Echolocation Calls of the Eleven Insectivorous Bats of Taiwan

臺灣 11 種食蟲性蝙蝠的回聲定位研究

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Abstract

Insectivorous bat emits ultrasound and listens to its echo in flight, the so-called echolocation call, to detect surrounding and to identify prey. Information on its patterns of different species is useful for the inventory survey, particularly when capturing is difficult. There are over 30 species of insectivorous bats in Taiwan, but such information was scarce. This study was intended to collect basic characters of echolocation calls of common insectivorous bats in Taiwan to establish their reference database for the intra- and inter-species identification. In March 2005 to November 2006, 249 individuals of 11 species of bats were caught with harp traps and mist nets around Taiwan and on the Kinmen Island. Ten parameters of the echo pulses were recorded and analyzed with the AnaBat system bat detector. Among these species *Rhinolophus monoceros* and *Hipposideros terasensis* emitted constant frequency (CF) type echo-calls; whereas the other 9 species had frequency modulated (FM) type echo-calls. For the former, the mean frequency (Fmean) and the constant part of the CF calls were 111.14 ± 2.57 kHz, respectively, for *R monoceros*, and 67.56 ± 1.53 kHz for *H. terasensis*. For the latter the mean frequency was 50.40 ± 3.91 kHz for *Pipistrellus abramus*, 45.41 ± 5.26 kHz for *Arielulus torquatus*, 46.91 ± 3.96 kHz for *Scotophilus kuhlii*, 34.55 ± 4.86 kHz for *Eptesicus serotinus horikawai*, 51.30 ± 8.86 kHz for *Miniopterus schreibersii*, 86.84 ± 10.30 kHz for *Murina puta*, 54.77 ± 3.19 kHz for *Myotis latirostris*, 54.05 ± 4.65 kHz for *Myotis* sp.2, and 57.55 ± 4.46 kHz for *Myotis* sp.3. Jamming avoidance responses to echolocation calls were observed in some of the colonies of *P. abramus* and *S. kuhlii*. Dialects were found among colonies of *Mi. schreibersii*.

摘 要

食蟲性蝙蝠以回聲定位偵測環境及分辨獵物。在進行蝙蝠調查時，研究人員可利用每種蝙蝠獨特的回聲定位來辨識物種，尤其是在不易以捕捉進行蝙蝠調查的地點。臺灣地區現已知有超過三十種的食蟲性蝙蝠，但其回聲定位資訊仍相當有限。本研究目的在於蒐錄臺灣地區常見食蟲性蝙蝠的回聲定位聲音，測量其音頻形值以建立作為辨識種類依據的資料庫，並藉以檢視種間及種內變異。自 2005 年 3 月至 2006 年 11 月，我們在臺灣與金門地區共計捕獲 11 種蝙蝠 249 隻個體，確定種類後以蝙蝠偵測器(AnaBat系統)錄音測量，單一脈波皆測量 10 個特徵值。其中臺灣小蹄鼻蝠(*Rhinolophus monoceros*)與臺灣葉鼻蝠(*Hipposideros terasensis*)為常頻式(CF)回聲音頻，其他 9 種則使用調頻式(FM)回聲音頻。臺灣小蹄鼻蝠的特徵音頻(Fc)約為 112 千赫(111.14 ± 2.57 千赫)，而臺灣葉鼻蝠約為 65 千赫(67.56 ± 1.53 千赫)。調頻式音頻的東亞家蝠(*Pipistrellus abramus*)的平均音頻(Fmean)為 50.40 ± 3.91 千赫，黃頸蝠(*Arielulus torquatus*)為 45.41 ± 5.26 千赫，高頭蝠(*Scotophilus kuhlii*)為 46.91 ± 3.96 千赫，堀川氏棕蝠(*Eptesicus serotinus horikawai*)為 34.55 ± 4.86 千赫，摺翅蝠(*Miniopterus schreibersii*)為 51.30 ± 8.86 千赫，臺灣管鼻蝠(*Murina puta*)為 86.84 ± 10.30 千赫，寬吻鼠耳蝠(*Myotis latirostris*)為 54.77 ± 3.19 千赫，長趾鼠耳蝠(*Myotis* sp.2)為 54.05 ± 4.65 千赫，以及長尾鼠耳蝠(*Myotis* sp.3)為 57.55 ± 4.46 千赫。此外，我們也發現東亞家蝠與高頭蝠在一隻以上的個體出現於同一區域時彼此的音頻會有避免干擾的調整，而不同地區的摺翅蝠則具有方言的現象。

Key words: echolocation, insectivorous bats, jamming avoidance, dialect, Taiwan

關鍵詞：回聲定位、食蟲性蝙蝠、避免干擾、方言、臺灣

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Introduction

Insectivorous bat uses echolocation call in flight in night to locate its position and to detect potential prey items (Kalko and Schnitzler 1989; Obrist 1995). A typical sequence of the call used in the prey detection has two phases: an approach-phase call during the time of pursuit, and a terminal-phase call (feeding buzzes) just before the capture (Griffin *et al*. 1960; Kalko and Schnitzler 1989). Search-phase calls are ideal for studying acoustic identification of species because they are emitted more often by foraging bats than other types of the calls and are more often encountered by investigators in the field (Fenton and Bell 1981; Fenton and Morris 1976).

Echolocation call structure may be described in terms of frequency and temporal parameters, of which duration, duty cycle, bandwidth, intensity etc. vary among species. The frequency has two categories: constant frequency (CF) that is a single tone at one frequency for a period of time, and frequency modulated (FM) that is a sweeping up or down in frequency for a period of time. A call may be made up of the combination of the two categories as CF/FM call (with a CF followed by FM component) (Vaughan *et al.* 1997; Schnitzler and Kalko 1998; Fenton 1999).

A search-phase call also exhibits a consistent sequence pattern with species- specificity (Ahlen 1981; Fenton and Bell 1981; O'Farrell *et al.* 1999; Schnitzler and Kolko 2001) but has intraspecific variation, resulting in obscurity in species distinction (Barelay 1999; Betts 1998; Brigham *et al.* 1989; Thomas *et al.* 1987). Also, echolocation call may vary among individuals of a species due to differences in size, age, sex (Buchler 1980; Heller and Helversen 1989; Jones *et al.* 1992 and 1994), foraging habitat, and microhabitat types (Jacobs 1999; Jensen and Miller 1999; Rydell 1990, 1993). The variation among populations from different geographic regions has been also demonstrated in some of the species (Parsons 1997; Thomas *et al.* 1987). With combination of the above factors, atmospheric attenuation, Doppler shift, directionality of emitted signal, and directionality of the detector may also cause wide ranges of intraspecific variation (Obrist 1995; Parsons 1997; Pye 1993), resulting in wide overlap of the calls among species. Therefore, a comprehensive knowledge on the intraspecific variation is important for the specific distinction (Barclay 1999; Betts 1998; Brigham *et al.* 1989; Thomas *et al.* 1987).

In Taiwan there are more than 30 insectivorous bats, of which many are endemic (Lin *et al.* 2004; Cheng *et al.* 2010). Information of their echolocation calls is very scarce. This study was intended to establish the reference database of echolocation calls of common insectivorous bats of Taiwan.

Materials and Methods

1. Bat capture and echo-call recording

We randomly selected some suitable sites in fields to set up harp traps and mist nets to catch flying bats in night around Taiwan and on the Kinmen Island. When a bat was caught, a small chemiluminescent tag (2.9*23 mm) was attached to its dorsal side of the body (Buchler 1976; Hovorka 1996). The bat was then taken to an open area, 100-300 m in diameter and less than 0.5 km from the capture site; it was released and its echolocation call when flying away was recorded.

The recording equipment used was consisted of an Anabat Ⅱ bat detector, a Zero Crossing Analysis Interface Module (ZCAIM), and a laptop computer with the Anabat software (Titley Electronics, Ballina, New South Wales, Australia). The Anabat Ⅱ detector was broadband (10-200 kHz), divide-by detector, which divided the frequencies of incoming signal by a preset division ratio (set at 16 in this study) to bring it within the audible ranges for the analysis. The signal then passed through ZCAIM where frequency information for the harmonic with the highest energy (usually the fundamental) was determined with the zero-crossing analysis, and the multiple harmonics were excluded. The ZCAIM was connected to a laptop computer to construct a oscillogram with the Anabat software (versions 6.2d or 5.7i), and saved it for later analysis. We also recorded the echolocation calls of *Rhinolophus monoceros* and *Miniopterus schreibersii* when they emerged from the roosts in dusk.

2. Data analysis

A typical sequence of echolocation call was found to be consisted of an approach-phase pulse and a terminal-phase pulse for feeding buzzes, and echoes, extraneous noise, and fragmentary pulses. The sequence was edited by quantitatively removal of non-search-phase portions by the filter options and remaining fragmentary calls by the Mark-off Points options in the software program Analook (version 4.9j, Titley Electronics). When the editing process was completed, the values of parameters for each of the pulses within the call sequence were saved for later statistic analysis. When edited call sequence had less than 5 pulses, it was excluded from the analysis. When the parameters were from the sequences of more than 5 individuals, they were used to examine the intrerpecific variation.

Ten parameters were examined. They were five frequency components, three time components and two slope components. The five frequency components were maximum frequency (Fmax), minimum frequency (Fmin), frequency at the knee (Fk), frequency of body (Fmean), and characteristic frequency (Fc). The three time components were total duration of the pulse (Dur), time into the pulse when the knee was reached (Tk), and time into the pulse when the characteristic frequency was reached (Tc). The two slope components were slope of the body (Sl) and characteristic section (Sc). The body was the flattest part of the call (lowest frequency change over time) equivalent to the narrow-band component (Caddle and Lumsden 1997).

3. Statistic analysis

Each of the parameters of the echo pulses of each species obtained was analyzed specifically with SAS software 9.13 and expressed as mean ± standard deviations and range. Multivariate discriminated function analysis (DFA) with cross-validation was used to examine the inter- and intra-specific variations. The DFA was performed with SPSS for Windows version 12 and the significant level was kept at $p < 0.05$.

