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同一山洞中五种蝙蝠的回声定位比较及生态位的分化

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摘要: 对同一山洞中 5 种蝙蝠的回声定位叫声和外部形态作了比较分析, 根据蝙蝠回声定位叫声、形态特征与捕食策略之间的联系, 并结合部分的野外观察研究, 推断其捕食生境及捕食策略, 并对洞中 5 种共栖蝙蝠的生态位分化进行了分析, 研究结果如下: (1) 南蝠(*Ia io*)在地面或树冠中间的开阔空间捕食个体较大的昆虫; (2) 大鼠耳蝠 (*Myotis myotis*) 主要以掠食性方式(gleaning)捕食森林或草地地表面的昆虫; (3) 黄大蹄蝠 (*Hipposideros pratti*)主要在树冠周围或树冠上方进行捕蝇器式(Fly-catching) (即倒挂于一固定枝条或地点, 探索周围飞行或接近的昆虫, 探索到后捕捉回原倒挂地点再进食) 或飞行捕食, 它主要捕食个体较大的甲虫; (4) 角菊头蝠(*Rhinolophus cornutus*)主要在较密集树木中(枝叶间)、农田及树木周围捕食体型较小的翼拍动昆虫; (5) 三叶蹄蝠 (*Aselliscus wheeleri*)是在树木、灌丛或在其周围空间内捕食较小的翼拍动昆虫, 但其食性可能与菊头蝠不同。根据以上研究结果, 认为这 5 种蝙蝠的取食生态位存在着明显的分化。

关键词: 蝙蝠; 回声定位叫声; 比较; 捕食策略; 生态位

The Echolocation Comparison and the Differentiation of Ecology Niche of Five Species Bats Live in One Cave

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Abstract: We captured five species of bats in one cave in Jingnan town of Xingyi district in Guizhou Province, China, these bats were great evening bat (*Ia io*), Large mouse-eared bat (*Myotis myotis*), Pratt's leaf-nosed bat (*Hipposideros pratti*), Little Japanese horseshoe bat (*Rhinolophus cornutus*) and Stoliczka's trident bat (*Aselliscus wheeleri*). We used the mist-net to capture these bats at the cave at 6:00 to 7:30 O'clock in the evening, then we carried these bats to the room where we used as a simple laboratory (6 m×5 m×3 m).

We started recording these bats' echolocation calls when they accustomed to the situation of the laboratory. We also measured the weight, body length, forearm length, wing length and wing width of these bats at the same time. We received the bats' echolocation calls by the Ultra Sound Detector (U30, Ultra Sound Advice, UK), the signals were inputted to Ultra Sound Processor, in which the frequency of these sounds were transformed to 1/10 of the original signals frequency. Then we recorded these signals by the digital recorder (Sony, MD-1, Frequency range: 30～20 000 Hz). We analyzed the recording signals with

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the software (Cool Edit 2000, Syntrillium Ltd., USA) in the personal computer, the sample rate is 44 100Hz for these sound signals, the sonogram and the frequency-power graph were analyzed by this software. The bats' call duration, the interval of the bats' call, the duty-cycle (the call's duration takes up the total period of the call and its interval) and some other parameters were measured based on the analysis.

We compared the echolocation characteristics of the five bats used the parameters that were put forward as before, the main results were referred in next part of the text. For the morphology compare, we measured the ratio of wing length to wing width (as a reference parameter for aspect ration, the square of wing span/wing area) and the ratio of body mass to forearm length (as a reference parameter for wing loading, the body mass/wing area).

According to the echolocation and morphology comparison of the five bats, we can attain several conclusions as follow: (1) The great evening bat has lower FMF, multi-harmonics echolocation, large body, higher ratio of wing length to wing width and higher wing loading. Based on the research by other scientists, bats with narrow wing and high wing loading most were fast flyer, and their flying agility was not well. Neuweiler thought that the bats with multi-harmonics FM calls were adapted to forage in the open area between canopy or on the surface of foliage or ground. And the lower FMF was fitted to forage larger insects or prey at long distance. According to the analysis and our field observe, the great evening bat was most probably foraged larger prey on the surface by gleaning foraging or foraged larger insects in the open area between tree canopy.

