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Citation	Mammal Study, 35(4), 227-233 https://doi.org/10.3106/041.035.0402
Issue Date	2010-12
Doc URL	http://hdl.handle.net/2115/47532
Type	article
File Information	MS35-4_227-233.pdf



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Seasonal change in the diet composition of the Asian parti-coloured bat *Vespertilio sinensis*

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Abstract. We determined the food habit of the Asian parti-coloured bat *Vespertilio sinensis* from May to August by analysing their faecal samples. Eight orders of insects were identified in the faeces. Lepidoptera, Diptera and Coleoptera had high frequencies of occurrence, but the proportion of each order varied with the sampling period. A comparison between diet composition and relative insect abundance showed that proportions of Coleoptera in the diet were larger than those in insect abundance. This pattern also was true for Lepidoptera in some sampling periods. In contrast, proportions of Diptera in the diet were lower than those in insect abundance, although Diptera was a major prey item. These results suggest that the diet composition of *V. sinensis* may be biased towards larger-sized taxa. Furthermore, the lack of any significant differences between diet composition and insect abundance for the other five orders suggested that the diet composition of *V. sinensis* is also influenced by the seasonal prevalence of each insect taxon.

Key words: diet, faecal analysis, insect abundance, *Vespertilio sinensis*.

Dietary information can provide fundamental insights into the ecology and behaviour of an animal. Food habits of insectivorous bats have been documented by numerous studies (reviewed in Jones and Rydell 2003). These studies have shown that diet composition varies with species, seasons and populations (e.g., Jones 1990; Hamilton and Barclay 1998; Funakoshi and Takeda 1998; Whitaker et al. 1999; Fukui et al. 2009), and reflect their feeding habitat and strategy (Siemers and Swift 2006). Thus, a description of diet for each bat species or population is essential for explaining the patterns of habitat use, and for predicting how major changes in insect communities resulting from human activities, such as pest control or habitat modification, will affect bats. Furthermore, a comparison of diet with insect abundance is necessary to analyse the presumed feeding behaviour. Understanding the diet composition of endangered species is important because population declines may be caused by the lack of prey in some instances. Moreover, information on the diet of bats, which often come into conflict with humans, may also be important for appropriate management of bats to promote their conservation

(e.g., alternative artificial roosts for bats could be installed near appropriate feeding habitats).

The Asian parti-coloured bat *Vespertilio sinensis* (formerly *V. superans*) is a medium-sized insectivorous species (forearm length = 43–53 mm [Fukui 2009], body weight = 14–30 g [Maeda 2005]) distributed in China, Mongolia, Ussuri, Korean Peninsula, Taiwan and Japan (Simmons 2005). From May to August, maternity colonies, which usually consist of tens to thousands of individuals, are formed by adult females and their offspring (Mukohyama 1996). It is thought that *V. sinensis* used to roost inside natural structures, such as tree holes and rock crevices; however, because the number of natural roosts has decreased due to recent deforestation, this species has been increasingly roosting in man-made structures (Fukui and Bat Research Group of Centennial Woods Fan Club 2001). Consequently, despite legal protection of bats, homeowners who resent bat noise, feces and urine, have increasingly resorted to extermination (Mukohyama 1996). To avoid such needless killing, appropriate measures could be provided. However, for *V. sinensis*, a large part of the ecological information,

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which could be used as baseline for management measures, is lacking. Previous studies have provided data on feeding activity and postnatal growth (Funakoshi and Uchida 1981) and roost preferences (Fukui et al., 2010) of *V. sinensis*. However, although Funakoshi and Uchida (1981) described diet composition during a limited season, seasonal trends in diet composition of this species have not been reported.

The aim of this study was to assess seasonal changes in the diet of *V. sinensis* and compare the diet with insect abundance as determined using light traps.

