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Diet of three sympatric insectivorous bat species on Ishigaki Island, Japan

Dai Fukui[1,*], Katsunori Okazaki[2], Kishio Maeda[3]

[1]JSPS Research Fellow, Hokkaido Research Center, Forestry and Forest Products Research Institute,
Hitsujigaoka-7, Toyohira, Sapporo, Hokkaido 062-8516, Japan
[2]Natural History Museum Kutchan, Kita-6, Higashi-7, Kutchan, Hokkaido 044-0006, Japan
[3]Nara University of Education, Takabatake-cho, Nara 630-8528, Japan

ABSTRACT: We determined the food habits of 3 sympatric species of insectivorous bats (*Rhinolophus perditus*, *Hipposideros turpis* and *Miniopterus fuscus*) from May 2001 to January 2003 on Ishigaki Island, in the Ryukyu archipelago, Japan, by analysing their faecal samples. We also measured wing morphology of these 3 species and assessed insect abundance near the roost. Diet composition differed between the 3 bat species throughout the survey period, except between *R. perditus* and *M. fuscus* from July to November 2002. *R. perditus* mainly consumed Coleoptera, Diptera, Lepidoptera and Hymenoptera, and the proportion of consumption of these insect orders changed seasonally. *H. turpis* mainly consumed Coleoptera from spring to summer. A large amount of *Anomala albopilosa* in particular seemed to be consumed. *M. fuscus* frequently consumed Diptera, Lepidoptera and Hymenoptera throughout the study period and Coleoptera in summer. Our results indicate resource partitioning between each species of bats; this partitioning may be caused by morphological differences between the 3 species of bats, which may result in different passive prey selection. Because of the variation in diet composition, habitats that maintain high insect diversity are required for bat assemblage. In the future, the preferred foraging habitats of the 3 species of bats should be studied, and the results of these studies should be combined with our results for establishing an appropriate conservation measure.

KEY WORDS: Food habit · Chiroptera · Endangered species · Conservation · Functional traits

INTRODUCTION

Insectivorous bats exhibit high species diversity (Simmons 2005). Quite often, multiple species are foraging sympatrically. Such coexisting bat species frequently differ in resource use in at least 1 niche dimension and thus avoid competition (Saunders & Barclay 1992, Arlettaz et al. 1997, Nicholls & Racey 2006). Several studies on mechanisms of resource partitioning have shown that differences in ecomorphological traits such as wing shape, body size and sensory cues are associated with differences in the access of bat species to food (Aldridge & Rautenbach 1987, Hickey et al. 1996, Swift & Racey 2002, Lee & McCracken 2004, Ma et al. 2004, Siemers & Schnitzler 2004, Zhang et al. 2005, Siemers & Swift 2006). An understanding of diet of sympatric insectivorous bats is necessary to explain the patterns of habitat use and resource partitioning and to predict how major changes in invertebrate communities associated with habitat manipulation will affect bat assemblage.

In the Ryukyu archipelago, which is located in the southern Japanese archipelago, 5 out of 9 microchiroptera species, except incidental species, are endemic to the area (Abe et al. 2005) and are mostly restricted to the remaining intact forests that are under pressure from other land uses (Ministry of Environment 2002). In fact, the island population of *Rhinolophus pumilus* on Miyako Island (treated as *R. p. miyakonis* by Yoshiyuki [1989] or *R. cornutus* by Simmons [2005]), where almost all forest lands have been converted to agricultural fields, is considered to be extinct because there has been no record of this species since 1971 (Abe et al. 2005).

In most parts of the Yaeyama Islands, southern Ryukyu archipelago, only 3 microchiropteran bat species, namely, the lesser leaf-nosed bat *Hipposideros turpis*, the Yaeyama least horseshoe bat *Rhinolophus perditus* and the southeast Asian long-fingered bat *Miniopterus fuscus*, are found and frequently use the caves together (Abe et al. 2005). *H. turpis* (average forearm length [FA]: 65 to 70 mm; Yoshiyuki 1989) is the northernmost species of the family Hipposideridae distributed only on the Yaeyama Islands, but it is thought that synonymous species are also distributed in south Thailand and Vietnam (Simmons 2005). *R. perditus* (FA: 40 mm; Yoshiyuki 1989) is a small Rhinolophidae species distributed only on the Yaeyama Islands. *M. fuscus* (FA: 44 mm; Yoshiyuki 1989) is also an endemic vespertilionid species distributed in the Ryukyu archipelago. All 3 species are listed as endangered species (EN) in the Japanese Red List (Ministry of Environment 2002). *H. turpis* and *M. fuscus* are also listed as Endangered and Vulnerable (VU) species, respectively, in the International Union for Conservation of Nature (IUCN) Red List (Hutson et al. 2001). Several caves for breeding and hibernating are known to exist on Ishigaki Island. However, in recent years, deforestation, roost destruction and tourism activities are creating serious problems for the island bat population. Therefore, conservation measures have to be established immediately. However, no ecological requirements, including the diet, of all the 3 species have been studied yet. The aim of the present study was to generate information on the diet of these 3 sympatric insectivorous bat species; these data can serve as background information for conservation measures.

MATERIALS AND METHODS

Study site. The study was conducted on Ishigaki Island, which is one of the southernmost islands in the Japanese archipelago (24° 20′ 4″ N, 124° 9′ 22″ E; Fig. 1), and has an area of 222.6 km². This island has a subtropical climate. The maximum, minimum and annual mean air temperatures are 34.7, 11.7 and 25.3°C, respectively. The annual precipitation is approximately 2000 mm.

On the island, there are many limestone caves and air-raid shelters from World War II, which are used by cave-dwelling bats. The nameless limestone cave (Cave A) and air-raid shelter (Shelter A) that we studied are located on the east side of the island, and the distance between the 2 roosts is approximately 5 km. Among the 3 species of insectivorous bats, *Rhinolophus perditus* and *Hipposideros turpis* roost in Cave A throughout the year but not in Shelter A. During the study period, the roosting population size of these 2 species was approximately 10 to 2100 and 10 to 450 ind., respectively. *Miniopterus fuscus* roosts in both Cave A and Shelter A. During the study period, *M. fuscus* used Cave A throughout the year, but used Shelter A from autumn to spring. The movements of *M. fuscus* between the 2 roosts were confirmed. The population size of *M. fuscus* was approximately 10 to 450 and 0 to 700 ind. at Cave A and Shelter A, respectively. Forest, sugarcane field and grassland are distributed in patches within a 3 km radius around the cave and air-raid shelter.