(2) The echolocation of large mouse-eared bat was multi-harmonics FM calls, but its FMF was higher than former, its call's duration was shorter than former. In addition, the mouse-eared bat had smaller body mass and length, relative broad wing shape and low wing loading. So it can be deduced that the mouse-eared bat adapted to fly with high agility, forage prey in near distance in more complex environment. The foraging strategy of mouse-eared bat was probably the second kind which suggested by Neuweiler, so the bat may has the gleaning foraging strategy on the surface of foliage or ground. The research results conducted by Arlettaz in field about the mouse-eared bat supported that the mouse-eared bat mainly preyed insects on the surface of forest ground or mellow ground. The results were matched with our analysis in this work.

(3) The Pratt's leaf-nosed bat had short CF-FM, multi-harmonics echolocation; its FMF was relative high to its big body mass. And it had narrow wing shape, high wing loading, so it might fly in high speed, lower flying agility. CF signal was apt to detect wing-beating insect, and the multi-harmonics could afford the fine structure of prey and the detail information of the habitat. So this bat might forage large prey in complex environment. But according to our field observe and research, the bat mainly preyed near the browns of trees or above the tree browns of the evergreen and deciduous broadleaf forest, it mainly foraged coleopteran insects by the survey of their diet. When we captured the bat flying back to cave in night, we found that there were residual bodies of insects in the mouth of the bat, so it may accustomed to prey at a fix site. For the all analyses above, we can deduce that this bat mainly forage prey as fly-catching (the bat hang on an given site or branch, scouting flying or approaching insects around, then it catch the insects back to the perch site to eat them) or aerial hawking.

(4) The little Japanese horseshoe bat's echolocation was typical long FM-CF-FM form, and only had one harmonics, its FMF was high and its call duration was longest in all the five bats. The long CF part of the echolocation was fitted to detect wing-beating prey by use of the Doppler's shift in complex environment, the high frequency of the echolocation was suited to detect prey in near distance. In addition, the horseshoe bat had small body mass, relative broad wing shape and lowest wing loading in all the five bats.

So it had good flying agility and suited to forage in narrow habitat. For all the above analyses, the bat may forage little wing-beating insects in dense foliages, farmland and trees around.

(5) The Stoliczka's trident bat's echolocation was short FM-CF-FM form, its FMF was highest in five bats, and it only has one harmonic. The high frequency CF signal was suited to detect wing-beating insects in complex environment in near distance, but the single harmonic was not good for the complex habitat, the mechanism about this problem was needed to discuss further. This bat had small body mass, broad wing shape and low wing loading, so it might fly at a low speed and had good flying agility. The observe in the fieldwork also supported that the bat mainly foraged lepidopteran and coleopteran insects under the crowns of broadleaf forest and in the brushwood.

Integrated the above analyses, we concluded that: the echolocation behaviors of the five species of bats were differentiated each other obviously, there were some differences in their foraging habitat, foraging strategy and theirs food, so the ecological niche of the five bats had obvious differentiation. In addition, the prey size of these five bats also had apparent differences.

Key words: bat; echolocation calls; comparison; foraging strategy; ecology niche

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蝙蝠属于哺乳纲翼手目(Chiroptera),因其是哺乳动物中唯一能够飞行的种类,而且小蝙蝠亚目(Microchiroptera)的蝙蝠主要依靠回声定位来寻找和捕食猎物[1],因此一直吸引了众多研究者的兴趣。关于蝙蝠飞行方面的一些研究工作已经揭示了翼形、捕食行为和飞行方式之间的联系[2,3];另外,许多关于回声定位的研究也显示了蝙蝠的不同回声定位类型和其生态特征之间的联系,尤其在其食物组成和捕食策略方面[4,5]。而关于蝙蝠的飞行、回声定位以及捕食策略之间联系的生态学研究还比较少[6]。

