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The activity time of the lesser bamboo bat, *Tylonycteris pachypus* (Chiroptera: Vespertilionidae)

Li-Biao Zhang[1,*], Fu-Min Wang[2], Qi Liu[1] & Li Wei[3]

[1]*Guangdong Public Laboratory of Wild Animal Conservation and Utilization & Guangdong Key Laboratory of Integrated Pest Management in Agriculture, Guangdong Entomological Institute, Guangzhou 510260, China.*
[2]*Guangdong Provincial Wildlife Rescue Center, Guangzhou 510520, China.*
[3]*College of Ecology, Lishui University, Lishui 323000, China.*
**Corresponding author. E-mail: zhanglb@gdei.gd.cn*

ABSTRACT. The activity time of the lesser bamboo bat, *Tylonycteris pachypus* (Temminck, 1840), was investigated at two observation locations in southern China: Longzhou and Guiping. Two bouts of activity (post dusk and predawn), with an intervening period of night roosting at diurnal roosts, were identified. The period of activity within each bout was usually less than 30 minutes. The activity periods of individuals belonging to the Longzhou population right after dusk and just before dawn lasted longer than those of the the Guiping population. We also found that the nocturnal emergence time of *T. pachypus* from the Longzhou population happened earlier than in the Guiping population. These findings indicate that the activity time of *T. pachypus* was quite short at night, and that different locations may affect the nocturnal activity rhythm of this species.

KEY WORDS. Activity period; emergence; return; *Tylonycteris pachypus*.

Most bats are nocturnal, foraging at night and resting in roosts during the day. Between activity bouts, they also spend time in night roosts (Anthony & Kunz 1997). The patterns of nocturnal activity vary dramatically among different species. O'Shea & Vaughan (1977) have reported that the pallid bat *Antrozous pallidus* (Le Conte, 1856) utilizes two foraging periods with an intervention period of night roosting. Some other species, such as *Euderma maculatum* (J.A. Allen, 1891), spend the entire night flying and foraging (Wai-Ping & Fenton 1988). Likewise, the duration of bouts has also been found to be different. For instance, *Eptesicus fuscus* (Beauvois, 1796) spends only 2 hours flying each night (Brigham 1991), while *Nacteris grandis* spends even less time in this activity (Fenton et al. 1990).

The timing and pattern of bat nocturnal activity may be influenced by environmental factors such as light levels (Lee & McCracken 2001), prey abundance (Erkert 1982), temperature (Catto et al. 1995), cloud (Kunz & Anthony 1996) and rain (Mcaney & Fairley 1988). Moreover, intrinsic biological factors such as predation risk (McWilliam 1989, Speakman 1991), colony size, age, sex, the reproductive status of individuals (Avery 1986, Rydell 1989, Korine et al. 1994, Clark et al. 2002, O'Donnell 2002), and interspecific competition (Swift & Racey 1983, Bonaccorso et al. 2006) may also impact the nocturnal activity of bats. The intensity of competition between or among sympatric related species is expected to be greater because they are morphologically similar, which is assumed to reflect niche similarity (Findley & Black 1983, Aldridge & Rautenbach 1987, Arita 1997). When common resources are limited, the niche theory predicts that resource partitioning (such as spatial and temporal niche) is necessary for species to coexist within a guild. They may forage in different habitats (Arlettaz 1999) and then feed on different diet items (Arlettaz et al. 1997), or forage during different times (Bonaccorso et al. 2006). In contrast, when their shared resources are not limited, species may forage concomitantly and for longer periods.

The lesser bamboo bat, *Tylonycteris pachypus* (Temminck, 1840) (Chiroptera: Vespertilionidae), and its sibling species, *Tylonycteris robustula* Thomas, 1915, are genetically closely related. The two species have similar morphological features (Medway & Marshall 1978). According to our field observations, which have been published in another contribution, the two species rarely roost together in the same internode, although they overlap in distribution. Also, they can alternate their use of the same internodes at different times or seasons (Zhang et al. 2004) and forage on similar categories of insects that occur sympatrically (Zhang et al. 2005a).