Insect abundance. We used malaise traps (height × length × width: 1 × 1 × 1 m; made of 0.5 mm mesh) to determine the approximate relative abundance of flying insects in the field at sites adjacent to Cave A
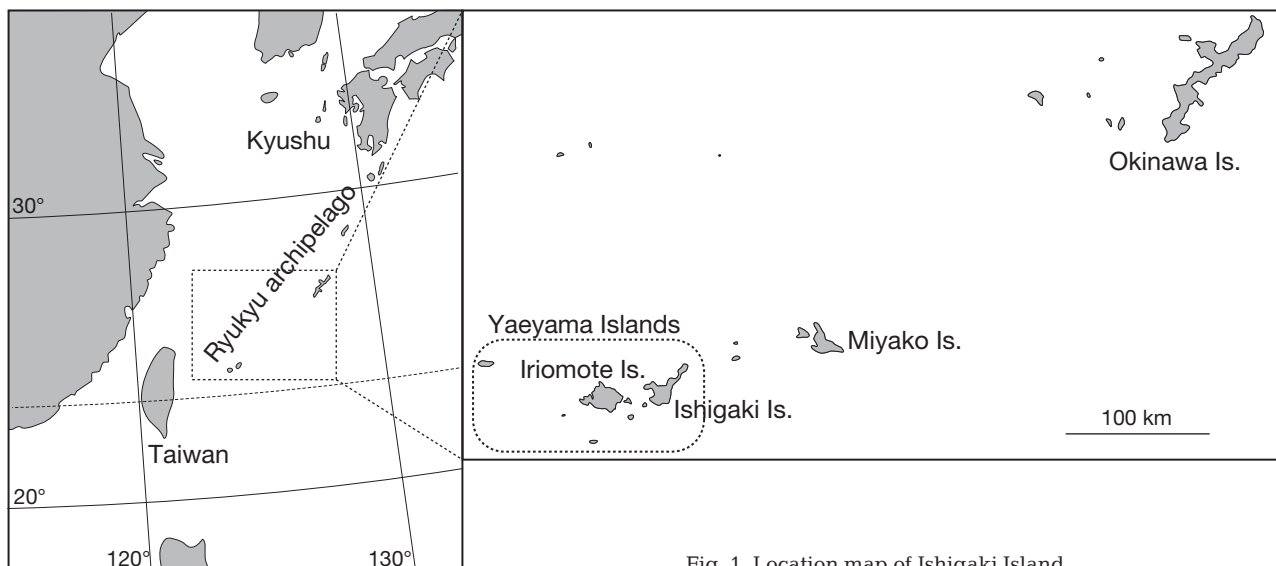

Fig. 1. Location map of Ishigaki Island

(< 200 m). These malaise traps consisted of 4 mesh panels (100 × 50 cm) assembled in a cross configuration. Insects were collected on 3 consecutive nights around the days when we collected faecal samples in 2002 and 2003. Each night from sunset to sunrise, we set up 9 traps at 9 trapping sites — 3 in grassland and 6 in the interior of natural broad-leaved forest dominated by *Trema orientalis*, *Pandanus odoratissimus* and *Oreocnide fruticosa* — at a height of 1.5 m. All trapping sites were fixed throughout the study periods. Samples collected in the malaise traps were preserved in 70% ethanol until analysis. Insect samples were identified to the level of order by using a 10× binocular microscope. Subsequently, the wet mass of each order was measured to the nearest 0.01 mg by using an electronic balance.

Diet analysis. For diet analysis, we collected faecal pellets from the caves or air-raid shelter every 1 or 2 mo throughout the survey period from May 2001 to January 2003 (May, June, July, August, October and November in 2001; January, March, May, June, July, September and November in 2002; January in 2003).

We could collect faecal pellets of *Rhinolophus perditus* in each survey month, except November 2001 and January and March 2002, when this species was hibernating. Faecal pellets of *Hipposideros turpis* were collected in each survey month, except January and March 2002 and January 2003, when this species was hibernating. In 2001, faecal pellets of *Miniopterus fuscus* were collected only in October, because this species formed colonies at inaccessible places in other months of this year. However, in 2002, we could collect

faecal pellets of *M. fuscus* in each survey month, except January and March 2002, when this species was hibernating.

Before collecting faecal pellets, we placed a plastic mesh sheet on the cave floor under the colonies of each bat species. We then collected 50 fresh faecal pellets on the next day and air-dried them for subsequent analysis. Each faecal pellet was tested separately after approximately 12 h in 10% KOH, and food items in the pellets were identified to the lowest possible taxonomic level — mostly to the level of order — by using a 40× binocular microscope. Because it is difficult to measure the relative volume of each item, the relative frequency of occurrence of different categories of prey was estimated for each sampling period and bat species.

Wing morphology. According to the method of Aldridge & Rautenbach (1987), we measured wing loading, the aspect ratio and the wingtip shape index of each bat species. These parameters were measured using a preserved specimen from Nara University of Education. The right or left half of the ventrally recumbent specimen with its wing fully extended was photographed against white paper next to a centimetre scale using a digital camera. Measurements of the wing area were performed on a Macintosh computer by using the public domain NIH image program. We excluded any specimens for which a record of body weight was not available, since this was required to calculate wing loading. The sample size for which wing morphology was measured for each species was 9, 2 and 7 for *Rhinolophus perditus*, *Hipposideros turpis* and *Miniopterus fuscus*, respectively.
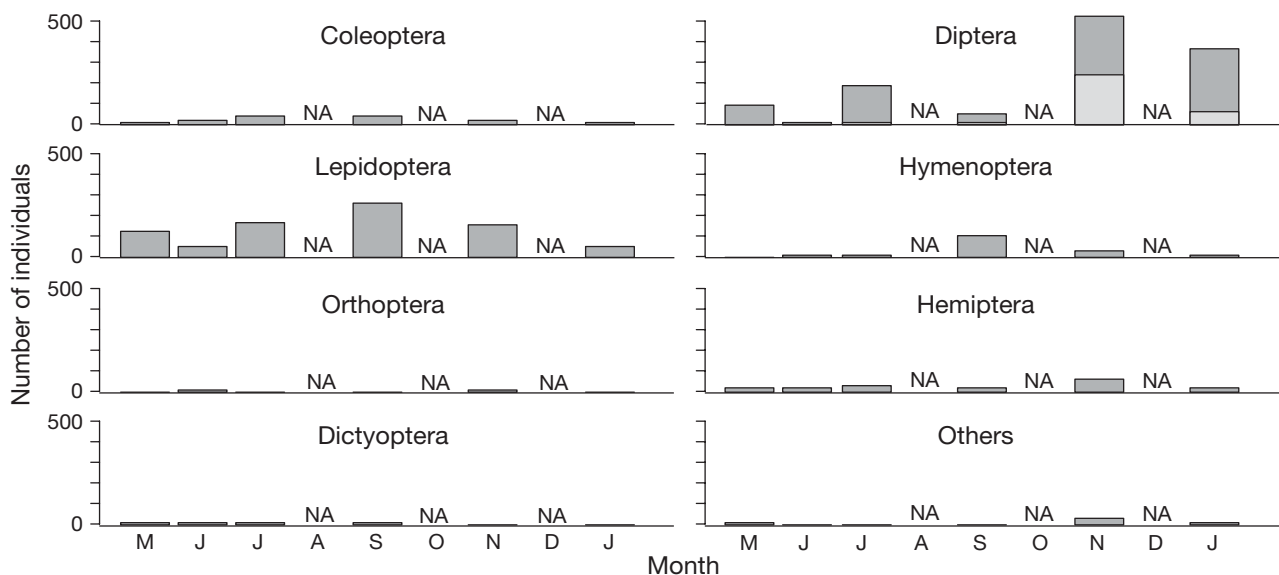