Results

In March 2005 to November 2006, echolocation calls were recorded from 249 individuals of 11 insectivorous bats, *Rhinolophus monoceros*, *Hipposideros terasensis*, *Arielulus torquatus*, *Pipistrellus abramus*, *Scotophilus kuhlii*, *Eptesicus serotinus horikawai*, *Miniopterus schreibersii*, *Murina puta*, *Myotis latirostris*, *Myotis* sp.2, and *Myotis* sp.3, in Taiwan and Kinmen. The echo pulses had two types: constant frequency (CF) type and frequency-modulated (FM) type. The echoes of *R. monoceros* and *H. terasensis* belonged to the CF type, whereas the echoes of *P. abramus*, *A. torquatus*, *S. kuhlii*, *E. serotinus horikawai*, *Mi. schreibersii*, *Mu. puta*, *My. latirostris*, *Myotis* sp.2, and *Myotis* sp.3 were the FM type. They are described as follows:

1. CF type echoes

(1) *Rhinolophus monoceros*

An echo pulse of *R. monoceros* had a two – frequency modulated part and a constant frequency part (Fig. 1). Its characters had Fmin of 96.50 ± 9.83 kHz, Fmax of 112.82 ± 2.09 kHz, Fc of 112.15 ± 3.0 kHz, and Fmean of 111.14 ± 2.57 kHz. The two-frequency modulated part had an initial frequency of around 86 kHz for 2.67 ± 4.56 ms from the start and 2.02 ± 1.60 ms from the constant frequency part to the end of the pulse. The constant frequency was approximately 112 kHz for 14.31 ± 9.41 ms. The total duration of the pulses was 18.94 ± 11.38 ms. Table 1 shows the other parameters of the echo pulses.

(2) *Hipposideros terasensis*

An echo pulse of *H. terasensis* had a one - frequency modulated part and a constant part (Fig. 2). The pulse was similar in shape to that of *R. monoceros* but distinguishable easily between the two species by the characters of the constant part. The main characters were Fmin 61.63 ± 2.30 kHz, Fmax 68.80 ± 1.90 kHz, Fc 68.41 ± 1.91 kHz, and Fmean 67.56 ± 1.53 kHz. The initial frequency of the pulse was around 65 kHz and had a prolonged constant part for 6.26 ± 2.32 ms. From the end of the constant part, the frequency showed a downward trend to 60 kHz to the end of the pulse. The total duration of the pulse was 8.44 ± 2.49 ms. Table 1 shows the other parameters of the echo calls.

2. FM type echoes：

(1) *Pipistrellus abramus*

Echo pulses of *P. abramus* were curvilinear in shape with the durations of 4.52 ± 1.69 ms (Fig. 3). They had Fmin of 47.68 ± 3.01 kHz, Fmax of 58.90 ± 10.12 kHz, Fc of 47.92 ± 3.38 kHz, and Fmean of 50.40 ± 3.91 kHz. The other characters are shown in Table 2.

(2) *Arielulus torquatus*

The echolocation pulses of *A. torquatus* were curvilinear in shape with the duration of 3.10 ± 1.07 ms (Fig. 4). They had Fmin of 39.50 ± 6.00 kHz, Fmax of 64.13 ± 10.43 kHz, Fc of 41.84 ± 5.57 kHz, and Fmean of 45.41 ± 5.26 kHz. The other characters are shown in Table 2.

(3) *Scotophilus kuhlii*

The shape of the echolocation calls of *S. kuhlii* was curvilinear with the duration of 4.19 ± 2.00 ms (Fig. 5). They had Fmin of 41.04 ± 2.27 kHz, Fmax of 65.62 ± 12.42 kHz, Fc of 41.64 ± 2.60 kHz, and Fmean of 46.91 ± 3.96 kHz. The other characters are shown in Table 2.

(4) *Eptesicus serotinus horikawai*

The shape of the echolocation calls of *E. serotinus horikawai* was curvilinear with the duration of 7.97 ± 3.18 ms (Fig. 6). They had Fmin of 29.52 ± 3.83 kHz, Fmax of 46.92 ± 10.91 kHz, Fc of 30.20 ± 4.64 kHz, and Fmean of 34.55 ± 4.86 kHz. The other characters are shown in Table 2.

(5) *Miniopterus schreibersii*

The shape of the echolocation calls of *Mi. schreibersii* was curvilinear with the duration of 3.74 ± 1.50 ms (Fig. 7). They had Fmin of 46.61 ± 5.64 kHz, Fmax of 66.40 ± 18.99 kHz, Fc of 47.01 ± 6.60 kHz, and Fmean of 51.30 ± 8.86 kHz. The other characters are shown in Table 2.

(6) *Murina puta*

The shape of the echolocation calls of *Mu. pupta* was linear with the duration of 1.33 ± 0.52 ms (Fig. 8). They had Fmin of 64.82 ± 10.52 kHz, Fmax of 115.50 ± 12.56 kHz, Fc of 100.06 ± 15.02 kHz, and Fmean of 86.84 ± 10.30 kHz. The other characters are shown in Table 2.

(7) *Myotis latirostris*

The shape of the echolocation calls of *My. latirostris* was curvilinear with the duration of 2.66 ± 0.75 ms (Fig. 9). They had Fmin of 49.78 ± 2.15 kHz, Fmax of 72.72 ± 14.15 kHz, Fc of 49.97 ± 2.37, and Fmean of 54.77 ± 3.19 kHz. The other characters are shown in Table 2.

(8) *Myotis* sp.2

The shape of the echolocation calls of *Myotis* sp.2 was curvilinear with the duration of 1.84 ± 0.68 ms (Fig. 10). They had Fmin of 48.14 ± 2.80 kHz, Fmax of 70.02 ± 13.29 Hz, Fc of 50.67 ± 5.67 kHz, and Fmean of 54.05 ± 4.65 kHz. The other characters are shown in Table 2.

(9) *Myotis* sp.3

The shape of the echolocation calls of *Myotis* sp.3 was linear with the duration of 1.07 ± 0.38 ms (Fig. 11). They had Fmin of 48.38 ± 2.76 kHz, Fmax of 76.98 ± 10.54 kHz, Fc of 61.99 ± 8.75 kHz, and Fmean of 57.55 ± 4.46 kHz. The other characters are shown in Table 2.

3. Species discrimination

(1) CF bats

Except the slope of characteristic section (Sc), the other 9 parameters of the echo pulses were significantly different between *R. monoceros* and *H. terasensis*, based on the Duncan's Multiple Range Test with the generalized linear model (GLM) procedure (Table1). There were a lot of discrepancies in the calls between the two bats, particularly in characteristic frequency (Fc), a character useful in specific distinction.

(2) FM bats

Based on the Duncan's Multiple Range Test with GLM procedure, the 9 species with the FM-type echoes could be separated into 8 groups (Groups A to H) by the pulse duration (Dur); 7 groups (group A to G) on Fmean and Fk, and Fmin and Tk, 6 groups (Group A to F) by Fc, Fmax and Tc; and 5 groups (Group A to E) by Sl and Sc (Table 2).

The best model was the stepwise discrimination analysis with the parameters Fk, Fmin, Dur, Sc, Fmax, Fmean, Tk and Fc, that produced an overall classification rate of 57.3% and the variance of 86.1% among the 9 species by the first two DFA function (Fig. 12). The frequency parameters including Fk, Fc, Fmean, and Fmin occupied the first fourth status in the first discriminating function. Furthermore, the most important parameter of the second function was time into the pulse when the knee was reached (Tk) (Table 3).

According to the first two discriminating factors, there were remarkable intra-species variations in *Mu. puta*, and *Myotis* sp.3 (Figs. 16 and 19). It was worth to point that the echo calls of *Mi. schreibersii* could be separated into two main groups by DF1 (Fig. 15). Based on the DF2, we separated echo calls of *A. torquatus* from those of *E. serotinus horikawai* (Figs.13 and 14). However, it was still difficult to distinguish the calls among *P. abramus*, *S. kuhlii*, *My. latirostris*, and *Myotis* sp.2 based on the DF1 and DF2 factors in our study (Figs. 18, 21, 17 and 20).

Discussion

Species-specific characters

The results of this study showed that *R. monoceros* and *H. terasensis* used CF type echolocation calls, whereas the other 9 species used FM type calls. The former two species could be distinguished easily by the oscillogram of their echolocation calls, but not for the latter 9 species. For these species, *Mu. puta* and *Myotis* sp.3 made a linear echo type call, while the remaining 7 species were the curvilinear echo type. The 10 echo parameters measured were found to be useful in identification of the 11 species studied. For the parameters, duration of pulse (Dur) was the most important in distinguishing the FM bat species. However, it was noted that *Mu. puta* and *Myotis* sp.3 were not distinguishable by the duration of pulse alone but by the frequency and the slope of the pulses. Furthermore, we found that *My. latirostris* and *Myotis* sp.2, were difficult to distinguish; they had a similar echo pattern, and more information is needed for the species identification.

Inter-specific variation

1. Jamming avoidance response

Fenton and Bell (1979) found that an individual of *My. volan* avoids interferences from other individual when feeding in the same area by modulating its own call, the so-called “jamming avoidance response” (Jones *et al.* 1994; Ulanovsky *et al.* 2004). Lee (2007) first reported *H. armiger*, a CF type species, to have the jamming avoidance response in Taiwan. In our study, we recorded two FM-type species, *P. abramus* and *S. kuhlii*, to have the jamming avoidance response in open field near the colony roost when different individuals emerged simultaneously (Figs. 22 and 23). One of co-active individuals would switch and adjust its echo to various calls to avoid the interferences.

2. Dialects

The results of the DFA analysis (Fig.15) showed the presence of two main groups of the FM type bats by DF1. There was a great discrepancy in the frequency among different geographical colonies of *Mi. schreibersii* (Fig. 24). The population from Taiwan emits the minimum frequency (Fmin) around 50 kHz, whereas the population from the Kinmen Island had approximately 40 kHz. Such geographic variation was also found for *V. darlingtoni* by Law *et al.* (2002) who call it "dialects." However, this paper first reports the dialect of bat in Taiwan.

Foraging strategies

Different types of echolocation calls used by insectivorous bats when flying in night may associate with their behavior and foraging strategies. Aerial foraging species always emit lower frequency calls to avoid the atmospheric reduced effect (Schnitzler and Kalko 1998). On the other hand, gleaner foraging species glean insects under the canopy or on the surface of vegetation by low-intensity, brief, and broadband calls to avoid overlap between their pulses and echoes when closing targets (Vaughan *et al.* 1997). Based on the echolocation data obtained and observation made in the wild, we concluded that *M. schreibersii*, *E. serotinus horikawai*, *S. kuhlii*, *A. torquatus*, *My. latirostris,* and *Myotis* sp.2 were the aerial foraging species, whereas *Mu. puta* and *Myotis* sp.3 were possible glean foraging species; they had the maneuverable feeding behavior and flied closer to the ground.

