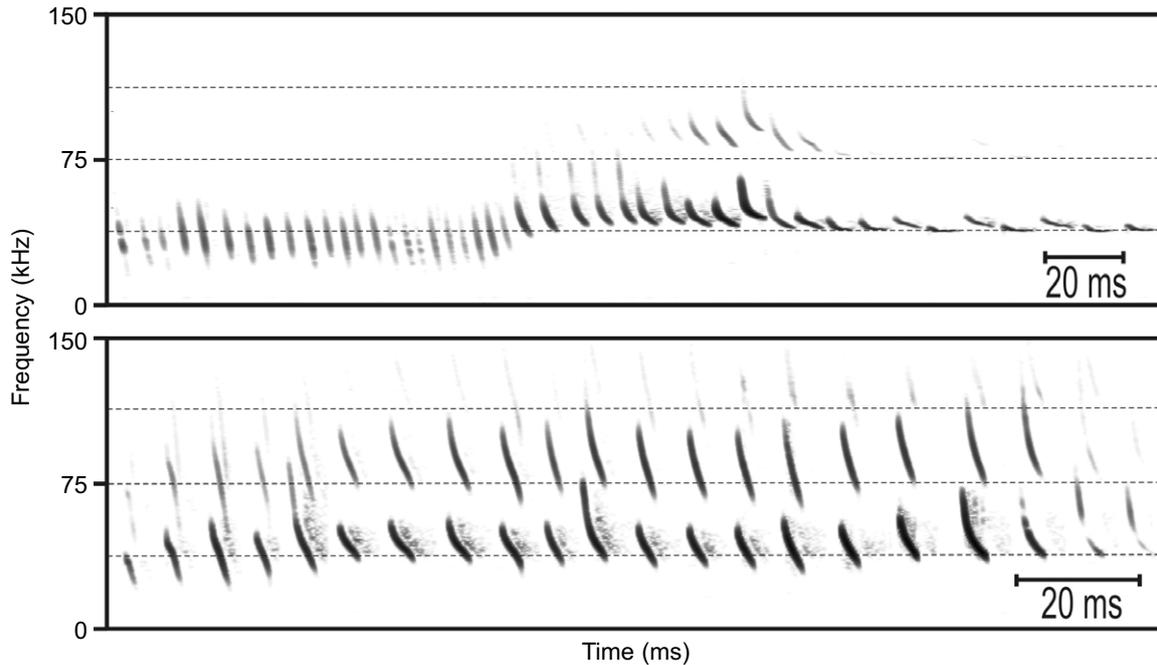
FIG. 3. Spectrograms of two examples of call sequences emitted by *M. minutus* while flying in open space after being released from the hand. Call interval have been removed. Notice the changes in acoustic parameters and call design

a landscape dominated by grassland savannah where the greatly varying height of the vegetation and its heterogeneous patch distribution was the most obvious feature. A large percentage of foraging passes, with alternation of call design, or with sudden changes from one call type to another, may be a vocal adaptation of hunting bats facing a constantly changing three-dimensional habitat structure in their flight path (Simmons and Stein, 1980).

Approach calls recorded in *M. minutus*, as in other bat species, are of higher bandwidth than preceding search signals and are therefore better suited for determining distance and prey position (Simmons and Stein, 1980; Siemers and Schnitzler, 2004). Although the pulse duration of approach calls

in *M. minutus* are relatively constant, they may sometimes increase. These relatively long approach calls contribute to increase duty cycle, which favors a higher flow of fluttering information that is important for prey evaluation, without creating problems of pulse/echo overlap (Mora *et al.*, 2004; Guillén-Servent and Ibáñez, 2007). Another unusual characteristic of the approach pulses in *M. minutus* is the shift to frequencies above the narrowband search pulse frequencies. Higher frequencies provide a better evaluation of prey in terms of size, form, depth and angular extension and texture (Simmons and Stein, 1980; Schmidt, 1988; Neuweiler, 1989). The final phase of capture in *M. minutus* is comparable to that observed in other bat species. Thus, broad-