Methods

Study site

This study was conducted in Centennial Woods Park, which is an isolated, broad-leaved forest (ca. 25 ha) in Kutchan (42°54'N, 140°45'E, altitude = 180 m), Hokkaido Prefecture, from the middle of May to early August 2000. The mean annual temperature is 6.7°C, and the annual rainfall is 1500 mm. The forest is dominated by Japanese poplar (*Populus maximowiczii*), Japanese white birch (*Betula platyphylla*) and alder (*Alnus japonica*), and is surrounded by extensive agricultural fields. There is a small pond (ca. 100 m²) 30 m from the roost, and a shallow stream (less than 1 m width) runs through the forest. Every year from early May to late August, pregnant females of *V. sinensis* congregate at a nursery roost (in the attic of an old garage) in the forest. The population increases to over 1,000 individuals in early August. From the middle of August to late August, all individuals disperse from the roost to an unknown area (Fukui and Bat Research Group of Centennial Woods Fan Club 2001).

Diet analysis

To assess diet composition, we conducted faecal analysis. To collect faecal pellets, a plastic mesh sheet (60 × 300 cm) was placed under the roost entrance. The next day, 50 fresh faecal pellets were collected and stored individually in 70% ethanol until analysis. Sampling was conducted every 10 days from the middle of May to early August. Each faecal pellet was tested after approximately 12 hr in 10% KOH, and arthropod items in the pellets were identified to the level of order using a 40 × binocular microscope. Because digestive efficiency may differ with each insect order and because there was a high proportion of unidentifiable material, it was difficult to measure the volume of consumed prey on the

basis of order. As an alternative, the presence or absence of each insect order, was recorded for each pellet. Out of the total sample of 50 pellets, the number in which items of each insect order were found was counted as the frequency of occurrence (r_x). Subsequently, the relative frequency of occurrence (%) of different categories of prey (R_x) was calculated for each sampling period using the following equation, in which the total number of insect orders found is indicated by “ n ”.

$$R_x = \frac{r_x}{\sum_{i=1}^n r_i} \times 100$$

Insect abundance

To measure relative abundance of each insect order, eight light traps with black lights were placed 1 m above the ground in open areas, such as grassland and forest edge, and randomly 10 to 100 m from the roost. All trapping sites were >30 m from the water bodies in the forest, and the distance between any pair of traps was greater than 30 m. The traps were not placed in the forest interior because the wing morphology of *V. sinensis* is characteristic of bats that fly mainly in open spaces (Norberg and Rayner 1987; D. Fukui, unpublished data), and that lack the maneuverability required to utilize cluttered spaces as a foraging habitat. At all trapping sites, feeding activities of Asian parti-coloured bats were observed by acoustic monitoring (D. Fukui, personal observation). All trapping sites were fixed throughout the survey period. The light traps consisted of four acrylic panels (100 × 50 cm) assembled in a cross configuration. In the centre of the four panels, a portable fluorescent light with black light (BF-662, National, Osaka) was installed. Trapped insects fell into a plastic bottle containing 70% ethanol through a funnel placed under the trap. Traps were run 3 hr from sunset on the same days as faecal sampling. Samples collected in the light traps were stored in 70% ethanol until analysis. Insect samples were identified to the level of order using a 10 × binocular microscope. Subsequently, the number of individuals of each order was counted as abundance, and the relative proportion of different insect orders was estimated for each sampling period. To estimate mean biomass per insect individual, the wet mass of each order was measured to the nearest 0.01 mg using an electronic balance.