The nocturnal activity rhythm of *T. pachypus* and *T. robustula* is still poorly known. In the present study we investigated the activity time (emergence time and foraging duration) of the lesser bamboo bat, *T. pachypus*, in two populations inhabiting Longzhou and Guiping Counties, Guangxi, south China, approximately 250 km apart from each other. *T. pachypus* is sympatric with *T. robustula* in Longzhou County, but occurs alone in Guiping County.

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MATERIAL AND METHODS

The study was carried out from March to November, in 2008 in Guangxi Province, south China. Two locations (Longzhou County, 21°10′N, 106°50′E, 116 m in elevation, and Guiping County, 23°09′N, 110°10′E, 68 m in elevation) were selected. Zhang et al. (2005a) had previously described the climate and vegetation of Longzhou County as having average annual temperature of 22.8°C and average annual precipitation of 1,180 mm (Fang 1995). Guiping County has a similar climate but the habitat is hilly rather than the typical karst of Longzhou County, with average annual temperature of 21.4°C and average annual precipitation of 1,727 mm (Fang 1995). Within both study areas, the bamboo, *Bambusa spinosa* Roxb, is abundant. This plant has enough internodes to provide enough suitable roost sites for both bat species. During data collection, *T. pachypus* and *T. robustula* were never found in the same roost at the same time, except on one occasion, when a single *T. pachypus* male and a single *T. robustula* male roosted in the same internode. In Longzhou County, bamboo is found in and around villages, while in Guiping County it is distributed along streams in areas that are somewhat far from villages.

Nocturnal observations were conducted from dusk to the next morning. Observers were split into two groups (two persons per group) and each group observed the activity time of *T. pachypus* in the two locations, at the same time. Normally, bamboo bats are faithful to their bamboo internodes for a short period (Zhang et al. 2004), which allowed us to continuously observe groups in the same internode from dusk to dawn. We selected a fixed bamboo forest in each location to conduct our observations. The bamboo bat colony in each forest had more than two hundred individuals. We swapped among different bamboo internodes on different days during the same month, and the size of the group in each of these internodes was normally over eight bats. In each location, the time of emergence and returning were recorded, respectively. Emergence time was defined as the time when the first bat individual flied out of its bamboo internode; the returning time was defined as the time when the first bat individual flied back into the bamboo roost, or attempted to do so. If no bat emerged from a bamboo internode after 20 minutes (confirmed by using a wire to check bat lairs), we terminated the observation on emergence time. Likewise, if no bat returned back to its bamboo internode we terminated the observation on returning time. The duration of activity was defined as the time period between emergence and returning, since it is difficult to observe the entire behavior of the bat after it flies out. Additionally, *T. pachypus* forages around or over their roost bamboo forest; for example, their foraging sites are nearby their roosts (Zhang et al. 2007). We also recorded air temperature at sunset and sunrise, and position of the roost site (via GPS, eTrex, Garmin Corp., Taiwan). The time of sunset and sunrise were read from a GPS. During the observation period, nocturnal observations were conducted for at least one week per month, normally in the middle of the month. Since *T. pachypus* is sympatric with *T. robustula* in Longzhou, we identified and confirmed the identify of *T. pachypus* using characteristics of its echolocation calls using a sound detector (D-980, Petterson Electronic AB, Uppsala) when individuals flied out or returned. This study was conducted according to the protocols approved by the Guangdong Entomological Institute Administrative Panel on Laboratory Animal Care.

A total of 75 night observations were conducted both in Longzhou and Guiping. When it was raining during the bat's normal activity period, the data of the corresponding night were omitted from both sites in the analysis. As a result, data on twelve night observations were discharged, and 63 night observations, one week per month, were analyzed. All data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov test and Bartlett test. We conducted Independent-Samples t-test for comparisons of emergence time, returning time and duration of activity between the Longzhou and Guiping populations, respectively. Then for comparisons of monthly variations in activity duration, we used One-Way ANOVA. Regression was used to analyze activity time and local air temperature. All statistical analyses were performed in SPSS 17.0 for Windows. Descriptive data were expressed as Mean ± SD, and the significant difference at 95% confidence level was calculated by Central Limit Theorem.