TABLE 2. Mean values (and SD) of acoustic parameters characterizing each call type identified in *M. minutus*. All *H*-values statistically significant, indicating significant differences among examined call types. Lowercase letters represent the results of a Student-Newman-Keuls post-hoc test applied to each parameter (identical letters mean no statistically significant difference between the means). *n* = the number of call sequences; freq = frequency

| Parameter | Call type | | | | | | | Kruskal-Wallis $H$ (6, $n$ = 262) $P < 0.001$ |
|---|---|---|---|---|---|---|---|---|
| | I $n$ = 30 | II $n$ = 45 | III $n$ = 58 | IV $n$ = 37 | V $n$ = 29 | VI $n$ = 33 | VII $n$ = 30 | |
| Duration (ms) | 9.30[a] (1.33) | 6.42[b] (2.08) | 5.42[c] (1.16) | 5.10[d] (0.95) | 4.95[d] (1.02) | 4.55[e] (0.96) | 3.71[f] (0.95) | 810.87 |
| Start freq (kHz) | 42.46[e] (3.31) | 58.92[d] (5.12) | 78.34[b] (6.74) | 86.99[a] (4.48) | 86.08[a] (4.60) | 74.57[c] (5.31) | 58.37[d] (5.72) | 1,246.46 |
| End freq (kHz) | 36.46[c] (2.01) | 39.51[a] (3.09) | 38.68[b] (4.61) | 40.19[a] (3.79) | 29.22[d] (5.50) | 26.13[e] (3.74) | 22.47[f] (4.88) | 1,001.91 |
| Slope (kHz/ms) | 0.67[g] (0.27) | 3.54[f] (1.79) | 7.65[e] (2.20) | 9.46[d] (1.95) | 12.02[a] (2.83) | 11.14[b] (2.63) | 10.08[c] (2.25) | 1,062.78 |
| Peak freq (kHz) | 38.43[g] (2.32) | 43.73[d] (2.32) | 44.80[c] (3.00) | 48.59[a] (4.58) | 45.91[b] (7.04) | 40.01[e] (4.77) | 36.94[f] (5.00) | 761.73 |
| Bandwidth (kHz) | 3.61[g] (1.63) | 13.59[f] (4.04) | 20.77[e] (4.49) | 32.77[c] (4.67) | 51.02[a] (5.94) | 36.33[b] (5.78) | 28.72[d] (5.11) | 1,253.46 |
| $Q_{10\text{-dB}}$ | 18.23[a] (7.79) | 5.95[b] (2.56) | 3.87[c] (1.58) | 2.91[d] (1.13) | 1.83[e] (0.75) | 1.91[e] (0.97) | 2.24[de] (1.34) | 1,089.41 |
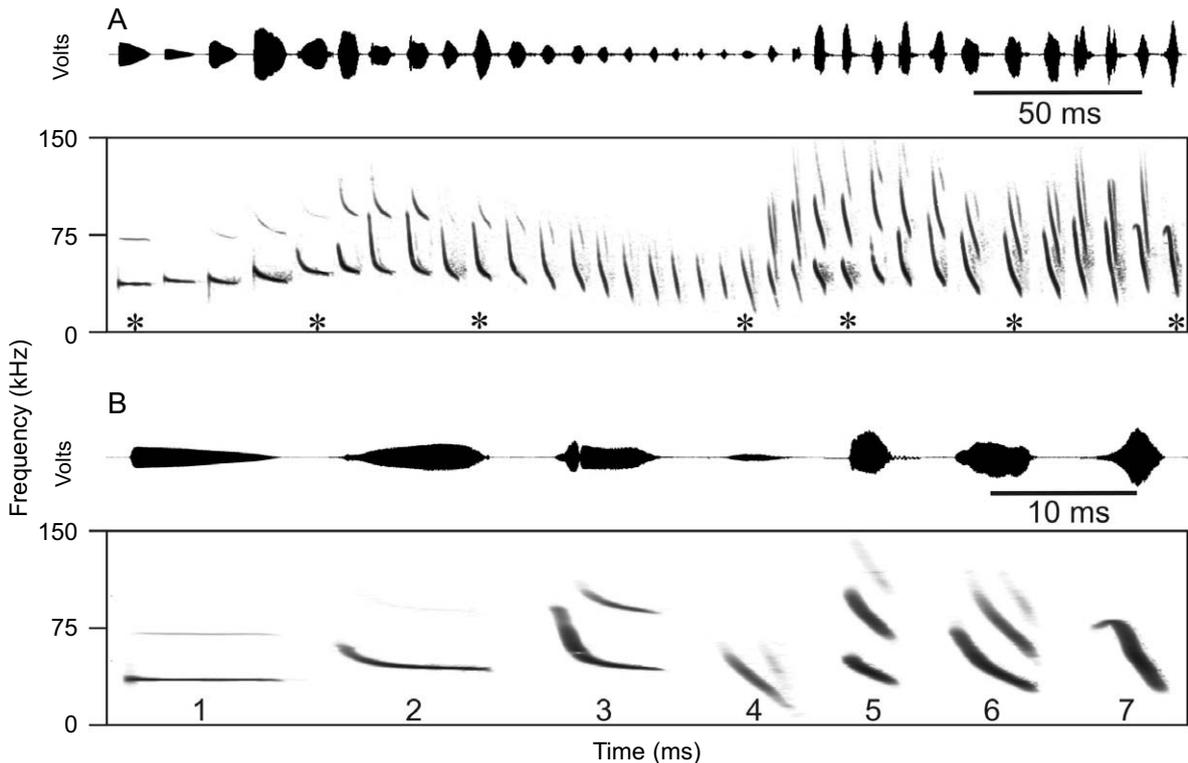
FIG. 4. A — Oscillograms (above) and spectrograms (below) of the calls in the echolocation inventory of *M. minutus*. Calls are shown by their general shape and acoustic characteristics. B — Details of the seven call types visually identified and marked with an asterisk in A. The selection was done by looking for differences in call design and acoustic parameters. Approach and final phase calls were not included in the analysis. Call designs: 1. short CF, 2. QCF, 3. FM/QCF, 4. FM, 5. multi-harmonic FM with no harmonic overlap, 6. multi-harmonic FM with harmonic overlap, and 7. QCF/FM