Table 1. Sample sizes, means, standard deviations and range of 10 parameters of the two insectivorous species using CF-type echolocation.calls (Dur, duration of pulse; Fmax, maximum frequency; Fmin, minimum frequency; Fmean, mean frequency; TK, time into the pulse when the knee is reached; FK, frequency at the knee; TC, time into the pulse when the characteristic frequency is reached; Fc, characteristic frequency; SI, initial slope of pulse; Sc, slope of the characteristic section; Ne, sample sizes sufficient for the statistic analysis; N, number of samples; and the grouping method was used for Duncan's Multiple Range Test by Generalized linear model (GLM)

表 1. 常頻式臺灣小蹄鼻蝠與臺灣葉鼻蝠的 10 個回聲定位音頻形値、樣本數、平均値、標準偏差及範圍。音頻形値包含持續時間(毫秒)、最高頻率(千赫)、最低頻率(千赫)、平均頻率(千赫)、起始音頻到轉折點時間(毫秒)、轉折點頻率(千赫)、起始音頻到特徵點時間(毫秒)、特徵點頻率(千赫)、起始斜率，以及特徵點斜率。以多變量分析並藉線性模式的鄧肯檢定作爲分群檢定。N 表示測錄蝙蝠數量，Ne 表示測錄分析蝙蝠回聲定位脈波數

Species (Ne/N)	Dur (ms)	Fmax (kHz)	Fmin (kHz)	Fmean (kHz)	Tk (ms)	Fk (kHz)	Tc (ms)	Fc (kHz)	S1 (kHz/ms)	Sc (kHz/ms)
R. monoceros	18.94	112.82	96.50	111.14	2.62	111.94	16.93	112.15	-440.99	-5.12
(197/19)	±11.39A	±2.09A	±9.83A	±2.57A	±4.56A	±3.04A	±10.53A	±3.04A	±733.33A	±97.29A
	0.30~	99.38~	80~	95.92~	0 ~	92.49~	0.15~	93.02~	-4304.75~	-866.04~
	54.80	115.94	113.48	114.58	41.53	115.11	53.21	115.11	1064.41	628.97
H. terasensis	8.44	68.80	61.63	67.56	0.39	68.26	6.65	68.41	-3.01	0.74

(191/54)	±2.49B	±1.90B	±2.30B	±1.53B	±0.71B	±1.88B	±2.47B	±1.91B	±92.37 B	±15.25A
	0.52~	65.04~	57.55~	62.02~	0~	64.00~	0.39~	61.54~	-702.70~	-8.97~
	15.77	71.75	70.80	71.23	8.05	71.75	14.15	71.11	224.55	206.87

Note: Significant different between A group and B group (Duncan's Multiple Range Test, $p < 0.05$).
註：A 與 B 為各音頻形值由鄧肯檢定分析顯示顯著的兩個分群排序。

Table 2. Sample sizes, types, means, standard deviations and range of 10 echoes parameters of 9 insectivorous bat species using FM-type echolocation calls (abbreviations similar to those denoted in Table 1)
表 2. 臺灣地區 9 種調頻式蝙蝠的 10 個回聲定位音頻形值、樣本數、平均值、標準偏差及範圍。音頻形值包含持續時間(毫秒)、最高頻率(千赫)、最低頻率(千赫)、平均頻率(千赫)、起始音頻到轉折點時間(毫秒)、轉折點頻率(千赫)、起始音頻到特徵點時間(毫秒)、特徵點頻率(千赫)、起始斜率，以及特徵點斜率。以多變量分析並藉線性模式的鄧肯檢定作為分群檢定。CL 表示曲線型，L 表示線型音頻。N 表示測錄蝙蝠數量，Ne 表示測錄分析蝙蝠回聲定位脈波數

Species (Ne/N)	Type	Dur (ms)	Fmax (kHz)	Fmin (kHz)	Fmean (kHz)	Tk (ms)	Fk (kHz)	Tc (ms)	Fc (kHz)	S1 (kHz/ms)	Sc (kHz/ms)
Pipistrellus	CL	4.52	58.90	47.68	50.40	1.34	50.55	4.28	47.92	188.56	41.22
abramus		±1.69B	±10.12E	±3.01C	±3.91D	±0.89D	± 3.89E	± 1.56B	± 3.38D	± 245.32E	± 55.30F
(270/45)		0.58~	42.11~	40.82~	41.44~	0~	42.11~	0.26~	40.82~	-1880.91~	-20.70~
		8.60	86.02	63.75	70.66	3.67	4.01	7.84	9.57	1047.81	408.17
Arielulus	CL	3.10	64.13	39.50	45.41	1.70	44.65	2.78	41.84	83.45	D147.13
torquatus		± 1.07E	± 10.43D	± 6.00F	±5.26F	±0.87C	± 6.11F	± 1.23D	±5.57E	± 1051.50F	±195.41
(135/7)		0.42~	44.82~	25.32~	35.13~	0~	32.13~	0.2~	30.25~	-3926.83~	-516.60~
		5.39	85.11	72.73	76.01	3.35	74.07	5.02	9.6	3056.11	748.90
Scotophilus	CL	4.19	65.62	41.04	46.91	2.05	44.48	3.79	41.64	313.16	87.81
kuhlii		± 2.00C	± 12.42D	± 2.27E	± 3.96E	±1.12B	± 2.86F	±1.96C	± 2.60E	±424.38D	± 87.84E
(467/46)		0.55~	39.22~	35.4~	37.74~	0~	37.3~	0.26~	35.56~	-4225.53~	-157.17~
		13.69	87.43	56.14	58.39	9.21	63.49	13	60.84	2023.61	685.29
Eptesicus	CL	7.97	46.92	29.52	34.55	3.75	33.57	7.38	30.20	165.29	66.90
serotinus		± 3.18A	± 10.91F	± 3.83G	± 4.86G	±2.21A	±5.03G	± 3.13A	± 4.64F	±407.07E	± 68.05E
horikawai											

(168/13)		1.01~	26.8~	23.15~	25.23~	0.20~	25.44~	0.66~	23.15~	-2190.96~	-1.78~
		22.49	76.92	54.24	58.35	14.43	62.75	20.98	59.04	2930.22	364.06
Miniopterus	CL	3.74	66.40	46.61	51.30	1.44	50.30	3.55	47.01	206.72	61.76
schreibersii		± 1.50D	± 18.99D	± 5.64D	± 8.86D	±0.92D	±6.95E	± 1.49C	± 6.60D	± 579.83E	± 75.71F
(335/13)		0.57~	40.10~	38.55~	39.75~	0~	40.10~	0.07~	39.02~	-3323.26~	-791.05~
		8.10	115.11	66.12	83.5	5.36	103.23	7.23	107.38	1688.80	467.52
Murina	L	1.33	115.05	64.82	86.84	0.20	108.24	0.44	100.06	384.47	537.78
puta		± 0.52H	±12.56A	±10.52A	±10.30A	± 0.27G	±15.02A	± 0.29F	±15.02A	± 797.59C	±339.42B
(91/6)		0.27~	88.40~	51.28~	70.48~	0~	65.04~	0.07~	59.48~	-3333.94~	-971.09~
		2.49	146.79	116.79	126.18	1.25	144.14	1.51	128.00	2484.83	1713.43
Myotis	CL	2.66±	72.72	49.78	54.77	1.22	53.32	2.58	49.97	501.27	84.38
latirostris		0.75F	± 14.15C	±2.15B	± 3.19C	±0.66E	± 2.74D	± 0.76D	± 2.37C	± 277.38B	±100.99E
(191/15)		0.59~	50.96~	44.82~	49.20~	0~	49.38~	0.29~	45.58~	-961.23~	5.5~
		4.23	101.91	55.36	64.23	3.06	71.11	4.23	59.7	1895.4	1287.82
Myotis sp.2	CL	1.84	70.02	48.14	54.05	0.80	55.18	1.66	50.67	459.47	233.60
		±0.68G	± 13.29C	± 2.80C	± 4.65C	± 0.52F	±6.99C	± 0.81E	± 5.67C	±428.01C	± 236.01C
(383/23)		0.60~	43.72~	38.19~	41.52~	0~	41.88~	0.14~	38.65~	-1963.86~	22.26~
		3.65	101.91	53.69	66.39	2.27	93.57	3.65	86.02	1338.55	1062.88
Myotis sp.3	L	1.07	76.98	48.38	57.55	0.22	69.44	0.49	61.99	708.18	634.67
		± 0.38H	± 10.54B	± 2.76C	± 4.46B	± 0.23G	± 9.17B	± 0.27F	± 8.75B	± 268.10A	±205.65A
(109/8)		0.54~	57.55~	41.13~	49.61~	0~	54.98~	0.10~	48.34~	-903.86~	-45.58~
		3.08	106.67	56.74	69.46	1.13	100.63	1.74	91.95	1557.11	1313.19

Note: Eight significant difference groups ranked from A to H by Duncan's Multiple Range Test.

註：A 至 H 爲各音頻形值由鄧肯檢定分析顯著的 8 個分群排序。

Table 3. Eigenvectors of the first two DFA functions (DF1 and DF2) for the 10 parameters of the echolocation calls 9 species of bats using the FM-type echo calls

表 3. 調頻式蝙蝠 10 個回聲定位音頻形值於判別分析第一與第二因子所占的特徵向量值

Parameters[1/]	DF1	DF2
Dur	-0.49411	0.838164
Fmax	-0.51956	-1.72225
Fmin	-0.19953	-1.47523
Fmean	0.837549	1.935487
Tk	-0.32372	0.75349
Fk	-0.36782	0.647562
Tc	0.882245	-0.72182
Fc	1.092281	-0.28172
Sl	0.133029	0.000699
Sc	0.356043	0.228875
Proportion	67.93904	86.08585

[1/] Abbreviation of the pulse parameters similar to those denoted in Table 1.

Fig. 1. The oscillogram of *R. monoceros* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 100 kHz and 115 kHz).