研究了贵州省生活于同一山洞的 5 种蝙蝠,这些种类在同一山洞中栖息、捕食,其中必然存在一定的生态位分化,使其在各自的适宜的生境中捕食而不致发生激烈的竞争。这 5 种蝙蝠都是以超声波回声定位进行捕食的,本文将结合 5 种蝙蝠飞行状态下超声波回声定位的分析及其与飞行有关的外部特征的比较,并结合对几种蝙蝠野外捕食行为的观察研究,推断这 5 种蝙蝠的捕食策略,探讨这些种类生态位的分化。

1 材料与方法

5 种蝙蝠捕自贵州省兴义市敬南乡山脚村飞龙洞(工作时间为 1999 年 7～8 月份及 2000 年 6 月份)。飞龙洞是典型的岩溶洞,有两个大洞口,洞顶离地面较高,最高处约 30m,洞长约 1000m,还有一个长约 500 多米的支洞。洞口外主要为一些陡峭的山丘,山上长有次生林,山脚下有地势较平坦的农田,周围的生态环境质量较好。主要的生境类型有针叶林、常绿落叶阔叶混交林、灌丛、草地和农田。

在飞龙洞,捕获到 5 种蝙蝠,即:南蝠 4 头(2 雄 2 雌)、大鼠耳蝠 10 头(8 雄 2 雌)、黄大蹄蝠 5 头(3 雄 2 雌)、角菊头蝠 3 头(2 雄 1 雌)、三叶蹄蝠 2 头(2 雄)。其中南蝠属于蝙蝠科南蝠属;大鼠耳蝠属于蝙蝠科鼠耳蝠属;黄大蹄蝠属于蹄蝠科蹄蝠属;三叶蹄蝠属于蹄蝠科三叶蹄蝠属;角菊头蝠属于菊头蝠科菊头蝠属。捕捉 5 种蝙蝠主要采取在支洞口及人为干扰较少的大洞口处挂上粘网,18:00～19:30 左右蝙蝠飞向洞外捕食时就被粘网挂住,此时研究人员立即将蝙蝠从粘网上取下。捕捉完成后将粘网取下,以免影响其他蝙蝠个体的飞行。蝙蝠捕捉后被带回到 6 m×5 m×3 m 的房间进行录音,随后测量蝙蝠的体重、体长、前臂长、翼长及翼宽等各种参数。录音时蝙蝠飞向工作人员,距离约 1 m 时进行录音。

实验中用超声波监听仪(U30, Ultra Sound Advice, UK)接收超声波,随后将超声波信号输入到超声波处理仪(PUSP,Ultra Sound Advice ,UK)中,将超声波频率转换为原频率的 1/10 后录制到数字式录音机(Sony, MD-1, 频率范围 30～20 000Hz)上。录入的声波信号用美国 Syntrillium 软件公司的 Cool Edit 2000 软件进行分析;采样频率为 44 100Hz,分析内容包括声波的声谱图和能量谱图。声谱图(哈明窗分析)分析精度为 256 波段,分析衰减为 60dB(对数能量值);能量谱图分析的 FFT 点数为 1024。另外,还对回声定位叫声的持续时间和间隔时间进行了测量,并计算出能率环(叫声持续时间占叫声持续时间及间隔时间