Statistics

Chi-square tests were used to compare diet composi-

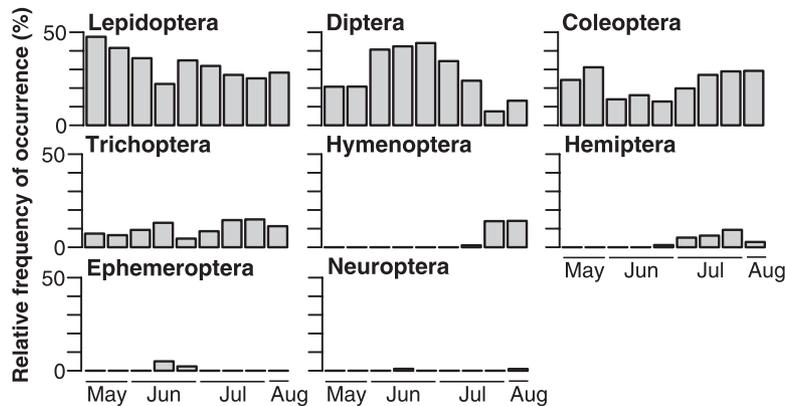


Fig. 1. Relative frequency of occurrence of each insect order in the diet. The number of pellets (out of 50) in which evidence of each insect order was found was counted as the frequency of occurrence. Subsequently, the relative frequency of occurrence (%) of each order was calculated by dividing the frequency of occurrence of each order by the sum of the frequencies of occurrence.

tion with insect abundance, and also to assess seasonal variation in diet composition and insect abundance. When chi-square tests revealed a difference between diet and insect abundance, the Bonferroni multiple comparison procedure was performed for each insect order as a post-hoc comparison. A value of $P < 0.05$ was considered statistically significant. All analyses were performed in the R environment for statistical computing (R Development Core Team 2008).

Results

Diet composition

A total of 450 faecal pellets were examined. Throughout the survey period, fragments of eight insect orders were found in the faecal pellets of *V. sinensis*. In total, Lepidoptera (mean relative percentage: 32.8%), Diptera (27.5%) and Coleoptera (22.6%) had high frequencies of occurrence (Fig. 1). The proportion of each order varied with the sampling period ($\chi^2 = 175.0$, $df = 32$, $P < 0.01$; Fig. 1). Lepidoptera had the highest relative percentage (47.6%) in May, after which its relative percentage gradually decreased. From early June to early July, Diptera was the most frequently occurring (40.7–44.2%) prey order, although Lepidoptera also showed a high frequency of occurrence (22.2–36.0%). From the middle of July to early August, Coleoptera was the most frequently occurring (27.1–29.2%) prey order, although Lepidoptera still showed a high frequency of occurrence (25.2–28.3%). Fragments of Trichoptera were found throughout the survey period and showed a moderate frequency of occurrence (13.1% in the middle of June, 14.6% in the middle of July, 15.0% in late July and 11.3% in early August). In late July and early August, Hymenoptera showed a moderate frequency of occurrence (14.0% and 14.2%, respectively); however, they were found only

from the middle of July to early August. Hemiptera were found in pellets from the latter half of the survey period, and the frequency of occurrence (9.3%) peaked in late July. Fragments of Ephemeroptera were found only in the middle of June and late June, and the frequency of occurrence was 5.1% and 2.3%, respectively. Neuroptera fragments were found only rarely in the middle of June and early August, with a frequency of occurrence of 1.0% and 0.9%, respectively.

Insect abundance

A total of 27,417 individuals from 10 orders were collected using light traps. Among the 10 orders, two orders (Orthoptera and Psocoptera) were excluded from our results because these two orders were rare (56 individuals) and not found in faecal pellets. No large insects, such as stag beetles, that would obviously not be available as prey for *V. sinensis*, were captured in this study.

There was a seasonal variation in the composition of insects ($\chi^2 = 266.6$, $df = 32$, $P < 0.01$; Fig. 2). In total, Diptera was the most abundant (mean relative proportion: 69.2%; Fig. 2). The relative proportion of Diptera was the highest in the middle of May (94.5%) and decreased gradually during the study period. In contrast, Coleoptera was not detected in the middle of May but increased gradually through the study period. Relative proportions of Lepidoptera varied from 4.6% to 43.2% with no distinct seasonal trend. Trichoptera was rare in the middle of May (relative proportion, 0.9%), but increased gradually until peaking in late June (15.5%). Hymenoptera and Hemiptera were relatively rare, but had a moderate frequency of occurrence (10.0% and 14.7%, respectively) in late July. Ephemeroptera were rare with frequencies of occurrence of 0.1% to 0.8% from early July to early August. Neuroptera were also rare with a frequency of occurrence of 0.1% from the