Fig. 2. Number of individuals of each insect order caught by malaise traps at forest sites. Pooled data of 6 traps in each survey period (3 consecutive nights) are shown. Light-coloured bar in Diptera represents Chironomidae. NA: no sampling
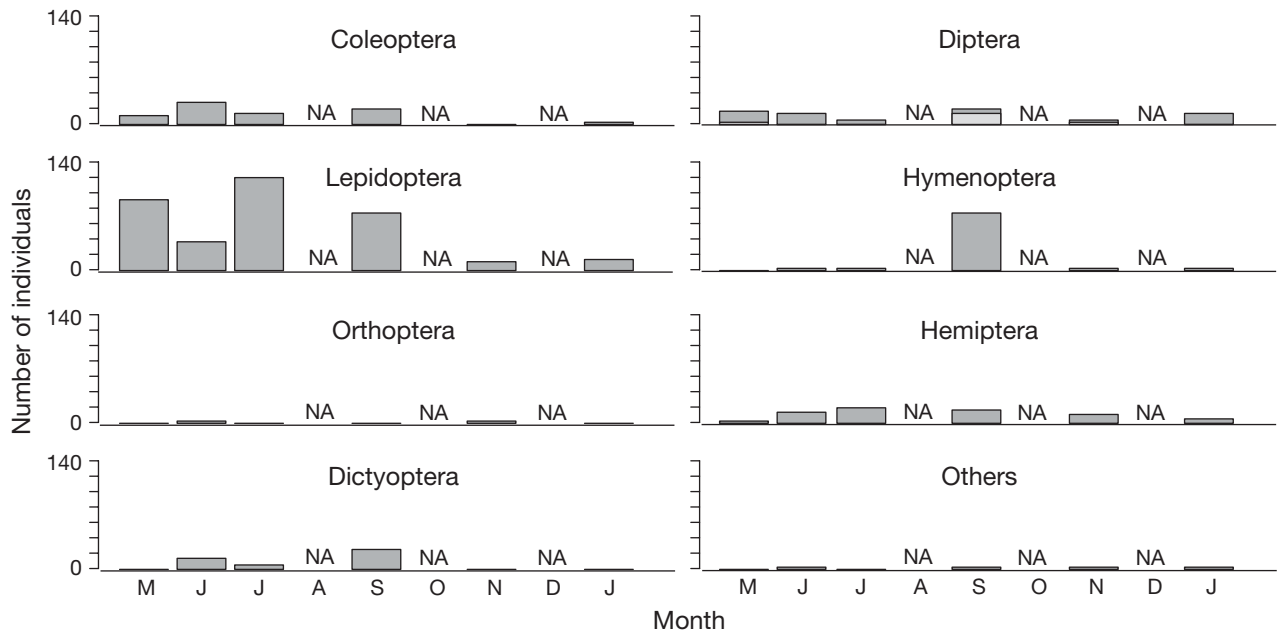
Fig. 3. Number of individuals of each insect order caught by malaise traps at grassland sites. Pooled data of 3 traps in each survey period (3 consecutive nights) are shown. Light-coloured bar in Diptera represents Chironomidae. NA: no sampling

Fig. 4. Wet mass of each insect order caught by malaise traps at forest sites. Pooled data of 6 traps in each survey period (3 consecutive nights) are shown. NA: no sampling

Statistics. Chi-squared tests were used to compare dietary composition between each bat species and to compare dietary composition with insect abundance. All analyses were performed in the R environment for statistical computing (R Development Core Team 2008) with an R program 'Resource Selection Programs' created by Okamura et al. (2004).