圖 1. 臺灣小蹄鼻蝠的回聲定位音頻波形圖。X 軸為時間軸(每格為 20 毫秒)，Y 軸為頻率(千赫)，特徵音頻範圍自 100 到 115 千赫。

Fig. 2. The oscillogram of *H. terasensis* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 65 kHz and 70 kHz).

圖 2. 臺灣葉鼻蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 65 到 70 千赫。

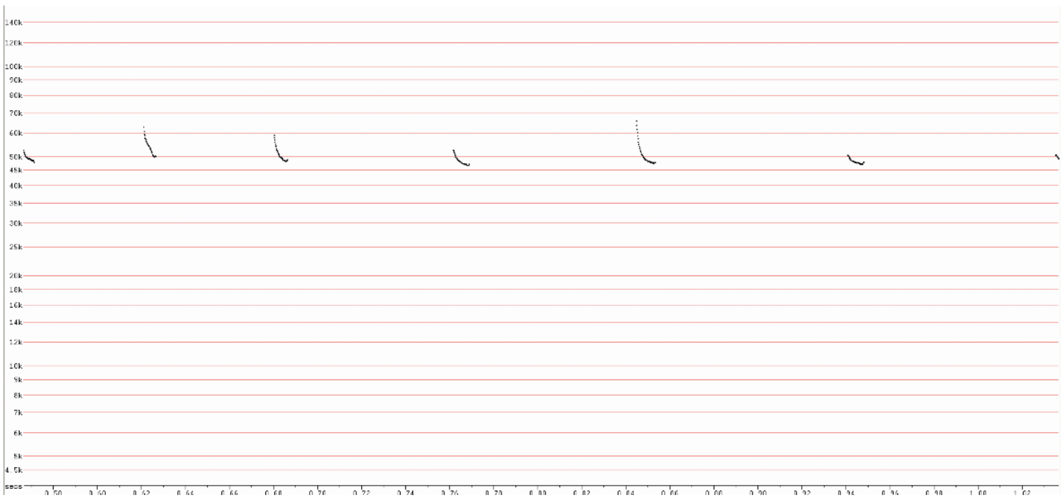

Fig. 3. The oscillogram of *P. abramus* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 40 kHz and 100 kHz).

圖 3. 東亞家蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 40 到 100 千赫。

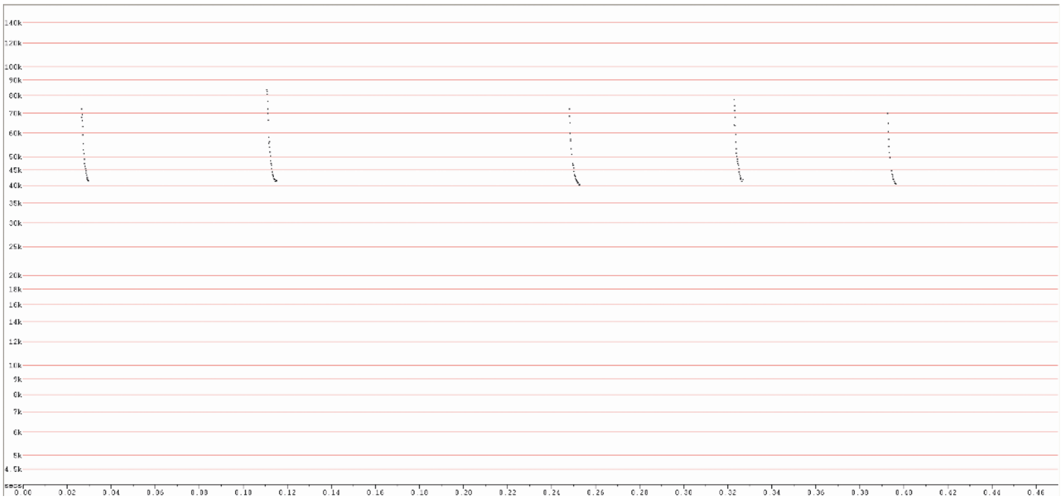

Fig. 4. The oscillogram of *A. torquatus* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 25 kHz and 70 kHz).

圖 4. 黃頭蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 25 到 70 千赫。

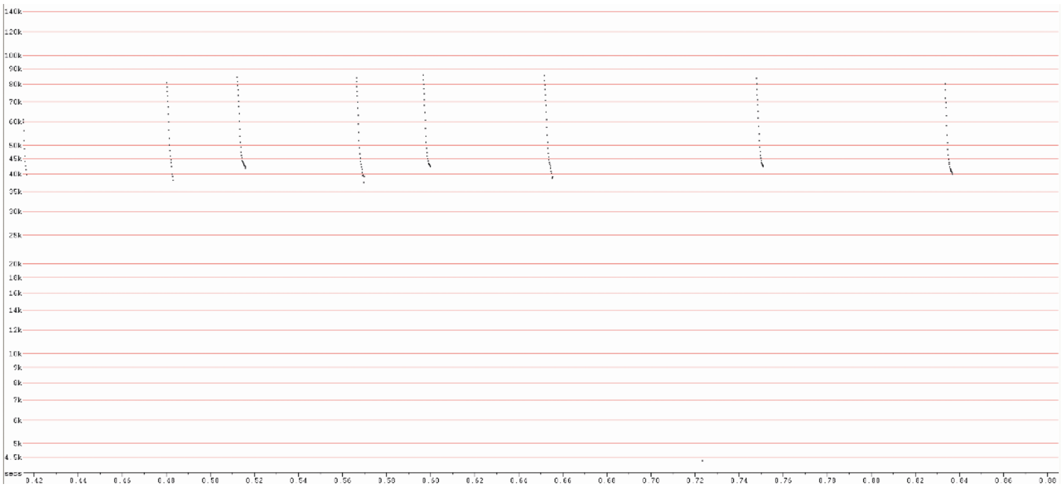

Fig. 5. The oscillogram of *S. kuhlii* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 35 kHz and 85 kHz).

圖 5. 高頭蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 35 到 85 千赫。

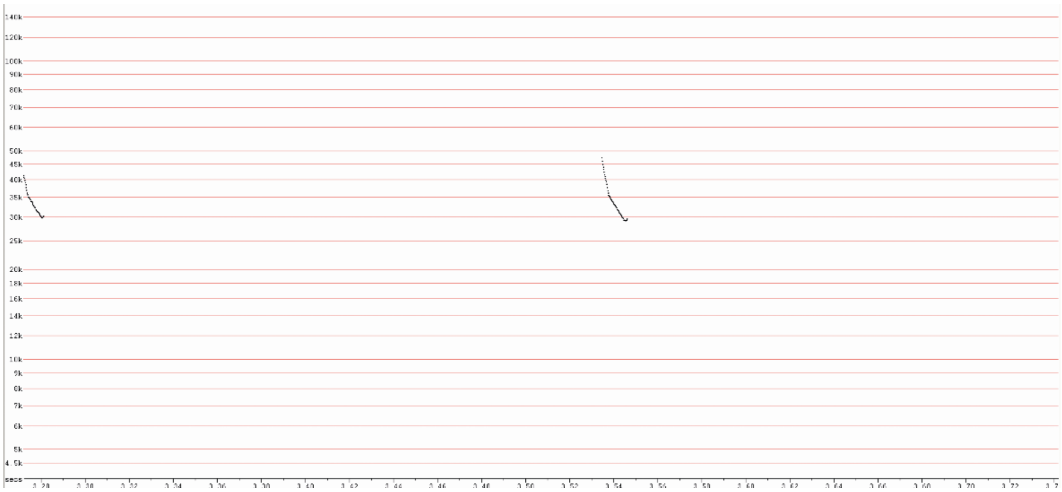

Fig. 6. The oscillogram of *E. serotinus horikawai* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between20 kHz and 60 kHz).

圖 6. 堀川氏棕蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 20 到 60 千赫。

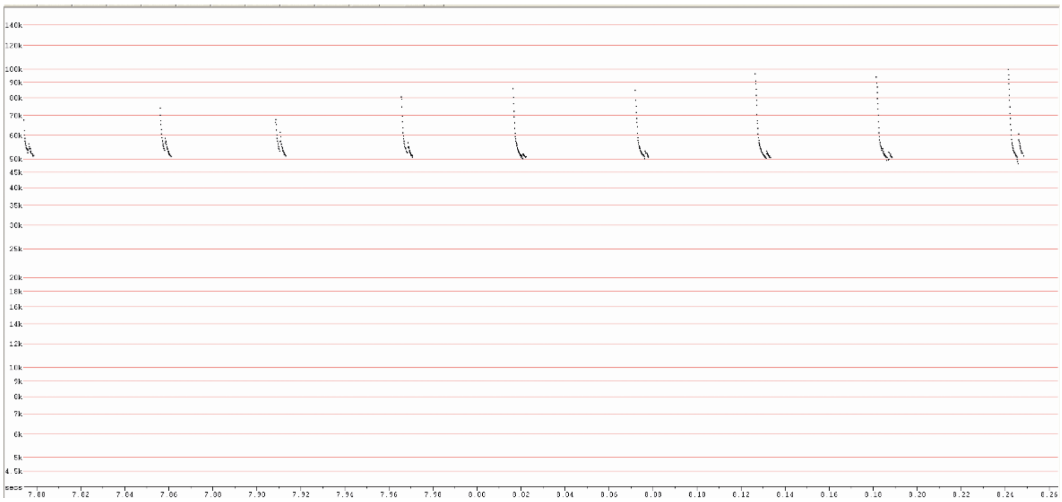

Fig. 7. The oscillogram of *Mi. schreibersii* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 50 kHz and 110 kHz).

圖 7. 摺翅蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 50 到 110 千赫。

Fig. 8. The oscillogram of *Mu. puta* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 40 kHz and 170 kHz).

圖 8. 臺灣管鼻蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 40 到 170 千赫。

Fig. 9. The oscillogram of *My. latirostris* (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 40 kHz and 100 kHz).

圖 9. 寬吻鼠耳蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 40 到 100 千赫。

Fig. 10. The oscillogram of *Myotis* sp.2 (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 40 kHz and 80 kHz).

圖 10. 長趾鼠耳蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，範圍自 40 到 80 千赫。

Fig. 11. The oscillogram of *Myotis* sp.3 (X-axis, time scale (20 ms each period); Y-axis, log frequency scale, and Fc between 35 kHz and 120 kHz).