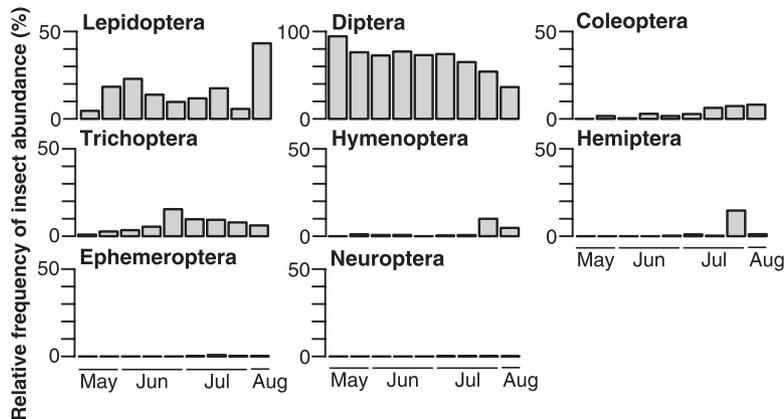


Fig. 2. Relative percentage of individuals of each insect order caught by light traps. Relative percentages were calculated by dividing the abundance of each insect order by the total insect abundance.

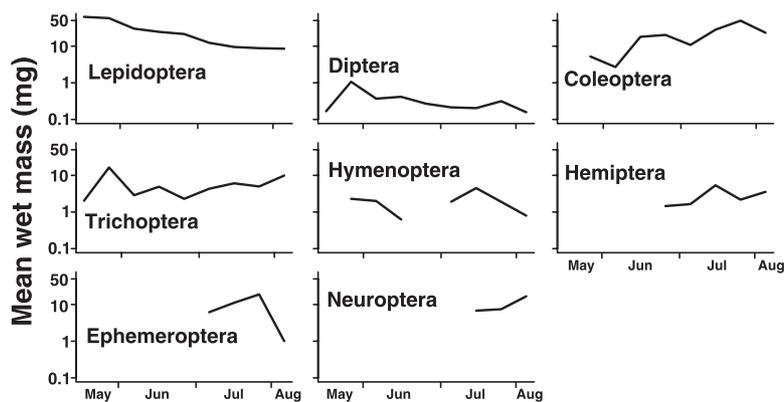


Fig. 3. Seasonal changes in mean wet mass per individual of each insect order caught by light traps. Data when no individual was caught are not shown.

middle of July to early August.

Mean wet mass per individual of Lepidoptera was the highest among the eight orders from May to early July (Fig. 3). From the middle of July, Coleoptera had the highest mean wet mass per individual, while that of Lepidoptera was still higher than most of the other orders. In contrast, mean wet mass per individual of Diptera was the lowest throughout the study period (Fig. 3). The other five insect orders had intermediate mean wet mass, except for Trichoptera in late May, Ephemeroptera in late June and Neuroptera in early August (Fig. 3).

Comparison between diet and insect abundance

The results of post-hoc comparisons showed that the relative proportion of Diptera in the diet was significantly lower than that in insect abundance throughout the survey periods (Table 1). In contrast, the proportion of Coleoptera in the diet was significantly higher than that in insect abundance throughout the survey period (Table 1). For Lepidoptera, the proportion in the diet was significantly higher than that in insect abundance in the middle of May, late May, late June, early July and late July, but not significantly different in other survey

periods (Table 1). For the remaining insect orders, there were no significant differences in proportions between diet and insect abundance throughout the survey periods (Table 1).

