Zoology 115 (2012) 22–29

Contents lists available at SciVerse ScienceDirect

Zoology

journal homepage: www.elsevier.de/zool

Ecomorphology, differentiated habitat use, and nocturnal activities of *Rhinolophus* and *Hipposideros* species in East Asian tropical forests

Ya-Fu Lee [a,b,*], Yen-Min Kuo [a,b], Wen-Chen Chu [a,1], Yu-Hsiu Lin [b,1,2], Hsing-Yi Chang [b,2], Wei-Ming Chen [a,2]

[a] *Department of Life Sciences, National Cheng Kung University, Tainan 701, Taiwan*
[b] *Institute of Biodiversity, National Cheng Kung University, Tainan 701, Taiwan*

ARTICLE INFO

Article history:
Received 20 January 2011
Received in revised form 12 July 2011
Accepted 29 July 2011

Keywords:
Bats
Echolocation
Habitat use
Wing morphology

ABSTRACT

We investigated the wing morphology and foraging distributions of sympatric *Rhinolophus* and *Hipposideros* species by acoustic sampling, measuring wing parameters, and observing bats in different settings of tropical East Asian forests, to evaluate their flexibility in habitat use and edge sensitivity. *R. formosae* and *H. terasensis* were more abundant at edges/in open habitats and shared the highest overlap, with *R. formosae* displaying the greatest breadth in habitat use, whereas *R. monoceros* had a higher abundance and feeding efficiency in forest interiors with a continuous canopy. *H. terasensis* was significantly larger and had higher wing loading and aspect ratio than *R. formosae* and *R. monoceros*, while *R. formosae* had higher wing loading but a lower aspect ratio than the smaller-sized *R. monoceros*. Shrubs and herbs were higher at sites where bats were captured than at those without bat captures, and *R. monoceros* and *R. formosae* were associated with greater canopy and ground coverage, respectively. *R. monoceros* always foraged while flying at lower heights close to the herb/shrub layers, while *H. terasensis* and *R. formosae* used perching to different extents, with *R. formosae* preferably using fly-catching techniques and appearing farther from the path in open forests rather than in forest interiors. Our results indicate that differences in wing parameters account for the different degrees of flexibility in habitat use, yet the deviations of call frequency from the expected values in *R. formosae* and *H. terasensis* suggest additional adaptations accounting for their flexibility in exploring habitats.

1. Introduction

Bats are the second-largest mammalian order (Simmons, 2005); many contribute to ecosystem functioning (Hodgkison et al., 2003; Kalka et al., 2008; Kunz et al., 2011) and even enhance human welfare (e.g., Lee and McCracken, 2005; Federico et al., 2008; Boyles et al., 2011). Over half of the extant bat species are plant-roosting to different degrees (Kunz and Lumsden, 2003), and many species rely heavily on woodlands for foraging (e.g., in temperate North America, Lacki et al., 2007). The globally increasing rates of fragmentation and alteration of tropical forests are an alarming threat to biodiversity (Achard et al., 2002), to which tropical species of forest-dwelling bats may be especially sensitive and vulnerable. For the dominant and ecologically diverse Neotropical phyllostomids, species richness and abundance tend to be lower at more disturbed sites (Medellín et al., 2000; Clarke et al., 2005), although the effects of forest fragmentation on bats vary among species and may be related to other factors (e.g., edge sensitivity and mobility of organisms; Meyer and Kalko, 2008; Meyer et al., 2008).

In the Palaeotropical/Australasian regions, microchiropterans mainly consist of insectivores (Hutson et al., 2001); many are relatively fast-flying, open space- or edge space-adapted generalists, such as certain groups in vespertilionids (e.g., *Pipistrellus*, *Eptesicus*, *Miniopterus*, *Scotophilus*, and *Chalinolobus*), emballonurids (e.g., *Taphozous*), and molossids (Norberg and Rayner, 1987). The responses of these species to forest fragmentation and disturbance are inconspicuous or often inconsistent (Crome and Richards, 1988; Fenton et al., 1998; Goodman et al., 2005). In contrast, clutter foragers that hunt in forest interiors may be more impacted by disturbances and more susceptible to the loss and modification of forest habitats (Pavey, 1998). Kingston et al. (2003) categorized these clutter foragers as key components of forest bat diversity of Indomalaya, notably but not exclusively including the second and third most speciose bat genera, the horseshoe

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* Corresponding author at: Department of Life Sciences, National Cheng Kung University, Tainan 701, Taiwan. Tel.: +886 6 2757575x65524; fax: +886 6 2742583.
E-mail address: yafulee@mail.ncku.edu.tw (Y.-F. Lee).