RESULTS

Based on our observations, the lesser bamboo bat *T. pachypus* normally feeds in and around bamboos in the forests in which they roost, and fly to foraging sites directly from their roost. The activity time of *T. pachypus* individuals in the two populations was characterized by two distinct bouts, one immediately after dusk and the second just before dawn. The duration of the activity within each bout was usually less than 30 minutes. The dusk (23.7 ± 8.39 min) and predawn (27.9 ± 14.79 min) activity periods of *T. pachypus* individuals were significantly longer in Longzhou than in Guiping (dusk: 21.2 ± 8.09 min; predawn: 25.4 ± 14.43 min) (dusk: $t = 2.374$, $p < 0.05$; predawn: $t = 2.857$, $p < 0.05$) (Fig. 1). A strong positive correlation was also observed between activity duration and air temperature at dusk and predawn in the two populations, respectively (Longzhou: $r_{dusk} = 0.891$, $r_{predawn} = 0.904$, respectively, both $p < 0.001$; Guiping: $r_{dusk} = 0.881$, $r_{predawn} = 0.837$, both $p < 0.001$) (Figs. 2-3). In addition, we found that the durations of activity of *T. pachypus* varied significantly in both populations from one month to another (Longzhou: $F = 4.069$, $p < 0.001$; Guiping: $F = 3.619$, $p < 0.001$) (Figs. 2-3).

The time of emergence obtained for the Longzhou population at post dusk (12.7 ± 0.62 min after sunset) was significantly earlier than for the Guiping population (14.7 ± 0.48 min) ($t = 2.37$, $p < 0.05$), but the returning time at predawn did not significantly differ between them (Longzhou: 17.3 ± 0.94

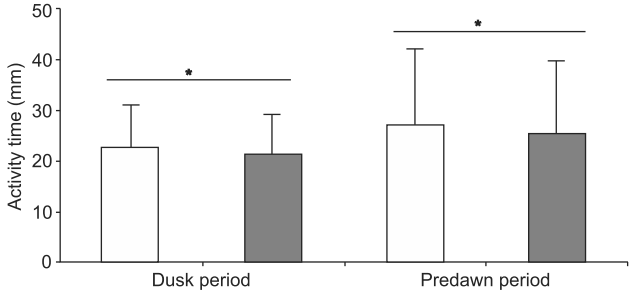

Figure 1. The foraging time of dusk (n = 63) and predawn (n = 63) periods of *Tylonycteris pachypus* in Longzhou County (empty column) and Guiping County (grey column), Guangxi, south China. All data are expressed as Mean ± SD. *p < 0.05.