Discussion

Numerous studies have assessed prey selectivity of bats in the field (e.g., Barclay 1985; Swift et al. 1985; Brigham 1990; Schultz 2000; Burles et al. 2008). In these studies, comparison between diet composition and insect abundance (resource availability) have been based on the assumption that these data were sampled without bias. However, Kunz (1988) and Whitaker (1995a) both suggested that data on resource availability should be viewed with great caution. There are no satisfactory methods of capture for assessing availability of insects to insectivorous bats (Kunz 1988). Bats feed in areas that cannot be sampled by most insect traps, and even if traps can be used, the insect species that are captured are biased by the types of traps. Moreover, some insects may not be "available" to bats. For example, detectable insect size is restricted by echolocation call structure

Table 1. Results from post-hoc comparison after chi-squared tests comparing diet composition with insect abundance collected by light traps

	May		June			July			August
	Middle	Late	Early	Middle	Late	Early	Middle	Late	Early
Lepidoptera	+	+	n.s.	n.s.	+	+	n.s.	+	n.s.
Diptera	–	–	–	–	–	–	–	–	–
Coleoptera	+	+	+	+	+	+	+	+	+
Trichoptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hymenoptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hemiptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ephemeroptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Neuroptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

+ or –: significantly higher or lower proportion in the diet, respectively ($P < 0.05$). n.s.: not significant.

(Jones and Rydell 2003; Houston et al. 2004), and some insect taxon have evolved ears that enable them to detect bat echolocation calls and avoid capture (Corcoran et al. 2009). In the present study, we compared diet composition with relative insect abundance on the basis of assumption that our insect data reflected the whole flying insect community structure (not availability) around the roost.

Vespertilio sinensis fed mainly on Lepidoptera, Diptera and Coleoptera throughout the survey period and moderately consumed Trichoptera (Fig. 1). In addition, Hymenoptera was consumed moderately in late July and early August. These results are quite different from those reported by Funakoshi and Uchida (1981), who found that prey items of this species (described as *V. superans superans*) in August included Coleoptera (86%), Lepidoptera (5%) and others (9%). Such intra-species variation in diet composition has been shown in several bat species (*Eptesicus nilssonii*: Rydell 1986, *Vespertilio murinus*: Rydell 1992, *Eptesicus fuscus*: Whitaker 1995b; Agosta and Morton 2003, *Pipistrellus abramus*: Hirai and Kimura 2004), and these differences might reflect variations in local insect abundance (Belwood and Fenton 1976; Whitaker 1995b). The maternity roost studied by Funakoshi and Uchida (1981) was situated on a small rocky island surrounded by ocean in Fukuoka prefecture (33°40'N, 130°13'E), 1380 km south-west from our study site, and was located in a warm-temperate zone, whereas our study area was located in a cool-temperate zone. It is likely that major differences between our results and Funakoshi and Uchida (1981) were caused by differences in habitat environment, which may influence insect community structure. Although Funakoshi and Uchida (1981) did not survey insect abundance, it is possible that Coleoptera

was more abundant in the feeding area of the bat population they studied. In contrast, Coleopteran abundance was relatively low at our study site (Fig. 2).

According to the results of chi-square tests, for three insect orders (Lepidoptera, Diptera and Coleoptera) proportions in the diet were significantly different from the proportions of those orders in insect abundance. Proportions of Coleoptera and Lepidoptera in the diet were larger than those in insect abundance, except for Lepidoptera in early June, the middle of June, the middle of July and early August (Table 1). In contrast, proportions of Diptera in the diet were lower than those in insect abundance (Table 1). Of these three orders, Coleoptera and Lepidoptera generally tended to have higher proportions of large-sized species, whereas Diptera tended to contain small-sized species (Siemann et al. 1996, 1999). In fact, our results using light traps showed that the mean wet mass per individual was highest for Coleoptera and Lepidoptera, and lowest for Diptera (Fig. 3). In general, numbers of individuals have unimodal relationships with body size within each taxonomic order (Siemann et al. 1996, 1999). Therefore, although size dispersion is unknown because we did not measure the wet mass of individuals, it is likely that Coleoptera and Lepidoptera in our study area contain large-sized individuals compared to Diptera and other orders.