RESULTS

Insect abundance

A total of 11 and 9 insect orders were collected at forest sites and grassland sites, respectively (Figs. 2, 3, 4 & 5, Appendix 1, available as supplementary
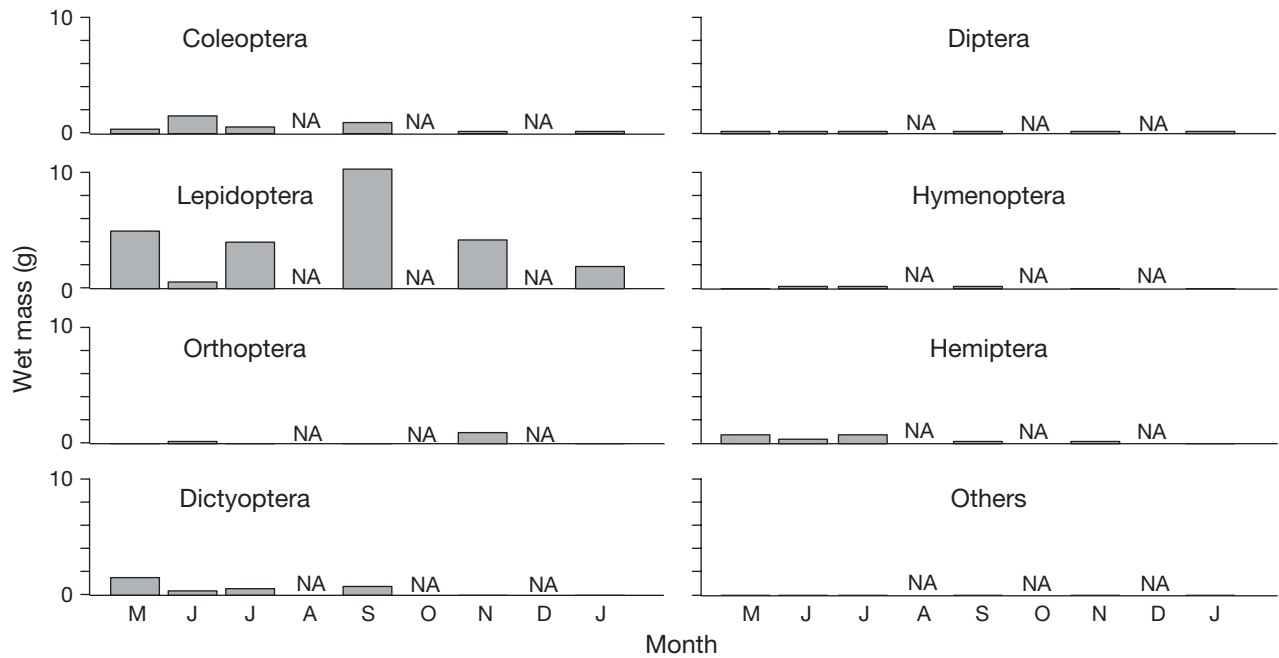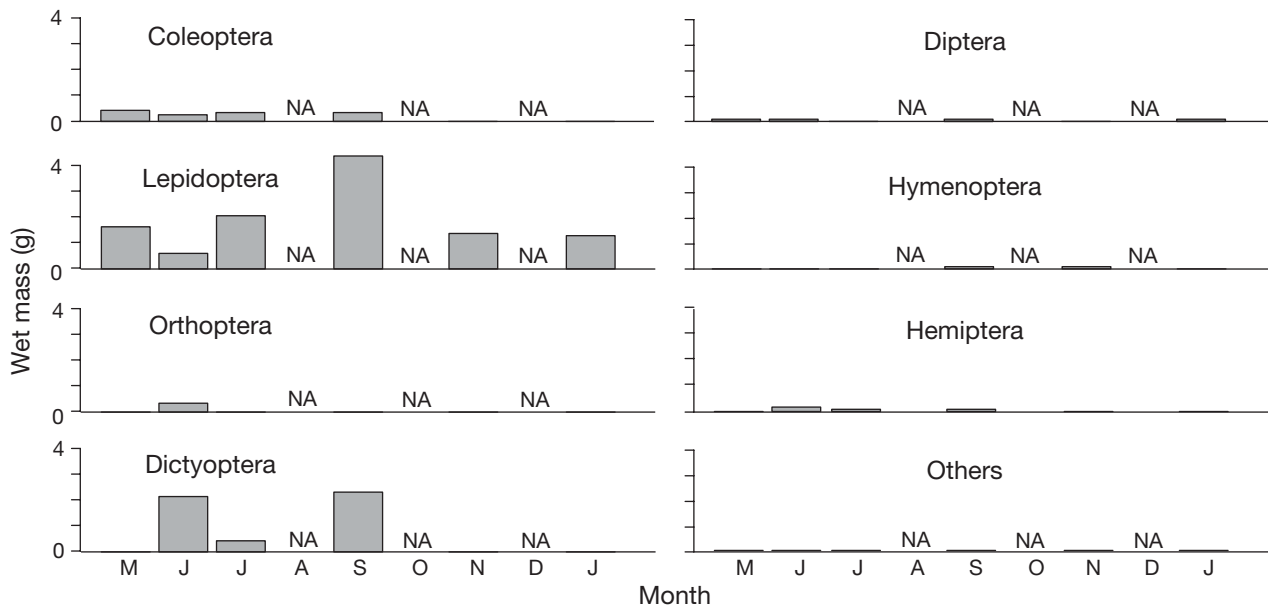
Fig. 5. Wet mass of each insect order caught by malaise traps at grassland sites. Pooled data of 3 traps in each survey period (3 consecutive nights) are shown. NA: no sampling

material at: www.int-res.com/articles/suppl/esr00156_app.pdf). In terms of the total number of individuals collected throughout the survey periods, Diptera was the most abundant at forest sites, but Lepidoptera was the most abundant at open sites. In contrast, in terms of the total volume (wet mass) collected throughout the survey periods, Lepidoptera was the most abundant at both forest and open sites. There was a seasonal variation in the composition of insects; for example, in terms of volume, Coleoptera was abundant from May to September at both forest and open sites, while Lepidoptera was the most abundant in August at both forest and open sites. Almost all Chironomidae were caught in November and January at forest sites.

Diet of *Rhinolophus perditus*

Throughout the survey period, fragments of 9 arthropod orders were found in the pellets of *Rhinolophus perditus* (Appendix 2, available as supplementary material at: www.int-res.com/articles/suppl/esr00156_app.pdf). Many Diptera were identified to belong to Chironomidae species. Coleoptera; Diptera, including Chironomidae; Lepidoptera; and Hymenoptera had a high frequency of occurrence (nearly 20% or more). However, the proportion of each order varied with the survey month and year. In 2001, Coleoptera had a high frequency of occurrence in pellets throughout the survey months; Lepidoptera, from May to July; Chironomidae, from June to August; and other Diptera and Hymenoptera, in October. In 2002 and 2003, Lepidoptera

had a high frequency of occurrence in pellets throughout the survey months; Coleoptera, from May to November; Chironomidae, in January; other Diptera, from June to November; Hymenoptera, from July to January; and Trichoptera, in June (Fig. 6).

Dietary composition of *Rhinolophus perditus* from May 2002 to January 2003 was compared with insect abundance at forest sites, because the results of wing morphology showed that *R. perditus* is suspected to forage in cluttered spaces (described below in 'Wing morphology'). Additionally, the results sometimes vary depending on which index of abundance ('number of individuals' or 'wet mass') is used. In the present study, we treated results as 'significant' only when both results were the same. The results of chi-squared tests showed that *R. perditus* consumes Coleoptera more frequently than the proportion of these insects in insect abundance in May, July and November; other Diptera, in June and September; Hymenoptera, in July and November; and Trichoptera, in June. On the other hand, Lepidoptera seems to be eaten less frequently in September; Hemiptera, in June and from September to January (Table 1).