圖 11. 長尾鼠耳蝠的回聲定位音頻波形圖。X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)，特徵音頻範圍自 35 到 120 千赫。

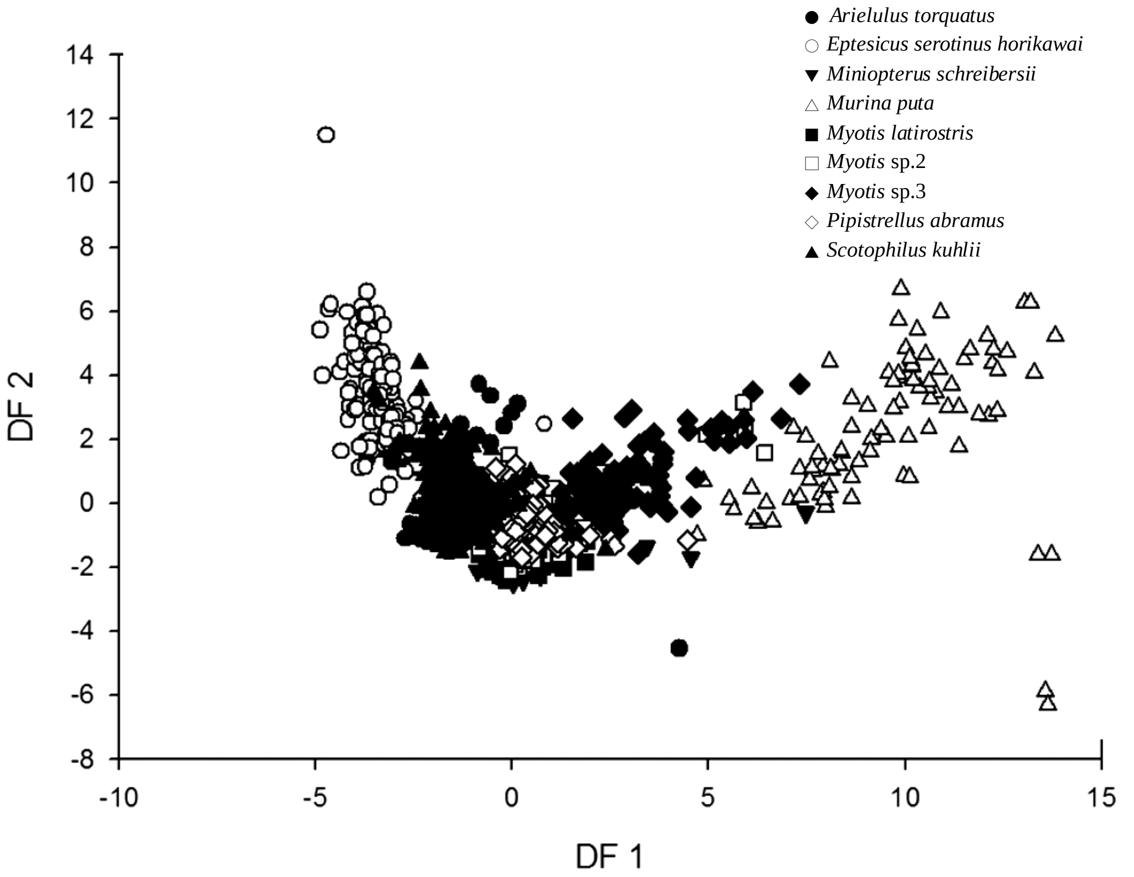

Fig. 12. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of the 9 species of FM-type bats.

圖 12. 調頻式蝙蝠音頻測量值於典型區別分析的落點圖。(DF1及DF2之各音頻形值所占的特徵向量值詳見表3)。

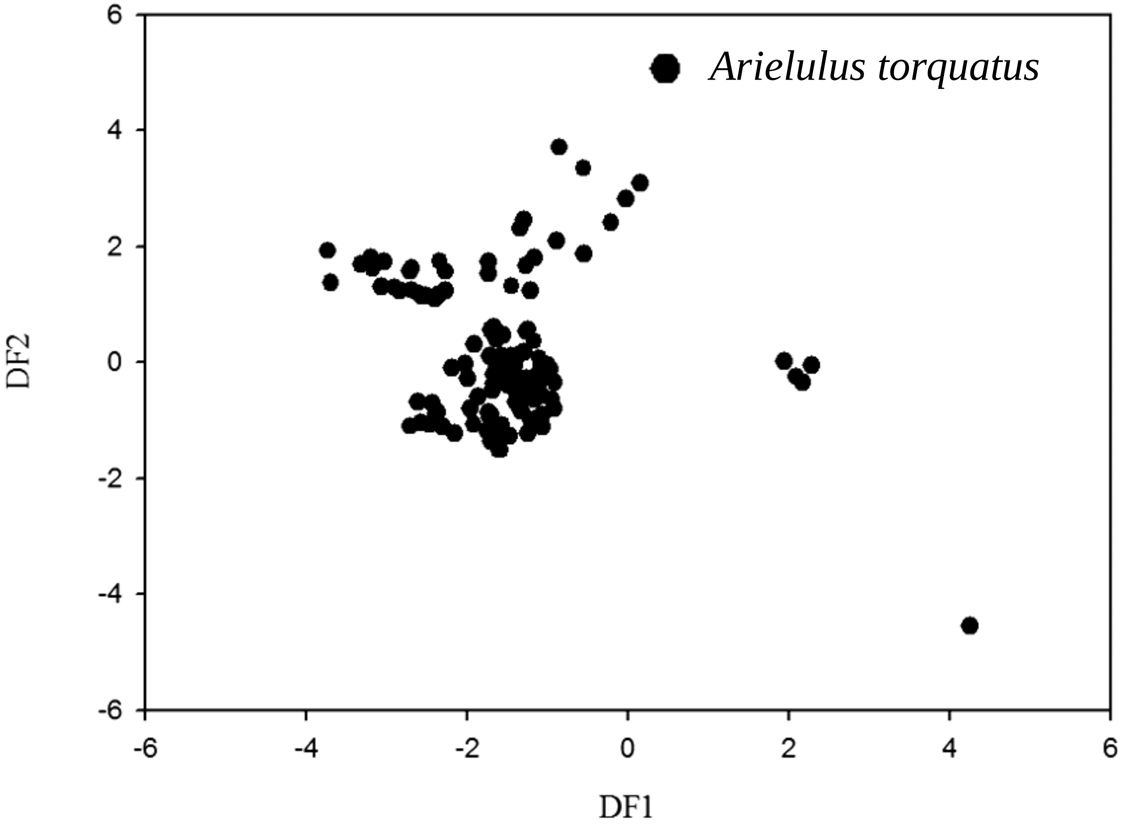

Fig. 13. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *A. torquatu*s.

圖 13. 以典型區別分析顯示黃頸蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占的特徵向量值詳見表 3)。

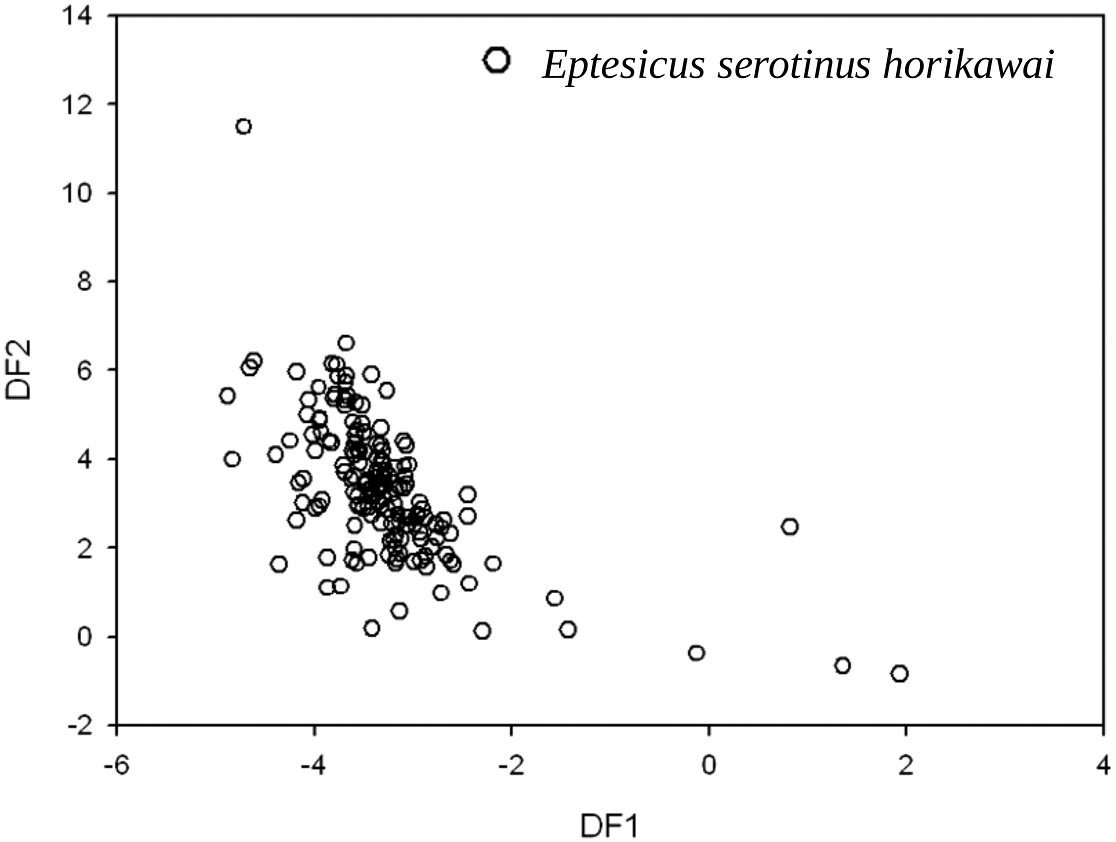

Fig. 14. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *E. serotinus horikawai*.