It is possible that high frequencies of occurrence of Coleoptera and Lepidoptera, which tend to contain large-sized species, were influenced by the echolocation call frequency of *V. sinensis*. According to the theoretical relationship between prey size and call frequency predicted by the Rayleigh effect, low frequency ultrasound (20–30 kHz) reflects poorly from small insects (<5.0 mm wing length; Houston et al. 2004). Thus, bats emitting low-frequency calls are unable to detect and consume

small insects. *Vespertilio sinensis*, which emits low-peak frequency calls (24.2 kHz, Fukui et al. 2004), is also thought to be unable to detect and consume small insects. This may be one reason why Lepidoptera and Coleoptera were consumed more frequently than Diptera.

Despite the prediction mentioned above, Diptera, which tend to contain small-sized species, were also frequently found in faecal pellets, especially in June (Fig. 1); however, relative proportions in the diet were lower than those in insect abundance (Table 1). Rydell (1992) found a high proportion of Chironomidae in faecal pellets from *V. murinus*, which is slightly smaller than *V. sinensis*. Further, several studies have shown that bats with low-frequency calls often feed on smaller prey than theoretically predicted (Rydell 1986; Jones 1995; Waters et al. 1995). With regard to the reasons, Jones and Rydell (2003) suggested the following two possibilities: (1) swarming prey may increase their conspicuousness both visually and acoustically and (2) bats may have flexible echolocation behaviour and sometimes make use of higher frequencies than normal. In addition, because we could not account for prey size, it is possible that *V. sinensis* consumed only large-sized Diptera as theoretical work by Houston et al. (2004) would suggest. In any case, our results showed that Diptera is one of the important prey categories for *V. sinensis* in addition to Lepidoptera and Coleoptera.

For the other five orders, there were no significant differences between diet composition and insect abundance. Hymenoptera and Hemiptera were found in both faecal pellets and light traps, mainly in the latter half of the survey period (Figs. 1 and 2). Ephemeroptera and Neuroptera were rarely found in both faecal pellets and light traps (Figs. 1 and 2). These results suggested that the diet composition of *V. sinensis* is not only biased towards larger sized taxa, but is also influenced by the seasonal prevalence of each insect order.

Our study revealed that *V. sinensis* consume diverse taxa of insects. The main insect orders Lepidoptera, Diptera and Coleoptera included many species of hygiene and agricultural pests. Funakoshi and Uchida (1981) estimated that daily food intake of lactating females of this species is about 6.4 g (ca. 36% of pre-feeding body weight). Our study roost, which consisted of more than 1000 individuals every year, is located in a small patch of forest, which is surrounded by extensive agricultural fields. If this species uses these agricultural fields as a feeding habitat, their ecological function in the agricultural ecosystem might be as influential as has been

shown for other insectivorous bat species (Cleveland et al. 2006; Federico et al. 2008; Williams-Guillén et al. 2008). In this case the conservation and management of *V. sinensis* in the study area is important for economic reasons. Further studies of factors such as population dynamics, feeding habitat and alternative artificial roosts (i.e. bat boxes) are needed to determine appropriate management measures.

Acknowledgments: We thank K. Okazaki for his kind help with the identification of insects. We are grateful to M. Miyazaki and the members of Centennial Woods Fan Club for their assistance in the field and to T. Aoi, K. Maeda, K. Funakoshi and members of Tomakomai Experimental Forest, Hokkaido University for their encouragement and valuable comments. We are sincerely grateful to Dr. David A. Hill for his helpful English proofreading. We also thank two anonymous referees for their useful comments. This work was partly supported by a Grant-in-Aid for JSPS Fellow (PD6525 to DF).

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Received 9 March 2010. Accepted 23 July 2010.