band, short, steep pulses provide superb resolution of target range and independence of range estimates on target velocity (Simmons and Stein, 1980).

*Call Plasticity*

*Mormopterus minutus* is a very flexible species in terms of echolocation and its signal repertoire incorporates call designs that can be found independently in the call inventories of other more stereotypic species. Short CF, QCF, FM/QCF, FM, multiharmonic FM, with or without harmonic overlap, and QCF/FM calls can be found in the species sonar behavior. This level of plasticity in *M. minutus* is partially shared by other species of small molossids (Simmons *et al*., 1978; Mora *et al*., 2004; Guillén-Servent and Ibáñez, 2007).

Two main factors may help to explain the call plasticity observed in *M. minutus*. As in several other bats, the flying condition might influence quantitative (Surlykke and Moss, 2000), and qualitative (Simmons *et al*., 1978; Mora *et al*., 2004; Guillén-Servent and Ibáñez, 2007) characteristics of the time-frequency design of the calls in this

species. For example, calls in cluttered spaces (i.e., vicinity of the roost, enclosed space) show usually FM broadband and multiharmonic designs covering more than 50 kHz and can thus provide a detailed target characterization (Simmons and Stein, 1980; Schmidt, 1988; Neuweiler, 1989), which is of considerable interest for a bat that is landing at very high speed on a palm or for a bat that is flying in new surroundings. Such vocal adaptation highlights the limited value of call libraries obtained from hand-released bats or from bats flying in confined spaces, which are frequently used to identify free-flying bats.