圖 14. 以典型區別分析顯示堀川氏棕蝠回聲定位音頻的落點圖。(DF1及DF2之各音頻形值所占特徵向量詳見表3)。

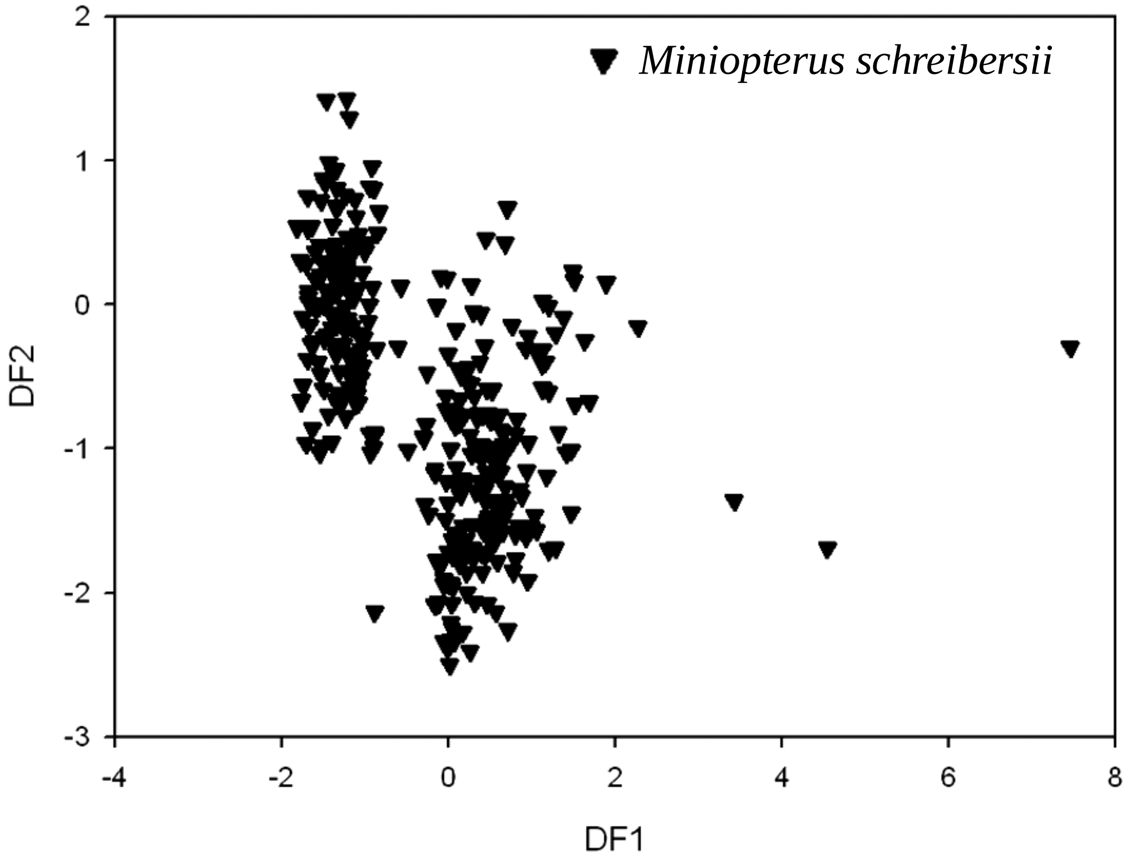

Fig. 15. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *Mi. schreibersii*.

圖 15. 以典型區別分析顯示摺翅蝠回聲定位音頻的落點圖。(DF1及DF2之各音頻形值所占特徵向量值詳見表3)。

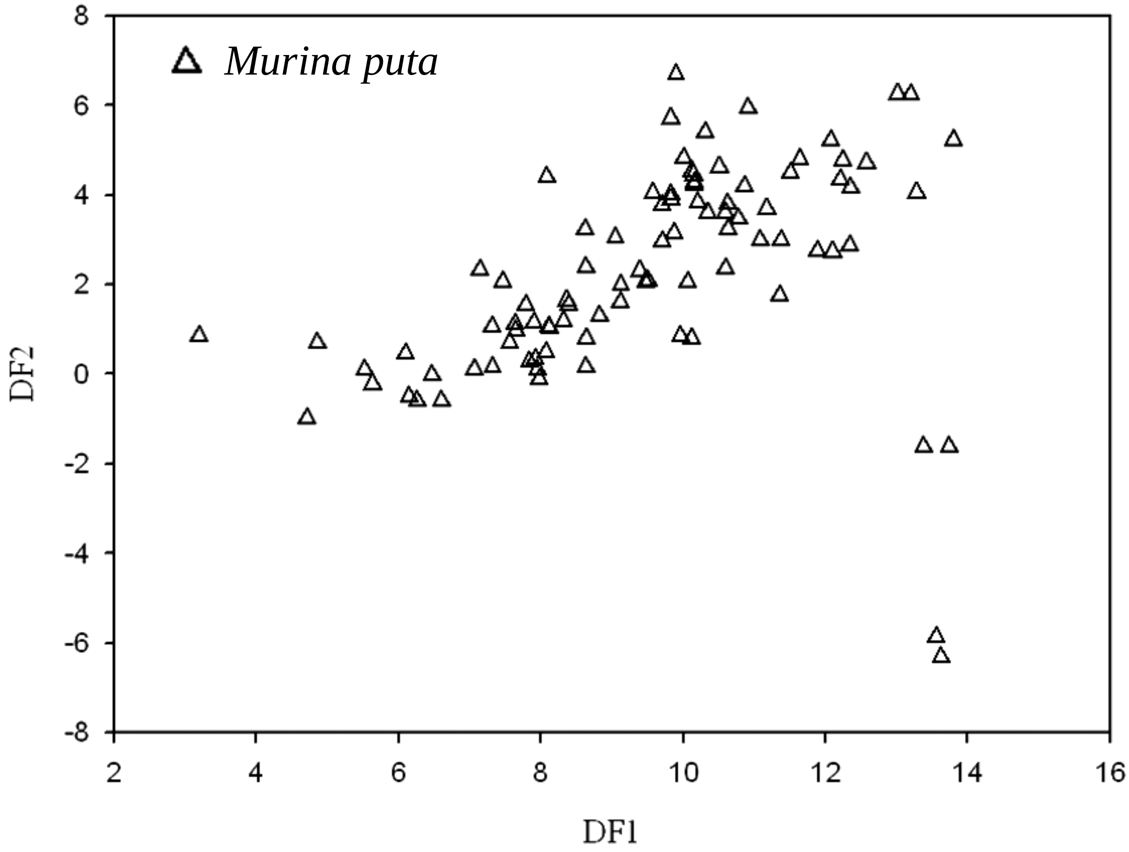

Fig. 16. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls *Mu. puta*.

圖 16. 以典型區別分析顯示臺灣管鼻蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量值詳見表 3)。

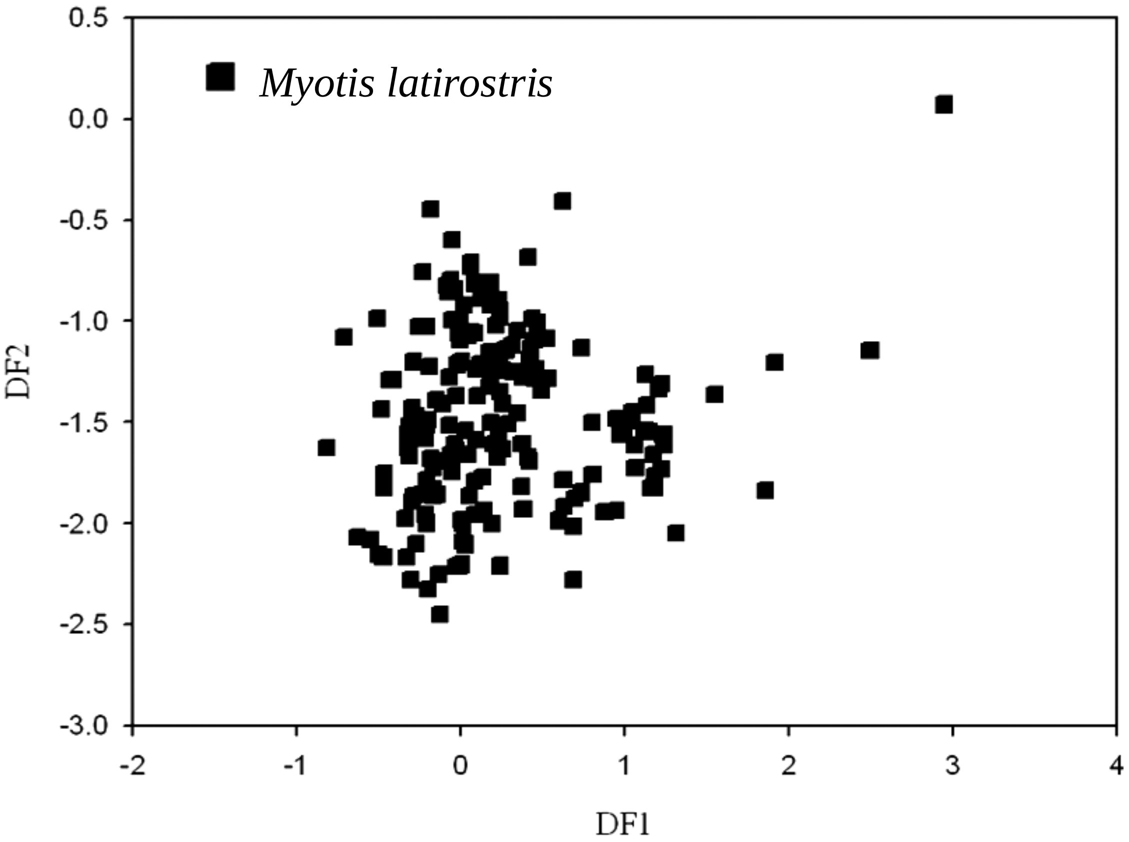

Fig. 17. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *My. latirostris*.