之和的百分比)。分析的数据均以平均值±标准差(X±SD)表示。

2　结果与分析

2.1　回声定位叫声的声谱分析

录音分析的结果表明,这 5 种蝙蝠回声定位叫声在种内雌雄个体之间的差异很小,从其声谱图上看基本上没有差异。因此在以下的超声波分析中未考虑性别差异。从图 1 中可以看出,在飞行状态下,南蝠回声定位叫声的声谱图为短 FM 型,一次完整的叫声脉冲包括 3～4 个谐波,其中第 4 个谐波仅出现于 7.6%的叫声中,第 3 个谐波虽出现于所有叫声中,但其能量较弱,第一及第二谐波叫声能量较强;大鼠耳蝠回声定位叫声的声谱图为比南蝠更短的短 FM 型,一次完整的叫声脉冲包括 2 个谐波,其中第一个谐波较强,第二个谐波较弱;黄大蹄蝠回声定位叫声的声谱图为 CF-FM 型,一次完整的叫声脉冲包括 3 个谐波,第二谐波最强,第一和第三谐波较弱,且在样本中出现率分别为 97.2%和 63.9%;角菊头蝠回声定位叫声的声谱图为 FM-CF-FM 型,一次完整的叫声脉冲包括 2 个谐波,其中第二谐波较强,第一谐波出现频率很少;三叶蹄蝠回声定位叫声的声谱图为长 FM-CF-FM 型,包括一个谐波,其中前调部分出现的比率为 54.5%。5 种蝙蝠的叫声频率、持续时间、间隔时间、频率范围、最大能量处频率及能率环见表 1。

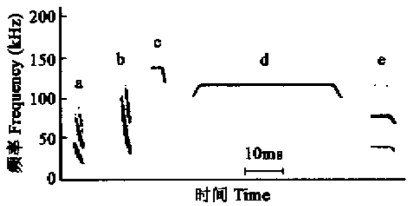

图 1　5 种蝙蝠回声定位叫声声谱图比较

Fig. 1　The comparison of ultrasound sonagrams of five bats

Notice: a 为南蝠 *Ia io*, b 为大鼠耳蝠 *Myotis myotis*, c 为三叶蹄蝠 *Aselliscus wheeleri*, d 为角菊头蝠 *Rhinolophus cornutus*, e 为黄大蹄蝠 *Hipposideros pratti*

表 1　5 种蝙蝠回声定位叫声的参数比较

Table 1　The comparison of characteristics of ultrasound of five species of bats

蝙蝠种类 Species of bats	南蝠(4)* *Ia io*	大鼠耳蝠(10) *Myotis myotis*	黄大蹄蝠(5) *Hipposiderospratti*	三叶蹄蝠(2) *Aselliscus wheeleri*	角菊头蝠(3) *Rhinolophus cornutus*
叫声次数 (1/s) The number of calls per second	25.3±11.0	16.6±6.1	22.7±6.2	23.9±10.5	14.3±3.4
叫声持续时间 (ms) Call duration	3.7±2.2	2.3±1.1	6.1±1.0	7.8±6.6	32.9±6.6
叫声间隔时间 (ms) Interval time	42.2±34.8	55.9±18.8	26.9±11.4	28.2±24.9	38.0±7.9
最大能量频率 FMF (kHz)	29.7±2.3	47.1±6.6	76.4±0.5	132.4±8.7	116.6±0.4
能率环 (%) Duty cycle	9.4	5.9	13.8	18.6	47.0
声谱图类型 Types of the sonagram	短调频型,多谐波 Short FM, multi-harmonics	短调频型,多谐波 Short FM, multi-harmonics	短恒频调频型,多谐波 Short CF-FM, multi-harmonics	短恒频调频型 Short CF-FM	长恒频调频型 Long CF-FM

* 蝙蝠名称后括号内数字为样本数 The number in the bracket behind the name of bats is sample size

2.2　蝙蝠外部形态特征统计结果

对从飞龙洞中捕获的 5 种蝙蝠(共 24 头)的外部特征进行了测量,其中包括:体重、头体长、前臂长、翼宽和翼长。本研究中,采用翼长/翼宽作为翼纵横比的参考值,体重/前臂长作为翼负荷的参考值,因为翼长/翼宽值的大小可以间接地反映出翼纵横比;而前臂长的大小,可以从一定程度上反映出翼面积的大小,故用此参数也有一定的说服力,可以反映出比较真实的情况。结果见表 2。