Diet of *Hipposideros turpis*

Throughout the survey period, fragments of 12 arthropod orders were found in the pellets of *Hipposideros turpis* (Appendix 3, available as supplementary material at: www.int-res.com/articles/suppl/esr00156_app.pdf). In Coleoptera, the scarab beetle
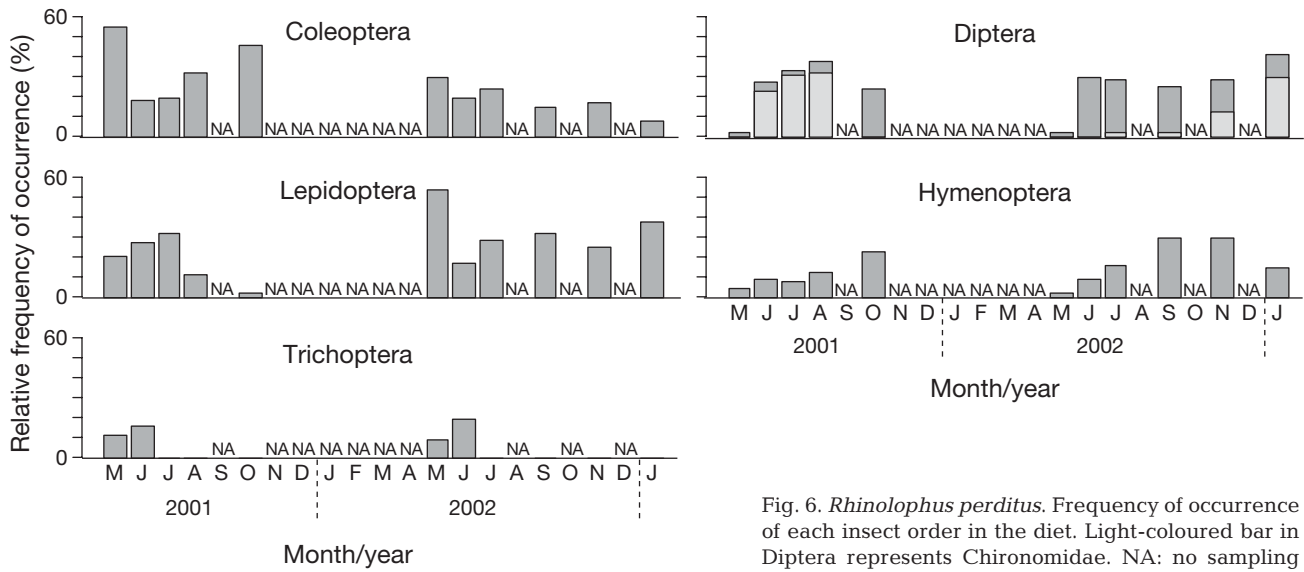
Fig. 6. *Rhinolophus perditus.* Frequency of occurrence of each insect order in the diet. Light-coloured bar in Diptera represents Chironomidae. NA: no sampling

Anomala albopilosa was identified. Coleoptera, including *A. albopilosa*, had a high frequency of occurrence. However, the proportion of each order varied with the survey month and year. *A. albopilosa* was the most abundant species according to the relative per-

Table 1. *Rhinolophus perditus.* Results from chi-squared tests comparing diet composition with insect abundance at the forest site in each survey period. +: significantly (p < 0.05) more frequently consumed than proportions of these insect taxon in insect abundance; –: significantly (p < 0.05) less frequently consumed than proportions of these insect taxon in insect abundance. Upper results in each period and for each taxon show the comparison between diet composition and number of individual insects. Lower results show the comparison between diet composition and wet mass of insects

			2002			2003
	May	Jun	Jul	Sep	Nov	Jan
Coleoptera	+	–	+		+	
	+		+		+	
Chironomidae					+	+
					–	
Other Diptera		+	+	+	+	
	–	+	–	+	–	–
Hemiptera		–	–	–	–	–
			–	–	–	–
Lepidoptera			–	–	–	–
			–		–	+
Hymenoptera			+	+	+	+
			+		+	
Orthoptera						
Neuroptera						
Trichoptera		+				
		+				
Araneae						

centage occurrence from May to October or July in both 2001 and 2002, whereas no fragments of this species were found in faecal samples collected in other months. In September 2002, other species of Coleoptera were the most abundant. In November 2001 and 2002, Trichoptera was the most abundant, although Orthoptera also had a high frequency of occurrence (Fig. 7).

The dietary composition of *Hipposideros turpis* from May to November 2002 was compared with insect abundance at forest sites, because the results of wing morphology showed that *H. turpis* is suspected to forage in cluttered spaces (described below in 'Wing morphology'). The results of chi-squared tests showed that *H. turpis* consumes *Anomala albopilosa* more frequently than the proportion of these insects in insect abundance from May to July; other species of Coleoptera, in September; and Trichoptera, from July to November. On the other hand, Lepidoptera seems to be eaten less frequently throughout the survey periods; Hemiptera, in May and June (Table 2).

Diet of *Miniopterus fuscus*

Throughout the survey period, fragments of 8 arthropod orders were found in the pellets of *Miniopterus fuscus* (Appendix 4, available as supplementary material at: www.int-res.com/articles/suppl/esr00156_app.pdf). Lepidoptera, Hymenoptera and Diptera had a high frequency of occurrence. However, the proportion of each order varied with the survey month and year. Lepidoptera had the highest relative percentage occurrence from October 2001 to September 2002. In November 2002, however,
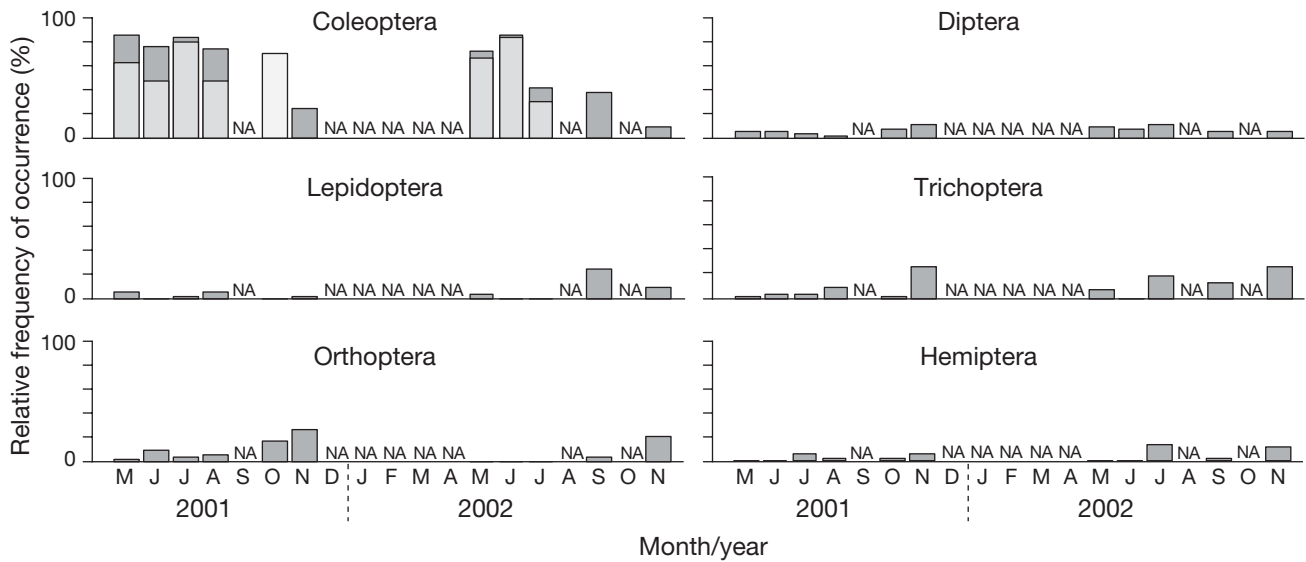
Fig. 7. *Hipposideros turpis.* Frequency of occurrence of each insect order in the diet. Light-coloured bar in Coleoptera represents *Anomala albopilosa*. NA: no sampling