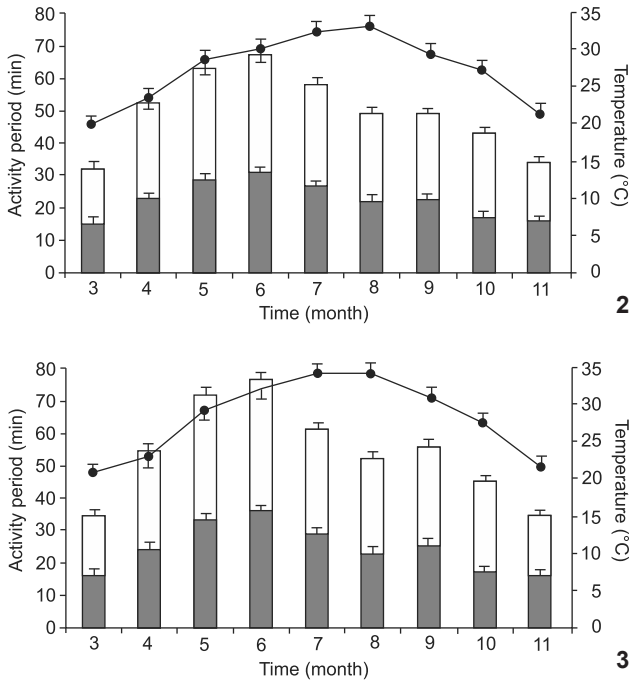

Figure 2-3. The total foraging time over one night (average value of seven nights for each month) of *Tylonycteris pachypus* in Longzhou County (2) and Guiping County (3). Solid portions indicate dusk foraging periods while hollow portions indicate dawn foraging periods. The dots indicate the average temperature.

min before sunrise, Guiping: 17.5 ± 0.62 min) (t = 1.38, p > 0.05) (Fig. 4). We also found that there is a significant correlation between the time of evening emergence and the average air temperature at sunset, and between time of predawn return and average air temperature at sunrise for both populations, respectively (Longzhou: $r_{emergence} = 0.882$, $r_{return} = -0.915$, respectively, both $p < 0.001$; Guiping: $r_{emergence} = 0.735$, $r_{return} = -0.826$, both $p < 0.001$).

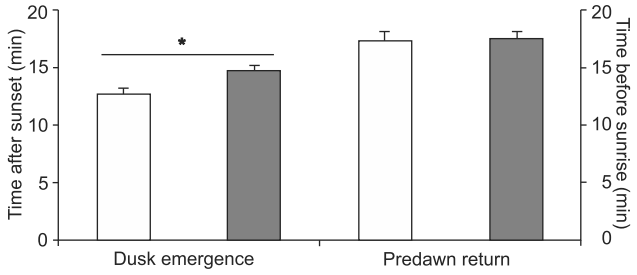

Figure 4. Time of dusk emergence (n = 63) and predawn returning (n = 63) of *Tylonycteris pachypus* in Longzhou County (empty column) and Guiping County (grey column), Guangxi, south China. All data are expressed as Mean ± SD. *p < 0.05.

DISCUSSION

Mammals that are characterized by energetically expensive modes of locomotion and which encounter limited (temporally) food supply tend to regulate their foraging behavior. Bat species usually emerge to feed after sunset and return before sunrise (Bateman & Vaughan 1974, O'Shea & Vaughan 1977, Duvergé et al. 2000). The timing of these activity bouts correspond to the time at dusk and predawn when insects are most abundant (Kunz 1974, Racey 1982, Racey & Swift 1985, Rydell 1993, Swift 1997). Based on previous studies, most bat species spend more than one hour each night in predation activities, and their nocturnal activity rhythm can be highly variable among different species. For instance, O'Shea & Vaughan (1977) have reported that the activity of pallid bats was characterized by two foraging periods with an intervening period of night roosting. Anthony et al. (1981) have also reported that the little brown bat typically has two foraging periods at night, which are divided by a short break in night roost. In the present study, we found that the night foraging time patterns of *T. pachypus* were characterized by two bouts: dusk and predawn, respectively. Within each bout, activity duration (time period from emergence to returning) was remarkably short, less than 30 minutes. This may be correlated with the fact that the lesser bamboo bat is one of the smallest bat species, and therefore individuals can spend relatively short periods of activity time to balance energy intake and the costs to maintain their high metabolic rate during flight (Speakman 2005). On the other hand, the roosting behavior of *T. pachypus* may also contribute to their short activity time. *T. pachypus* roosts within bamboo internodes, and these restricted spaces may limit the activity of bats and subsequently reduce their energy consumption. Moreover, the short foraging distance away from their internode roosts decrease flight time as well as energy consumption (Zhang et al. 2007).