表 2 5 种蝙蝠身体形态的各项参数值

Table 2 The comparison of body parameters of five species of bats

蝙蝠种类 The species of bats	体重 Body mass (g)	头体长 Body length (mm)	前臂长 Forearm length (mm)	翼宽 Wing width (mm)	翼长 Wing length (mm)	翼长/翼宽 The ratio of wing length to wing width	体重/前臂长 The ratio of mass to forearm length
南蝠 *Ia io*	52.3	93.2	73.7	85.6	230.0	2.7	0.7
大鼠耳蝠 *Myotis myotis*	25.2	71.5	63.7	86.8	192.0	2.2	0.4
黄大蹄蝠 *Hipposideros pratti*	58.7	87.8	93.4	104.5	249.7	2.4	0.6
三叶蹄蝠 *Aselliscus wheeleri*	6.0	41.0	43.8	54.2	116.5	2.1	0.1
角菊头蝠 *Rhinolophus cornutus*	4.6	32.7	38.0	50.9	94.9	1.9	0.1

* 样本数同表 1 The sample size is same as table 1

3 讨论

蝙蝠的回声定位行为及相关的形态特征与其捕食策略及捕食生境有着密切的联系。在飞龙洞中，我们发现了南蝠、大鼠耳蝠、黄大蹄蝠、角菊头蝠和三叶蹄蝠，根据生态位分化的原理，这 5 种共栖同一山洞的蝙蝠在捕食生境及捕食猎物上必然有一定的分化，这样才能避免过度的竞争。

Neuweiler[4]认为具有多谐波调频声的蝙蝠适于在各种较为复杂的环境中捕食，如在树冠之间的开阔空间进行捕食，在树叶上或地面上进行拾遗式(gleaning)捕食等。南蝠的回声定位叫声为短 FM 型，具有 3 个谐波，所以它可能属于此种类型。南蝠回声定位信号的最大能量频率集中在 29.7±2.3kHz 范围内，而较低的叫声频率适合在远距离内捕食个体较大的昆虫或猎物[6]。此外，南蝠的翼长与翼宽值很高，体重与前臂长的比值也很高，这说明南蝠为快速飞行者，同时飞行的灵活性不高。因此，南蝠不适合在树叶间捕食，因为此处空间太小，太繁乱，南蝠无法自如地捕食猎物。根据野外观察，南蝠可能捕食地面上的个体较大的猎物，另外南蝠也可能在树冠中间的开阔空间飞行捕食个体较大的昆虫。

大鼠耳蝠的回声定位叫声与南蝠相类似，同样为 FM 类型，具有多谐波，但回声定位叫声最大能量处频率(47.6±6.6kHz)比南蝠略高，持续时间(2.3±1.1ms)比南蝠短，这说明大鼠耳蝠的猎物搜索范围比南蝠的小，而且捕食生境更复杂[6]。此外，大鼠耳蝠的翼长与翼宽的比值小于南蝠，说明其翼相对较宽，而体重与前臂长比值较小，意味着大鼠耳蝠具有较小的翼负荷，因而也具有较高的飞行灵敏性，适合在较为狭窄、较为繁乱的空间内捕食。所以大鼠耳蝠的捕食策略为 Neuweiler[4]所提到的第二种，即在树叶上或地面上进行拾遗式捕食。Arlettaz[7,8]在野外研究了大鼠耳蝠的捕食策略后得出，大鼠耳蝠主要捕食森林或草地地表面的昆虫，其捕食方式为拾遗式(gleaning)捕食。这一结果也与本文分析所得结论相符。