Diptera was the most frequently occurring prey order, although Lepidoptera also showed a high frequency of occurrence. Moreover, in November 2002, 41.6% of Diptera were identified as Chironomidae, whereas no fragments of this family were found in faecal samples collected in other months. From October 2001 to September 2002, Diptera showed moderate frequency

Table 2. *Hipposideros turpis.* Results from chi-squared tests comparing diet composition with insect abundance at the forest site in each survey period. See Table 1 for symbol definitions

	2002				
	May	Jun	Jul	Sep	Nov
Anomala albopilosa	+	+	+		
	+	+	+		
Other Coleoptera			–	+	
				+	
Diptera	–				–
Hemiptera	–	–			
	–	–			
Lepidoptera	–	–	–	–	–
	–	–		–	
Hymenoptera			–	–	
Orthoptera					+
Neuroptera					
Trichoptera			+	+	+
			+	+	+
Araneae					
Odonata					
Lepidoptera (larvae)					
Blattaria					

of occurrence; furthermore, Hymenoptera showed moderate frequency of occurrence throughout the survey period. Orthoptera was found only in October 2001, although it had a relatively high frequency of occurrence in that month. Coleoptera showed moderate frequency of occurrence from May to July 2002 (Fig. 8).

The dietary composition of *Miniopterus fuscus* from May to November 2002 was compared with insect abundance at grassland sites, because the results of wing morphology showed that *M. fuscus* is suspected to forage in open spaces (described below in 'Wing morphology'). The results of chi-squared tests showed that *M. fuscus* consumes Hymenoptera more frequently than the proportion of these insects in insect abundance from May to July; other species of Diptera, in July. On the other hand, Lepidoptera seems to be eaten less frequently in July; Hemiptera, in July and September; and Chironomidae in November (Table 3).

Interspecies variation

Diet composition significantly differed between *Rhinolophus perditus* and *Hipposideros turpis* and between *H. turpis* and *Miniopterus fuscus* throughout the survey period (chi-squared test, p < 0.001; Table 4). On the other hand, diet composition significantly differed between *R. perditus* and *M. fuscus* in October 2001 and May and June 2002 (chi-squared test, p < 0.001), but it did not significantly differ from July to November 2002 (chi-squared test, p > 0.01; Table 4).
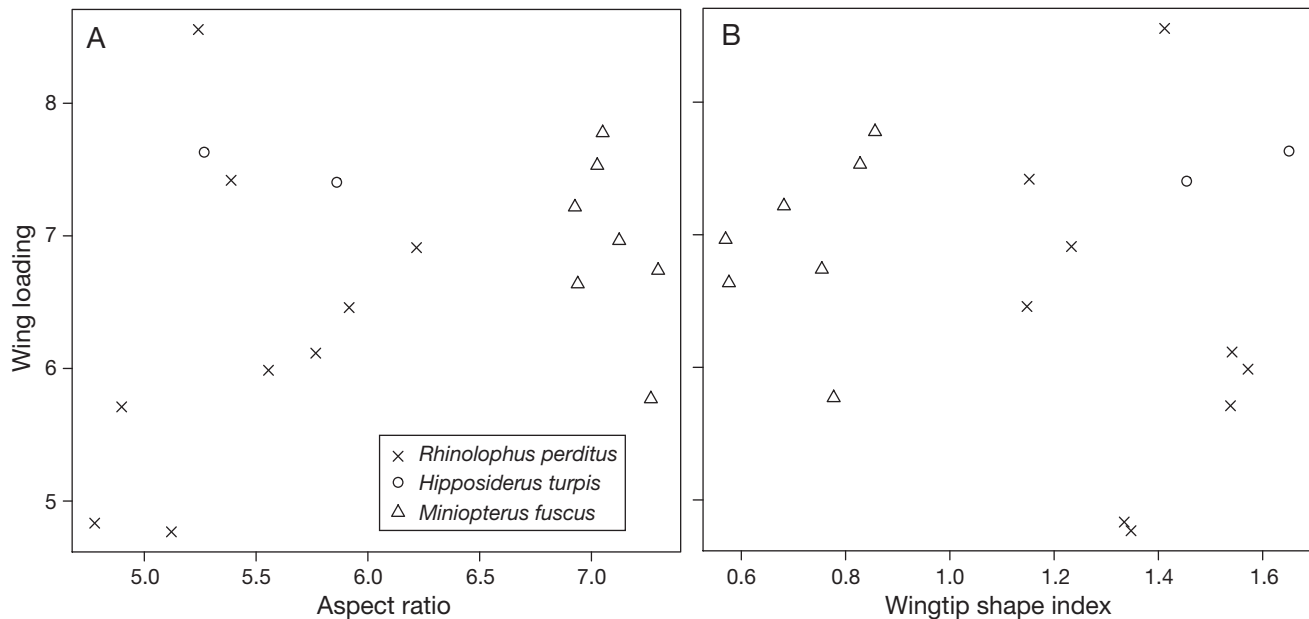
Table 3. *Miniopterus fuscus*. Results from chi-squared tests comparing diet composition with insect abundance at the grassland site in each survey period. See Table 1 for symbol definitions

	May	Jun	2002 Jul	Sep	Nov
Coleoptera					
Chironomidae				−	+
				−	
Other Diptera		+	+		+
			+		
Hemiptera		−		−	
		−	−	−	−
Lepidoptera		+	−		−
			−		
Hymenoptera	+	+	+	+	+
	+	+	+		
Orthoptera					
Neuroptera					
Psocodea					

Wing morphology

The aspect ratio of *Miniopterus fuscus* was higher than those of the other 2 species (*t*-test: $t = 8.80$, 9.09, df = 14, 7, respectively, $p < 0.05$), but there was no difference between *Rhinolophus perditus* and *Hipposideros turpis* ($t = 0.35$, df = 9, $p = 0.73$; Fig. 9A). The wingtip shape index of *M. fuscus* was lower than those of the other 2 species ($t = 8.78$, 8.74, df = 14, 7, respectively, $p < 0.05$), but there was no difference between *R. perditus* and *H. turpis* ($t = 1.48$, df = 9, $p = 0.17$; Fig. 9B). Whereas, there were no differences in wing loading between the 3 species (*R. perditus* and *H. turpis*: $t = 1.36$, df = 9, $p = 0.21$; *R. perditus* and *M. fuscus*: $t = 1.26$, df = 14, $p = 0.23$; *H. turpis* and *M. fuscus*: $t = 1.15$, df = 7, $p = 0.29$; Fig. 9).