Our results indicate that in Longzhou County *T. pachypus* emerges earlier and forages for longer periods of time than that in Guiping County. On average, the activity time of individuals in Longzhou each night is approximately five minutes,

which is longer than that in Guiping. Although this increase is small in magnitude, it represents a 10% increase in average activity time. The different activity behavior in different locations may have resulted from many factors such as the effect of interspecific competition (Swift & Racey 1983, Bonaccorso et al. 2006), variations in prey abundance (Erkert 1982), predation risk (McWilliam 1989, Speakman 1991), and colony size (Avery 1986, Rydell 1989, Korine et al. 1994, Clark et al. 2002, O'Donnell 2002). Both *T. pachypus* and *T. robustula* eat similar categories of insects when they occur sympatrically, although the prey of the later is somewhat larger than that of the former (Zhang et al. 2005a). In conclusion, in Longzhou where both sibling species are sympatric, the activity time of *T. pachypus* may be affected by *T. robustula*.

Many authors have documented seasonal fluctuations in emergence and returning time of bats (Bateman & Vaughan 1974, O'Shea & Vaughan 1977, Duvergé et al. 2000). Pallid bats emerge earlier in the summer sunset when compared with spring and autumn sunsets (O'Shea & Vaughan 1977). Lee & McCracken (2001) have also reported that the timing of evening emergence and returning of the Mexican free-tailed bats, *Tadarida brasiliensis* (I. Geoffroy, 1824), are correlated with the time of sunset and sunrise, and that bats are more likely to emerge earlier in relation to earlier sunset time during late summer, when compared with spring to early summer. They also return progressively later at dawn, which is associated with sunrise in the entire season. We found that the dawn returning times of *T. pachypus* were correlated with sunrise from March to November. In this study, *T. pachypus* emerged only 5-10 minutes after sunset during summer, but 10-20 minutes during spring and autumn. Pallid bats emerged 20-40 minutes after sunset (O'Shea & Vaughan 1977) and greater horseshoe bats emerged 45-53 minutes after sunset (Duvergé et al. 2000). Kunz et al. (1995) have pointed out that increased energetic demands during pregnancy and lactation could cause females, especially those lactating, to spend twice or even three times as much time foraging than bats that are neither pregnant nor lactating. As a result, emerging earlier in the evening and returning later at dawn will give these bats more time to feed, but at the cost of a greater danger of predation (Fenton 1995, Speakman et al. 1995, Rydell et al. 1996). Our results indicate that the activity time of flat-headed bats is longer in summer than in spring and in autumn. This may be influenced by prey activity, reproductive status and energy demands (Richards 1989). Female flat-headed bats usually become pregnant in May, and give birth and lactate in June (Zhang et al. 2005b). During this time, reproductive females would require more energy to maintain the increased physiological requirements of pregnancy and lactation, which is reflected in their increased activity time.

Seasonal fluctuations in activity patterns can be influenced by many factors, such as ambient temperature and/or prey availability (Anthony et al. 1981, Rydell 1989, Maier 1992). In the present study, the bamboo bats emerged earlier and returned latter when the ambient temperature was higher, which resulted in a positive association between high ambient temperature and increased activity. In March and November, when temperatures were relatively low, the activity periods of bamboo bats were obviously short than from April to October. Reduced activity in lower temperatures has also been demonstrated for many other insectivorous bat species (e.g., Anthony et al. 1981, Kronwitter 1988, Rydell 1989, Maier 1992, Catto et al. 1995). This negative influence may be a reflection of decreased food availability, because insect activity throughout the night is positively correlated with temperatures (Taylor 1963, Lewis & Taylor 1964).

In conclusion, our findings suggest that the lesser bamboo bat spends relatively short time being active, even less than half hour each bout. This behavior may be correlated with the high-energy demand for this tiny mammal to be able to fly. Secondly, our findings suggest that the activity behavior of the lesser bamboo bat, including emergence time and activity duration, varies in different locations. The variation in activity may result from many factors such as the effect of sibling sympactric species, and variations in prey abundance, predation risk, and colony size in different locations. Further studies should be conducted to confirm the factors that influence the variations in bat activity.

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