黄大蹄蝠叫声属于短 CF-FM 型，具有 3 个谐波，最大能量处频率(FMF)为 76.4±0.5kHz，能率环为 13.8%。黄大蹄蝠采用 CF 叫声，而 CF 信号适合探测翼拍动的昆虫，最大能量处频率(FMF)较高，因此它可能在近距离捕食[6]。后部的 FM 组分可以为黄大蹄蝠提供猎物的精细结构和详尽的信息。叫声中包括 3 个谐波，说明其捕食环境较为复杂，因为蝙蝠在复杂环境里捕食昆虫时，可以采取两种不同策略[1]，一是运用多普勒效应，二是增加谐波的数目。从黄大蹄蝠的外部特征来看，它具有较长的翼——翼长与宽的比值较大，所以飞行速度较快；具有较重的体重——体重与前臂长的比值较高，所以其翼负荷也较大，因而飞行的灵敏性较差。从它较大的体型与体重分析，捕食一些较大的猎物才会提高其捕食效率，满足其生活的能量需求。由野外观察可知，黄大蹄蝠主要在常绿落叶阔叶混交林的林冠周围及上方开阔的空间捕食。黄大蹄蝠是以较大的鞘翅目甲虫为食的，在洞口附近其栖居点或停留点的下面，发现了大量的粪便及昆虫的残体；在网捕过程中还发现，飞回洞中的黄大蹄蝠，口中仍有未吃完的昆虫或猎物的残体，说明它习惯于倒挂在某处捕食。综合黄大蹄蝠的回声定位叫声的特点、外形特征以及野外的观察，可以推断出黄大蹄蝠主要在树冠周围及上方开阔空间进行捕蝇器式(Fly-catching)（即倒挂于一固定枝条或地点，探索周围飞行或接近的昆虫，探索到后捕捉回原倒挂地点再进食）或飞行中的捕食。

角菊头蝠回声定位叫声含有一个谐波，是典型的长 FM-CF-FM 型，最大能量处频率(FMF)为 116.6±

0.4kHz,能率环为 47.0%。一般地,在开阔空间中的长距离回声定位是通过低音频率完成的,而在叶群中和其周围的短距离的回声定位则是在高频率下进行的[6]。值得注意的是,角菊头蝠的回声定位叫声持续时间是 5 种蝙蝠中最长的,长的 CF 叫声适于利用多谱勒变化分辨猎物翼的摆动[9],使回声定位的频率及强度都发生规律性的变化,这样角菊头蝠就能够从复杂的环境噪音中分辨出翼摆动的猎物。所以,角菊头蝠很可能在树木的枝叶及树木之间的狭窄空间内捕食。最大能量处频率(FMF)很高,可以推断出其猎物的体形很小。从其外部特征来分析,角菊头蝠具有相对宽的翼——翼长与翼宽的比值较小,具有较小的体重——体重与前臂长的比值在 5 种蝙蝠中最低,可以断定其飞行速度较慢而且灵敏性很高。综上所述,角菊头蝠可能是在树木枝叶或在其周围狭窄空间内捕食较小的翼拍动昆虫。

三叶蹄蝠也是短 FM-CF-FM 型,只有一个谐波,最大能量处频率为 132.4±8.7kHz,能率环为 18.6%。研究表明[10],频率低的声波波长较长,适于在长距离范围探测个体较大的猎物;相应地,频率高的声波波长短,适于探测近距离、个体较小的猎物。三叶蹄蝠的频率是 5 种蝙蝠中最高的,而且叫声主要为 CF 组分,因此可以推断它是在近距离内捕食个体很小的翼拍动昆虫,其后部调频的存在,使蝙蝠能够更好地收集猎物的详细信息,以成功地在空中捕食猎物并避开障碍物。叫声中只含一个谐波,这与它在复杂空间捕食不太适合,其作用机制还有待于进一步探讨。从外部特征来看,三叶蹄蝠有相对宽的翼以及相对轻的体重,即较低的翼长与宽的比值和体重与前臂长的比值,说明三叶蹄蝠飞行速度较慢,行动灵敏性很好,它可能在较小空间内进行飞行捕食。野外的观察研究也证实三叶蹄蝠主要在阔叶林的林下及灌丛中捕食以鳞翅目及鞘翅目为主的昆虫。

综合上面的分析,可以得出以下的推论:5 种蝙蝠的回声定位行为差异显著,在捕食生境及捕食策略上也存在着一定的差异,因此其生态位存在着明显的分化,另外从野外的观察及体形方面的测量数据来看,这几种蝙蝠在捕食猎物的大小上也有较大的差异。

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