Fig. 8. *Miniopterus fuscus*. Frequency of occurrence of each insect order in the diet. Light-coloured bar in Diptera represents Chironomidae. NA: no sampling

Table 4. Results from chi-squared tests comparing the diet between each bat species separately for each survey period. Prey categories that did not occur in the faeces of either of the 2 species in a given period were excluded from the chi-squared (chi-sq) test for that night (therefore, the degrees of freedom [df] differ between nights). November 2001 and January 2003 are not shown because diet of only 1 species was analysed. Rp: *Rhinolophus perditus*; Ht: *Hipposideros turpis*; Mf: *Miniopterus fuscus*. Bold print represents significant difference ($p < 0.001$)

		2001 May	Jun	Jul	Aug	Oct	2002 May	Jun	Jul	Sep	Nov
Rp × Ht	chi-sq	**68.85**	**90.78**	**109.93**	**81.87**	**105.19**	**53.65**	**75.86**	**89.18**	**51.77**	**98.37**
	df	**8**	**9**	**8**	**9**	**7**	**7**	**7**	**10**	**9**	**11**
	p	**0.0026**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Rp × Hf	chi-sq	–	–	–	–	**81.68**	22.62	32.18	6.5	10.29	14.06
	df	–	–	–	–	**5**	6	6	5	5	6
	p	–	–	–	–	**<0.0001**	0.0009	<0.0001	0.26	0.07	0.029
Ht × Hf	chi-sq	–	–	–	–	**97.52**	**53.87**	**63.54**	**75.89**	**46.71**	**89.43**
	df	–	–	–	–	**6**	**6**	**4**	**9**	**8**	**12**
	p	–	–	–	–	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**

Fig. 9. Scatterplot of aspect ratio and wing loading (A) and wingtip shape index and wing loading (B) of the 3 bat species

DISCUSSION

Dietary composition has been widely studied for many species of Rhinolophidae (Whitaker & Black 1976, Findley & Black 1983, Jones 1990, Funakoshi & Takeda 1998, Wei et al. 2006, Ma et al. 2008). In these studies, Lepidoptera was the most dominant prey for almost all Rhinolophidae species. In our study, Lepidoptera was the most abundant prey throughout the survey periods, but the other 3 orders (Coleoptera, Diptera and Hymenoptera) were also abundant, and the most dominant prey taxon varied with the survey periods (Fig. 6). However, although the proportion of each order in the diet of *Rhinolophus perditus* differs from that of other Rhinolophidae species, these 4 insect orders are also common prey of other Rhinolophidae species. Ma et al. (2008) discussed that the highly specialized ability for insect detection constrains Rhinolophidae to the consumption of these 4 insect orders. *R. perditus* can pick up the wing beats of their prey, even in echo-cluttered environments, by acoustic glints that are prey-specific modulations in the constant frequency component of the returning echo, which are induced by the alternating wing movements relative to the bats. Therefore, they can consume mainly nocturnal and actively flying insects such as Lepidoptera, Diptera, Coleoptera and Hymenoptera. The diet of *R. perditus* seems to be influenced by such echolocation characteristics.

Among the 4 insect orders that were abundant in the diet of *Rhinolophus perditus*, Coleoptera, Diptera and Hymenoptera were consumed more frequently than

the proportions of these insects in insect abundance (Table 1). We cannot explain the exact mechanisms behind prey selection, because all insect capture methods are biased towards catching insects of a certain size, mass, or flight behaviour (Muirhead-Thomson 1991), and it is difficult to estimate the accurate abundance of insect community. However, it seems quite probable that Coleoptera, Diptera and Hymenoptera are important resources for *R. perditus*.

In the present study, the remains of Diptera in the pellets of *Rhinolophus perditus* were frequently identified to belong to adult Chironomidae, but the frequency of occurrence varied with the survey period. In 2001, Chironomidae was frequently consumed in summer. On the other hand, in 2002 and 2003, it was consumed in November and January (Appendix 2). During these periods, Chironomidae was also frequently captured by malaise traps (Appendix 1). The emergence season of Chironomidae varies with species and year (Armitage 1995). Although insect abundance in 2001 was not surveyed, there is a possibility that *R. perditus* forage on Chironomidae positively in the season of their emergence.

Although there is no information on the diet of *Hipposideros turpis*, the diets of several Hipposideridae species have been studied previously (Whitaker & Black 1976, Vaughan 1977, Findley & Black 1983, Aldridge & Rautenbach 1987, Eckrich & Neuweiler 1988, Zubaid 1988, Jones et al. 1993, Pavey & Burwell 1997, 2000, Bowie et al. 1999, Pavey et al. 2001, Razakarivony et al. 2005, Li et al. 2007, Rakotoarivelo et al. 2007). These previous investigations have revealed

that Lepidoptera (moths) or Coleoptera (beetles) or both dominate in the diet of hipposiderid bats. In our study, Coleoptera was the most frequently occurring prey order from May to October (Fig. 7). According to previous studies, almost all hipposiderid bats that consume mainly Coleoptera seem to be larger species (Vaughan 1977, Aldridge & Rautenbach 1987, Eckrich & Neuweiler 1988, Zubaid 1988, Pavey & Burwell 1997, Razakarivony et al. 2005, Rakotoarivelo et al. 2007; but see Jones et al. 1993). In bats, larger species tend to have higher bite force (Aguirre et al. 2002). Because of the variation in prey hardness, bite performance influences the diet composition of bats (Aguirre et al. 2003). This trend is more pronounced in high duty cycle bats (Rhinolophidae and Hipposideridae; Bogdanowicz et al. 1999). Our results are in agreement with this trend.

The scarab beetle *Anomala albopilosa* in particular dominated the diet of *Hipposideros turpis* from May to October and in July in both 2001 and 2002 (Fig. 7). *A. albopilosa* is a middle-sized beetle (17 to 22 mm), and its adult emerges from May to August on Miyako Island, which is adjacent to Ishigaki Island (Higa et al. 1978). However, no *A. albopilosa* individuals were collected in our study by using malaise traps. As mentioned earlier, it is difficult to estimate the accurate abundance of insects. In this instance, it is possible that our malaise traps are not suited to capture *A. albopilosa* or that *A. albopilosa* does not use habitats where we set traps. The former possibility is more feasible because adult *A. albopilosa* feed on a broad range of leaves, including tree species around our traps. Therefore, we cannot draw conclusions on prey selection based on our results. However, it seems quite probable that *H. turpis* positively selects and consumes a large amount of *A. albopilosa* in summer, and this beetle species is an important resource for *H. turpis*. The high degree of dependence on *A. albopilosa* in summer implies that *H. turpis* is more likely to be affected by changes in insect composition (i.e. through land use change). Moreover, Trichoptera and Orthoptera are also important resources because these orders were consumed more frequently than their proportion in insect abundance after depletion of Coleoptera (Table 2).