Another source of call plasticity in *M. minutus* relates to the presence of conspecifics. A number of studies indicate the potential for individual recognition by echolocation call signatures emitted by bats while foraging (Masters *et al*., 1995). Vocal signatures in *M. minutus* revealed large differences between call designs of different individuals when they were flying together with conspecifics. Thus, our results indicate that *M. minutus* has the vocal plasticity to differentiate self-calls when flying in
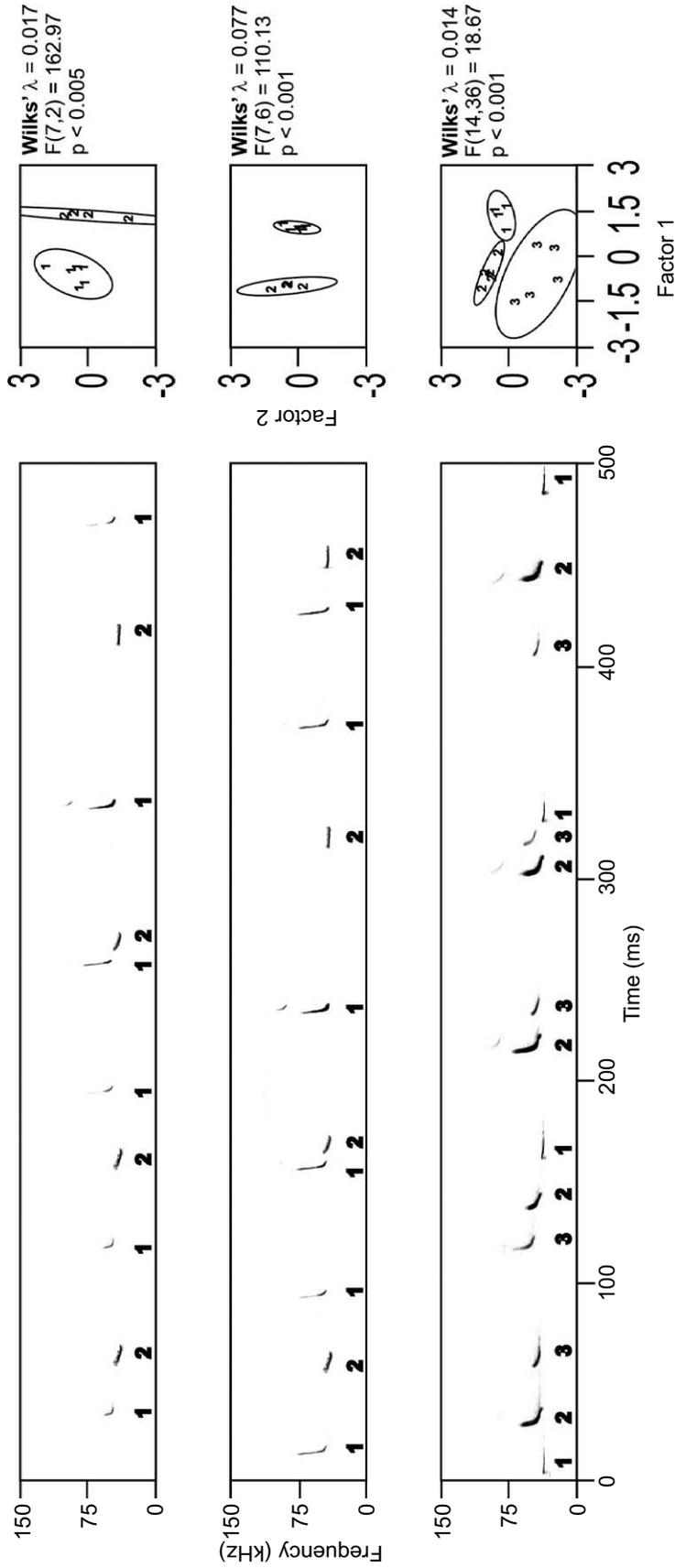
FIG. 5. Spectrograms of three examples of call sequences emitted by *M. minutus* while flying together with conspecifics. Scatter plot of the Principal Component Analysis and results of ANOVA for each sequence are shown at the right side of the spectrogram panels. Notice that calls from different individuals are group together

groups, but suggests that vocal signatures in the species may be very flexible, as proposed for *Nycticeius cubanus* (Mora *et al.*, 2005).

If the number of call designs can be seen as an indication of the number of different perceptual tasks a given species can solve (Simmons and Stein, 1980), then the plastic echolocation inventory of *M. minutus* may confer a behavioral advantage that enables them to exploit different habitats and/or food resources, as evidenced in the natural history of the species (Silva, 1979). In other bat species (e.g., *Myotis evotis*; Faure and Barclay, 1994) one signal design is modified in its time-frequency structure and consequently in its acoustic properties to solve different perceptual tasks. In the *Myotis* species, for example, the echolocation call inventories can be derived from a sigmoidal call type by changing duration, bandwidth and harmonic composition of the three elements that distinguish the basic design (Siemers and Schnitzler, 2004).

The echolocation plasticity of the genus *Myotis* is emulated in molossids like *T. brasiliensis* (Simmons *et al.*, 1978) and *M. molossus* (Mora *et al.*, 2004) that use several stereotyped call designs which are associated with specific acoustic environments. In *M. minutus*, however, several call designs are distinguished, each of which can show a high degree of flexibility. The advantages of manipulating one signal design, as shown by vespertilionids, with the advantages of emitting several call designs as shown by molossids, are thus combined within the same sonar inventory in *M. minutus*. Future controlled studies will be necessary to determine which factors shape the call plasticity observed in *M. minutus*.

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