[1] Present address: Taiwan Endemic Species Research Institute, Nantou 552, Taiwan.

[2] These authors contributed equally to this work.

0944-2006/$ – see front matter © 2012 Elsevier GmbH. All rights reserved.
doi:10.1016/j.zool.2011.07.006

bats *Rhinolophus* and the Old World leaf-nosed bats *Hipposideros* (Simmons, 2005).

Species in these two groups differ from other insectivorous bats by emitting high duty cycle constant-frequency (CF) and frequency-modulated (FM) calls (or more specifically defined as FM–CF–FM calls for *Rhinolophus*; Jones and Rayner, 1989; Neuweiler et al., 1987). Their calls are often at higher frequencies, scale more negatively with body mass than those of bats from other families, and utilize Doppler-shift compensation to resolve the problem of masking effects (Jones, 1999). These echolocation and auditory characteristics allow *Rhinolophus* and *Hipposideros* to detect insect wing beats in narrow, highly cluttered spaces in forest interiors and within foliage (Neuweiler, 1989; Schnitzler and Kalko, 2001). A low wing loading and aspect ratio also favor a close association of *Rhinolophus* with vegetation. *Hipposideros* resemble *Rhinolophus* with a similarly low wing loading, but their relatively higher aspect ratio suggests faster flight and a greater adaptation to a more open area (Norberg and Rayner, 1987; Norberg, 1994). Nevertheless, species specialized for narrow spaces may not be exclusively restricted to these areas and often exploit additional types of habitats (Fenton, 1990; Schnitzler et al., 2003).

The detection range of high-frequency calls is affected by atmospheric attenuation; however, the long, pure-tone (CF) component aided by Doppler shifts may free rhinolophids from this constraint. Doppler-shift compensation may be less complete in *Hipposideros* (Habersetzer et al., 1984), but these bats often emit shorter pulses at higher frequencies compared to rhinolophids of a similar size (Jones, 1999). Rhinolophids and hipposiderids are frequently found associated with sheltered, warm environments close to or within forests (Pavey, 1998; Goiti et al., 2003), although they might not visit all types of woodlands (Russo et al., 2002). Yet, *Rhinolophus* and *Hipposideros* can also forage in less cluttered environments along forest and vegetation edges or even in open habitats (e.g., Bell and Fenton, 1984; Siemers and Ivanova, 2004; Goiti et al., 2006). These bats may leave forests to seek different types of prey or different types of habitats in different seasons due to changes in prey abundance (e.g., *R. ferrumequinum*, Jones et al., 1995; *H. diadema*, Pavey and Burwell, 2000). Thus, behavioral flexibility is expected, and variations among species may be high in these species-rich groups.

We present the first attempt to investigate the nocturnal distributions and activities of Eastern Asian tropical forest rhinolophids and hipposiderids and to evaluate their flexibility in habitat use. Given a general similarity in the echolocation calls of these two groups, we tested the hypothesis that differences in wing parameters result in different degrees of flexibility or patterns of habitat use (Bogdanowicz et al., 1999). Specifically, we predicted that (i) species with higher wing loading and aspect ratios, typically characterized by faster flight, would be less adapted to highly cluttered environments in forest interiors and, thus, would be more active in edges and/or open forests. In addition, we predicted that (ii) species with similar wing parameters but higher call frequencies would be less flexible in exploiting forest edges and open forests.