圖 17. 以典型區別分析顯示寬吻鼠耳蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量詳見表 3)。

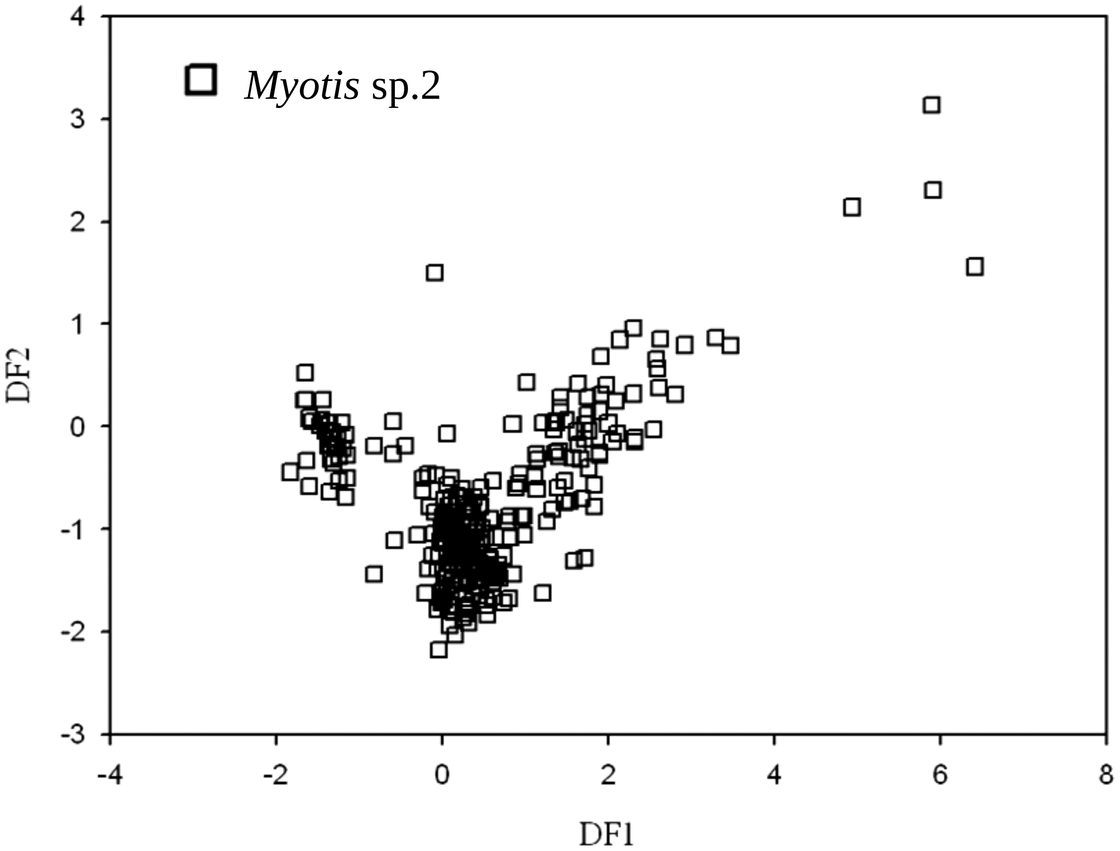

Fig. 18. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls *Myotis* sp.2.

圖 18. 以典型區別分析顯示長趾鼠耳蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量詳見表 3)。

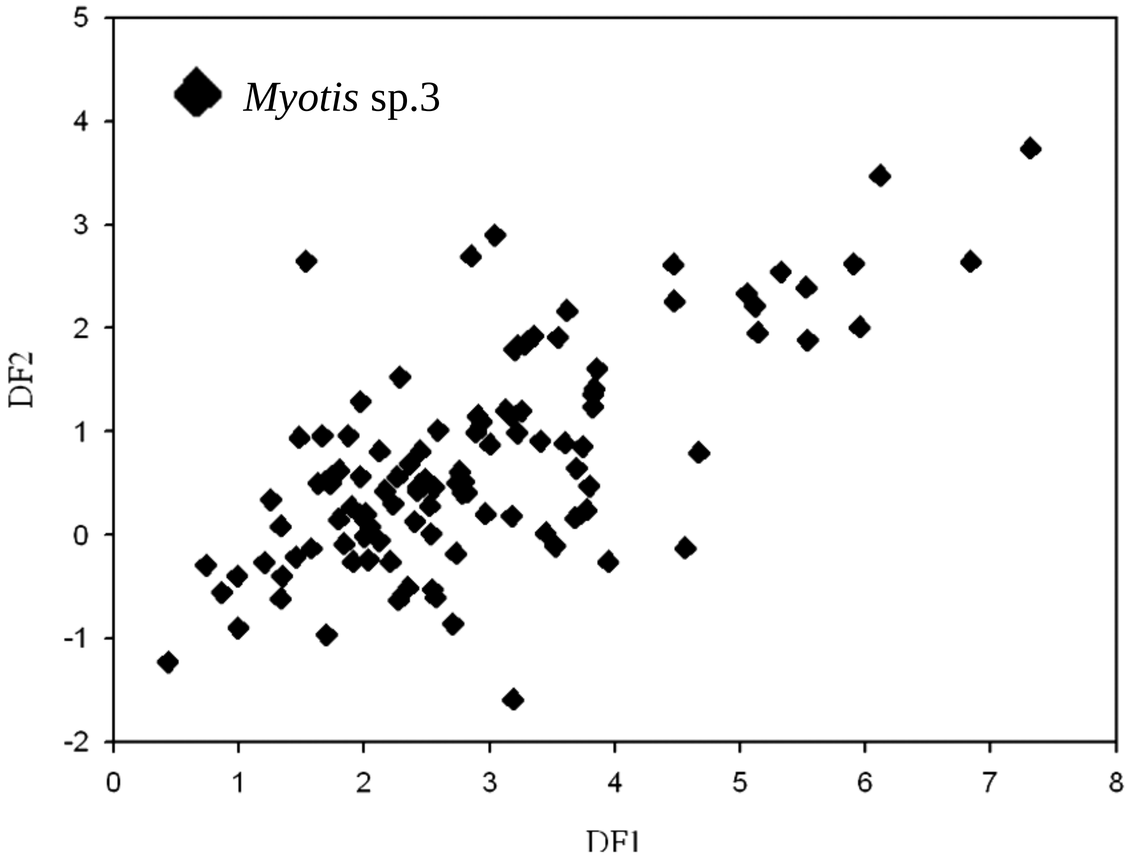

Fig. 19. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *Myotis* sp.3.

圖 19. 以典型區別分析顯示長尾鼠耳蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量詳見表 3)。

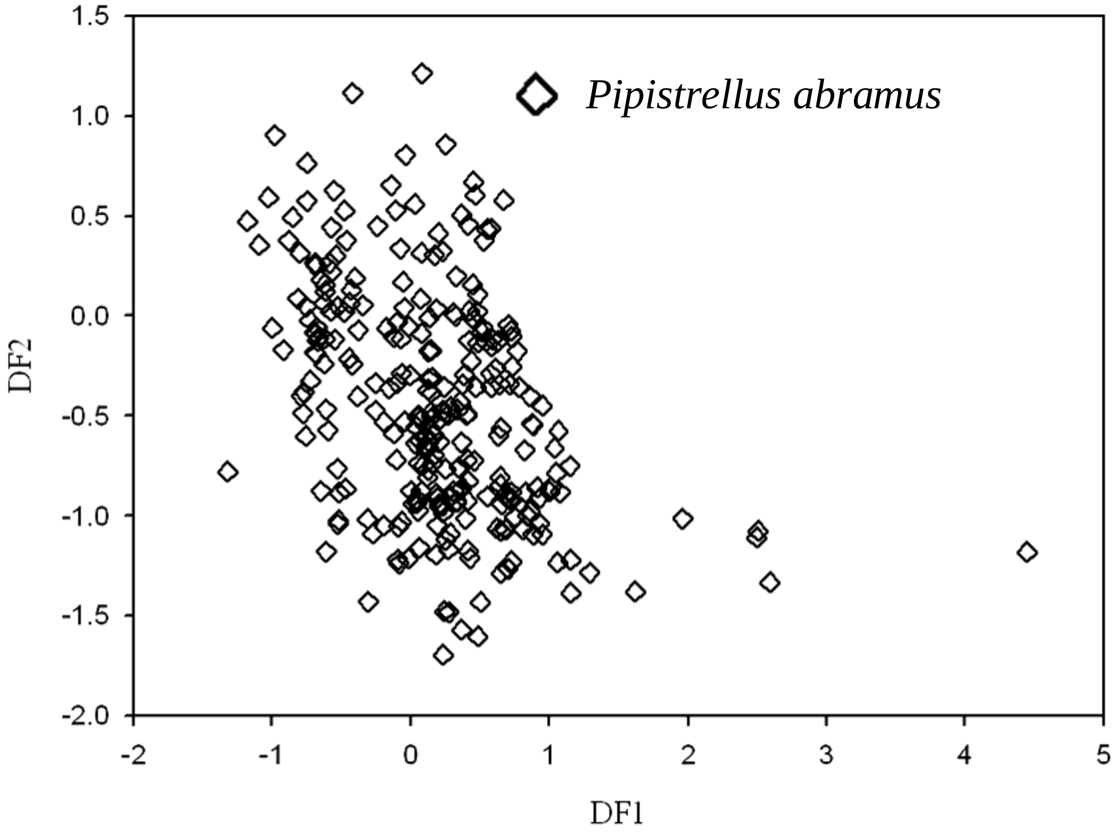

Fig. 20. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *P. abramus*.