The larva of *Anomala albopilosa* is one of the most serious sugar-cane pests in the Ryukyu archipelago, and, sometimes, a heavy infestation with larval *A. albopilosa* occurs (Teruya et al. 1977). Therefore, a high proportion of *A. albopilosa* in the diet of *Hipposideros turpis* from May to October and July raises the possibility that *H. turpis* might play an important role in controlling the pest population on the island.

The diets of several *Miniopterus* species have been studied previously at various places (Whitaker & Black 1976, Findley & Black 1983, Funakoshi & Takeda 1998, Razakarivony et al. 2005, Rakotoarivelo et al. 2007); however, there is still a lack of information on the diet of *M. fuscus*. The diet composition of *Miniopterus* species varies with the study. In Zambia, *M. schreibersii* consumes Isoptera, Lepidoptera and Coleoptera (Whitaker & Black 1976, Findley & Black 1983). In Madagascar, *M. manavi* consumes mainly Lepidoptera, Coleoptera and Hemiptera (Rakotoarivelo et al. 2007). In Kyushu, Japan, Lepidoptera, Diptera and Trichoptera are the dominant prey items of *M. fuliginosus* (Funakoshi & Uchida 1975, Funakoshi & Takeda 1998). Compared to these studies, our study showed that Lepidoptera, Hymenoptera and Diptera were the dominant prey items (Fig. 8). Among these orders, Hymenoptera in particular rarely occurs in the diet of other *Miniopterus* species (but see Razakarivony et al. 2005). In contrast, prey types frequently found in the diet of other *Miniopterus* species, such as Isoptera and Hemiptera, were not found in the diet of *M. fuscus*. It is possible that the absence of Isoptera was due to prey availability at our study site, because we caught no Isoptera during the study period. On the other hand, *M. fuscus* seems to avoid or not have access to Hemiptera because we caught Hemiptera as well as Coleoptera, Diptera and Hymenoptera. Comparison of diet and insect abundance revealed that Diptera and Hymenoptera seem to be important resources for *M. fuscus* (Table 3).

Resource partitioning, in which different species prey on insects of different groups, has been widely reported in insectivorous bats (Black 1974, Husar 1976, Fenton et al. 1977, Hickey et al. 1996, Funakoshi & Takeda 1998, Zhang et al. 2005). There are multiple possible mechanisms of insect resource partitioning: (1) consumed insects vary with the wing morphology that influences flight space (e.g. open space and cluttered space; Norberg & Rayner 1987) because insect availability may differ with space and (2) the consumed insects are also affected by echolocation call design (Schnitzler et al. 2003) and body size because these factors affect insect detection and food size, respectively. Species-specific differences in these traits lead to 'passive selection' of insect resources. Therefore, bats with different traits consume different resources, and 'passively' partition the resource.

Our data indicate resource partitioning because the relative proportion of each insect order in the diet of each bat species was different. The diet composition of *Hipposideros turpis* in particular was quite different from those of the other 2 species.

Among the 3 species, the wing morphology of *Miniopterus fuscus* was apparently different from those of *Rhinolophus perditus* and *Hipposideros turpis* (Fig. 9). Because only a few specimens were investigated in the present study, the results of statistical analysis might be affected by low test power. However, in general, the genus *Miniopterus* has longer wings than do

Rhinilophidae and Hipposideridae and has been predicted to use both open and cluttered spaces for feeding (Norberg & Rayner 1987). On Ishigaki Island, we have not captured *M. fuscus* in cluttered spaces (D. Fukui unpubl. data). Therefore, *M. fuscus* in our study area is suspected to use open spaces, although Jacobs (1999) showed that a closely related species (*M. schreibersii*) of *M. fuscus* flies in both open and cluttered spaces. On the other hand, *R. perditus* and *H. turpis* has been predicted to use cluttered spaces because their lower aspect ratio and higher wingtip shape index may lead to slow and manoeuvrable flight (Norberg & Rayner 1987). Moreover, only *M. fuscus* emits typical frequency-modulated (FM) calls (D. Fukui unpubl. data), while the other 2 species emit constant-frequency (CF) calls (Matsumura 2005). Because of the difference in these functional traits between *M. fuscus* and the other 2 species, they 'passively' partition foraging space and food resources, and there may not be competition for resources.

Rhinolophus perditus and *Hipposideros turpis* have similar wing morphology (Fig. 9) and echolocation structure (Matsumura 2005). Both species emit CF calls to detect prey, although the frequencies are different (97 and 82 kHz, respectively; Matsumura 2005); they also have relatively short wings that are adapted to flying in cluttered space. Therefore, these 2 species seem to use similar types of foraging spaces with the same level of clutter. However, the diet compositions of these species were quite different throughout the survey period. While *H. turpis* mainly forages on scarab beetle, *R. perditus* forages on Hymenoptera, Lepidoptera, Coleoptera and Chironomidae. There are 2 possible explanations for this difference: (1) the different body size of the 2 species i.e. their different evolution is reflected in different morphological traits which causes resource partitioning. *H. turpis* is larger than *R. perditus* and appears to have a stronger biting force. Therefore, *H. turpis* can forage on larger and harder prey, such as beetle, while *R. perditus* can consume only smaller prey, such as chironomids; (2) there is a possibility that these 2 species could also partition resources vertically i.e. exploitative competition (Arlettaz et al. 1997). To verify these hypotheses the diet of these species should be analysed in the region where each species occur allopatrically.

Our results reveal that diverse insects are consumed by the bat assemblage on Ishigaki Island. This implies that habitats that maintain high insect diversity are required for bat assemblages. Moreover, extensive consumption of the serious sugarcane pest *Anomala albopilosa* by *Hipposideros turpis* implies that the reduction in the *H. turpis* population will also affect the agro-ecosystem. Sugarcane is the dominant crop on Ishigaki Island. Thus, to maintain the agricultural economy on the island, bat conservation measures should be established. In the future, the preferred foraging habitats of the 3 species of bats should be studied directly by monitoring techniques such as radio-tracking, and the results of these studies should be combined with our results for establishing appropriate conservation measures.

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