2. Materials and methods

2.1. Study area

Field work took place in the Guijijaou Experimental Forest (GEF) and the Hengchun Tropical Botanical Garden (HTBG; 120°48′E, 20°58′N, ca. 450 ha, 200–300 m in elevation) in Kenting, Hengchun Peninsula, southern Taiwan. Mean monthly temperatures reach 28 °C in July through August and are generally above 20 °C in the coldest months, and an annual rainfall of 2200–2300 mm typifies the tropical climate (Guijijaou Weather Station data, Taiwan Forestry Research Institute).

Formosan woolly horseshoe bats (*Rhinolophus formosae*), Formosan lesser horseshoe bats (*Rhinolophus monoceros*), and Formosan leaf-nosed bats (*Hipposideros terasensis*) are endemic to Taiwan and common species in this area (Lee et al., 2007). Autumn maple trees (*Bischofia javanica*), bark figs (*Ficus benjamina*), and coast persimmons (*Diospyros maritima*) are characteristic species of the canopy layer of the monsoon reef-karst forest. Philippine drypetes (*Drypetes littoralis*) and Taiwan aglaia (*Aglaia formosana*) dominate reef tops, and in reef valleys, vegetation includes Formosan nato trees (*Palaquium formosanum*), Taiwan ebony (*Diospyros discolor*), Philippine ebony persimmon (*Diospyros ferrea* var. *buxifolia*), and Papala kepau (*Pisonia umbellifera*). Smaller woodland remnants, grass patches, and the HTBG comprising primary/secondary forest fragments or mixed-species forestry plantations surround the GEF along its southern and southwestern borders (Lee et al., 2007).

2.2. Acoustic monitoring of nocturnal activity

We established and mapped (1:5000) number-labeled grids (200 m × 200 m) that covered a total area of ca. 120 ha and incorporated three types of habitats: forest interiors (13 grids), forest edges (6 grids) and open forests (12 grids). Using the grid we set up seven transect lines of different lengths (1145.7 ± 93.8 m; 8.02 km in total), based on terrain and accessibility. Each line comprised various numbers of monitoring zones that were roughly equal in length, equivalent to that of a grid, plus 10 m of searching area on both sides of the line. Three transects, containing 14 zones in all, meandered through open forests in the HTBG, where tree densities are the lowest and vegetation is subject to regular management practices, such as understory clearance. At forest edges, two transects with a total of seven zones ran roughly in parallel along the karst ridges that form the boundary of the forest interior. Two transects with a total of 11 zones were situated in the forest interiors, penetrating the GEF forest toward the north and east, respectively, and characterized by the highest tree densities and high canopy and herb layers (Lee et al., 2010). Forest edges and open forests represent background cluttered space, whereas forest interiors correspond to highly cluttered spaces (Schnitzler et al., 2003).

We conducted monthly acoustic monitoring to assess bat activity from April 2002 to August 2004. On clear, calm nights each census was simultaneously conducted by two teams of two individuals each, one team in open forests and the other in forest edges and interiors, covering all transects. In cases when only two members were available, the surveys were conducted over two successive nights. While the exact start and stop times of each census varied, they always began within 20 min after sunset and ended after all transects were assessed, usually at approximately midnight. Censuses resumed from June 2007 to May 2008, with additional monitoring from midnight to early dawn following the same procedure. The monitoring sequence (between transects and within each transect) was randomly alternated to reduce the effect of time on bat activity and potential personal bias. We used bat detectors (D230; Pettersson Elektronik AB, Uppsala, Sweden), which were hand-held at a height of 1.3–1.5 m, in the heterodyne mode to monitor echolocation calls. Monitoring focused on, and was switched continuously among, distinct pure-tone (CF) frequencies of ca. 39–42 kHz for *R. formosae*, 66–69 kHz for *H. terasensis*, and 105–115 kHz for *R. monoceros* (Lin et al., 2004; Y.F. Lee, unpubl. data). Upon each acoustic encounter of echolocation calls, we visually confirmed the species and tallied the number of bats present at the site or made a best estimate, using the naked eye or binoculars (Leica 10 × 25 BN; Leica Camera AG, Solms, Germany) aided by spotlights or headlights as necessary.