圖 20. 以典型區別分析顯示東亞家蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量詳見表 3)。

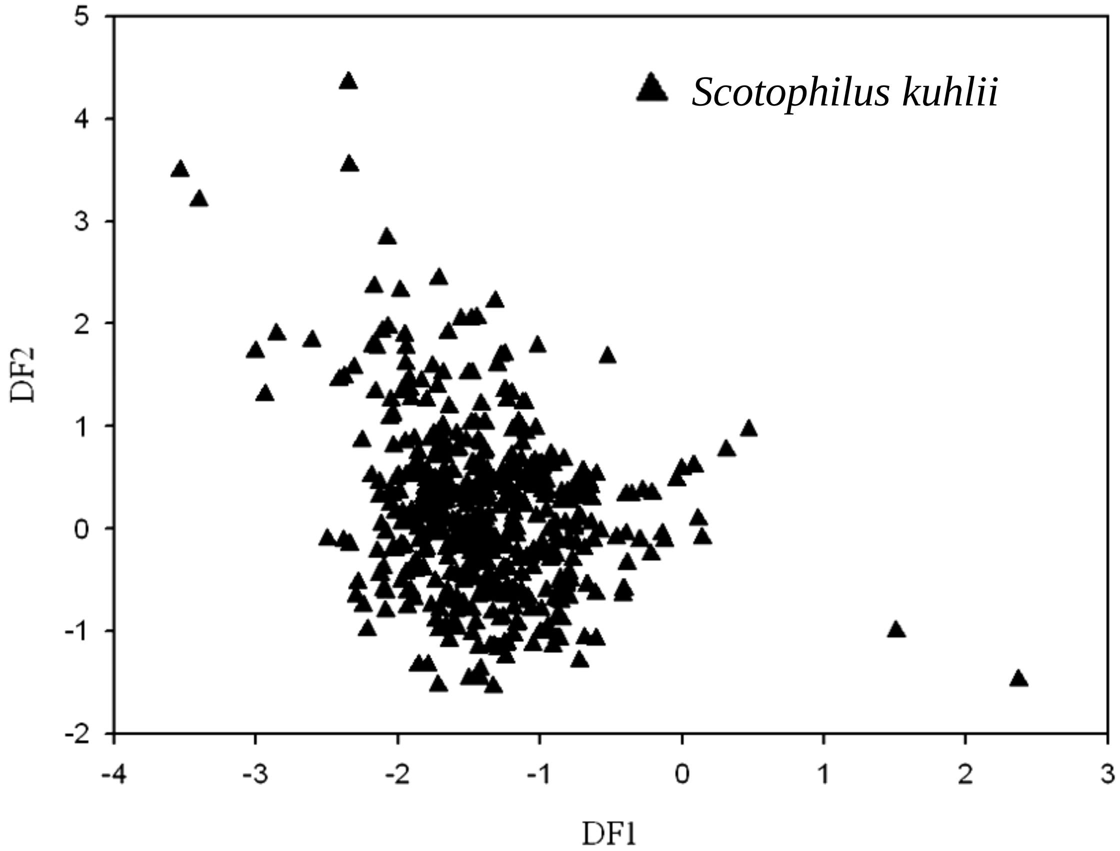

Fig. 21. Relationhips of the eigenvectors between the first two DFA functions (DF1 and DF2 in Table 3) for the 10 parameters of the echolocation calls of *S. kuhlii*.

圖 21. 以典型區別分析顯示高頭蝠回聲定位音頻的落點圖。(DF1 及 DF2 之各音頻形值所占特徵向量詳見表 3)。

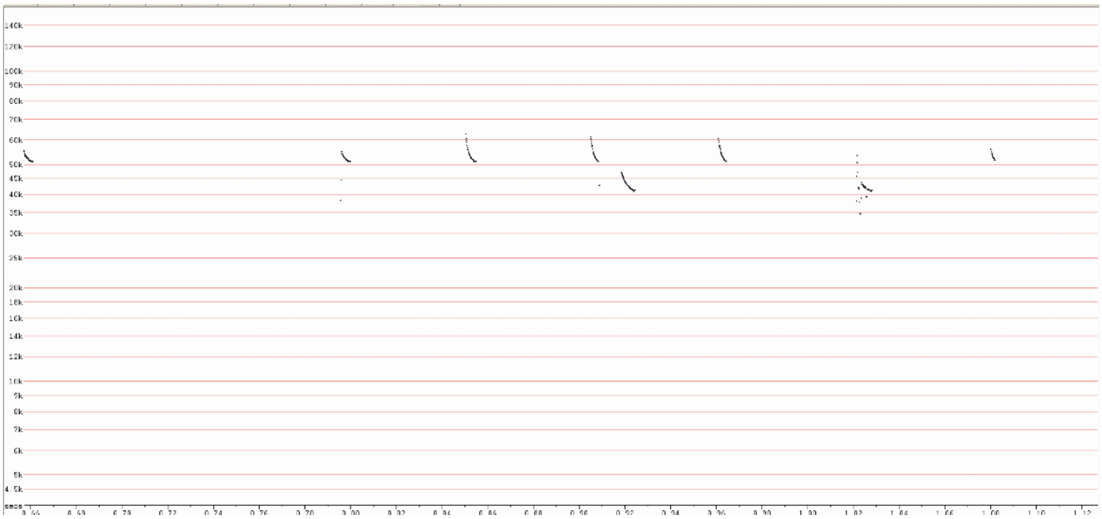

Fig. 22. The oscillogram showing jamming avoidance (overlapping plus) of *P. abramus* (X-axis, time scale (10 ms each period); Y-axis, log frequency scale).
圖 22. 東亞家蝠的避免干擾音頻調整現象，圖中爲共域兩隻個體的音頻波形圖；X 軸爲時間軸(每格爲 10 毫秒)，Y 軸爲頻率(千赫)。

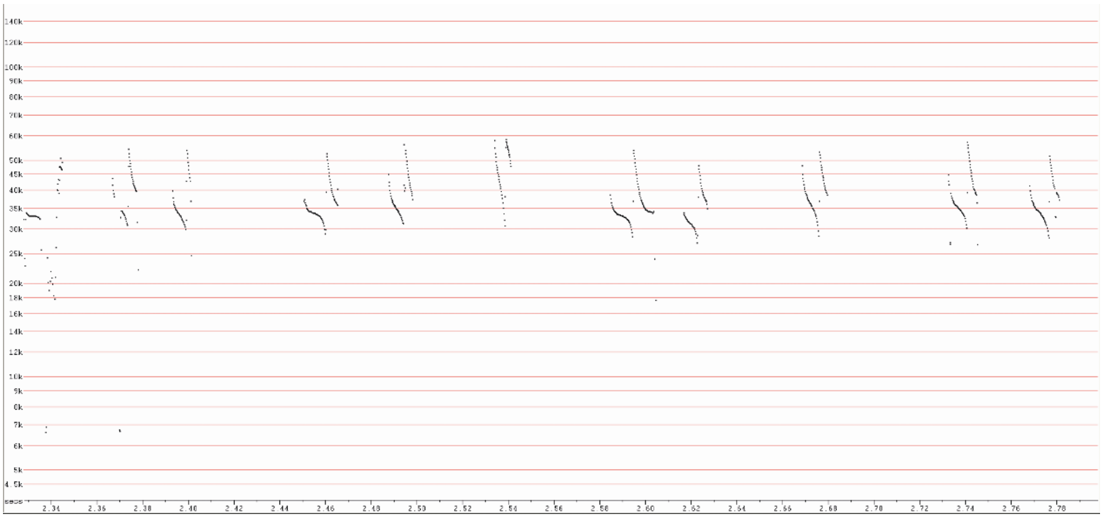

Fig. 23. The oscillogram showing jamming avoidance (overlapping plus) of *S. kuhlii* (X-axis, time scale (10 ms each period); Y-axis, log frequency scale).
圖 23. 高頭蝠的避免干擾音頻調整現象，圖中爲多隻高頭蝠共域飛行的音頻波形圖；X 軸爲時間軸(每格爲 10 毫秒)，Y 軸爲頻率(千赫)。

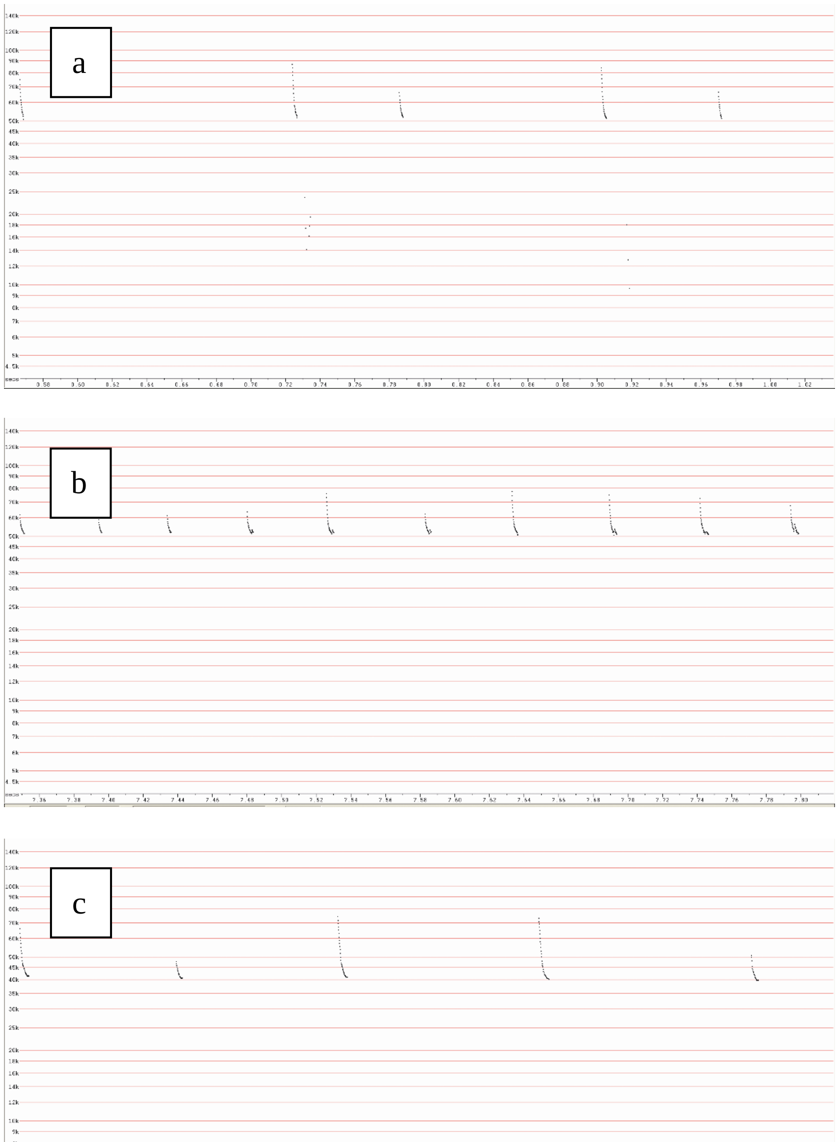

Fig. 24. The oscillograms of *Mi. schreibersii* showing different dialetics from 3 colonies: (a) Rueifang, New Taipei City, northern Taiwan (50.79~115.11 kHz); (b) Qishan, Kaohsiung, southern Taiwan, ranging (47.2~100 kHz); and (c) Lieyu, Kinmen Island (38.55~77.67 kHz) (X-axis, time scale (20 ms each period); Y-axis, log frequency scale).

圖 24. 不同地區摺翅蝠的回聲定位音頻頻譜圖，(a)瑞芳區，新北市，北臺灣，音頻範圍 50.79~115.11 千赫(b)旗山區，高雄，南臺灣，音頻範圍 47.2~100 千赫(c)列嶼，金門地區，音頻範圍 38.55~77.67 千赫。此種差異現象稱爲「方言」；X 軸爲時間軸(每格爲 20 毫秒)，Y 軸爲頻率(千赫)。

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