Food Habits of Japanese Pipistrelles *Pipistrellus abramus* (Chiroptera: Vespertilionidae) in Northern Taiwan

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Ya-Fu Lee and Ling-Ling Lee (2005) Food habits of Japanese pipistrelles *Pipistrellus abramus* (Chiroptera: Vespertilionidae) in northern Taiwan. *Zoological Studies* **44**(1): 95-101. The composition and seasonal variation in the diet of Japanese pipistrelles, *Pipistrellus abramus*, were studied by analyzing fecal samples collected from May 1988 to June 1990 in Chutung, northern Taiwan. The diet of these bats contained a variety of insects (12 orders) and spiders. The majority of pellets examined (86.3%) contained 3 to 6 prey items (mean = 4.2 ± 0.1). In decreasing order, beetles, dipterans, hymenopterans, caddisflies, moths, true bugs, and homopterans were the most frequently found (95.9% in total frequency of occurrence) and accounted for the highest volume percentages (96.7% in total) in the feces. The dietary heterogeneity index (DHI) of Japanese pipistrelles was 9.25, but this varied among monthly samples, and we found no apparent seasonal patterns. Both overall DHI values (9.43; 9.39) and the 95% confidence limits (8.17~11.05; 8.41~11.39) appeared to be greater in the period of mid-summer to fall, and in the winter months, than in the period of Apr. to mid- summer (8.67; 7.52~10.18), respectively. The diets of the bats over the 3 seasonal periods were similar, with only minor variations. Hymenopterans, moths, and caddisflies were more frequently taken, while true bugs and homopterans less frequently taken by bats after mid-July. Bats appeared to consume higher proportions of homopterans in the 1st than in the 3rd period, but higher proportions of true bugs in the 2nd than in either the 1st or 3rd periods; whereas higher proportions of hymenopterans were consistently taken in the 1st sampling year. http://www.sinica.edu.tw/zool/zoolstud/44.1/95.pdf

Key words: Chiroptera, Bats, *Pipistrellus abramus*, Diet

Over the last several decades, many empirical studies on food habits of bats have generated enormous amounts of data essential to our understanding of foraging behavior and ecology of insect-eating bats (e.g., Rose 1967, Belwood and Fenton 1976, Fenton and Thomas 1980, Barclay 1985, Jones 1990, Rydell 1992, Churchill 1994, Shiel et al. 1998, Lee and McCracken 2002 2004). The majority of those studies, however, unavoidably focused on New World species, those of temperate Eurasia, and to a lesser extent, on African and Australian species. With few exceptions (e.g., Eckrich and Neuweiler 1988, Whitaker et al. 1999), we still know very little about the food habits of the majority of species of insectivorous bats in most parts of Asia.

The Japanese pipistrelle, *Pipistrellus abramus*, is widely distributed in eastern and southern Asia from Siberia, Japan, Korea, eastern China, and Taiwan, to northern Vietnam, Burma, and India (Corbet and Hill 1992, Koopman 1993, Simmons 2005). These bats live in caves, tree cavities, and crevices, as well as in man-made structures such as houses and churches (Funakoshi and Uchida 1978). Some aspects of the population and reproductive biology of this species have been studied in Japan (Funakoshi and Uchida 1978, 1982, Uchida et al. 1988), Taiwan (Lu 1988, Ke 1995, Lee 1995), and China (Huang and Huang 1982), respectively. Their

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close relative in Europe, the common pipistrelle (*P. pipistrellus*), has a broad and general diet (up to 10 insect orders) achieved by an opportunistic foraging mode (Swift et al. 1985, Hoare 1991, Sullivan et al. 1993, Barlow 1997). Information regarding of of food habits of Japanese pipistrelles, however, is still scanty anywhere within their distribution range.

Funakoshi and Uchida (1978) reported on the diet of Japanese pipistrelles in Fukuoka, Japan, but only presented the frequency of occurrence of food items. Yang (1996) studied the diet of this species in Yunlin, south-central Taiwan, however, only during the generally defined non-hibernating period (i.e., roughly between Apr. and Oct.; Funakoshi and Uchida 1978). Funakoshi and Uchida (1978) noted that as far north as ~33°N, Japanese pipistrelles still emerge on warmer days in Feb. and Mar. In subtropical Taiwan, although less active in winter, these bats constantly emerge and forage on warmer evenings (Lee 1995, Y. F. Lee unpubl. data). Thus, a complete picture of the diet of this species over the entire time frame in a subtropical region is needed. This study reports on the food habits of Japanese pipistrelles based on a full-year sampling in northern Taiwan; we also tests whether the diet varied at different times of the year.

MATERIALS AND METHODS

Study sites

Fieldwork took place in rural Chutung (24° 42'N, 121°6'E, 165 m elevation), a hilly region of northern Taiwan, between May 1988 and June 1990. A Japanese pipistrelle colony roosted within the roof of a traditional Taiwanese tile and wooden house. The house, built in early 1960s, is located at the valley of Shangping Creek, and is surrounded by rice paddies, bamboo woods, and secondary forests mainly comprised of *Acacia confusa*. The number of bats dwelling within the roof fluctuated over time; however, there were usually a couple of hundred bats present during most times of the spring and summer (Lu 1988, L.L. Lee unpubl. data). Most individuals emerged and returned by passing through clefts in the upper portion of the front porch.

Fecal sampling

We collected fecal pellets twice each month during the study period. Pellets were collected at dawn from the ground in front of the porch in the front yard. The landowner would routinely sweep the ground every morning to clean it or because the paved area was needed as a place to sun-dry crops, thus our morning collections each month represented the digestive products of bats from the previous night's foraging. We normally selected 10-20 of the largest intact pellets. The bats enter into an intermittent seasonal torpor after mid-fall and particularly in the winter months, nightly activity of bats outside the roost declines sharply, as does the amount of feces on the ground. During such periods, we collected as many pellets as were available.

Dietary analysis

Fecal analysis followed the method of Whitaker (1988). We soaked each pellet in a petri dish with 70% ethyl alcohol to soften it, and then dissected it with a dissecting needle and fine forceps. Prey fragments were sorted and identified under a dissecting microscope (10 x 20 magnification) with reference to insect keys (Borror et al. 1989) and voucher specimens of locally collected insects. The percent volume of each prey in a pellet was estimated with the aid of grid paper (10 x 10 units) attached to the bottom of the petri dish. We could only confidently identify prey items to order, due to sufficient mastication by the bats, and we recognize that we may have underestimated the presence of some soft-bodied insects in the feces.

The frequency of occurrence and the percent volume of each prey item in the feces were determined for each insect taxon identified. The frequency of occurrence provides a standardized measure, ranging from 0% to 100%, of the commonness of each prey item in the bats' diet (McAney et al. 1991). We calculated the frequency of occurrence as the number of fecal pellets in which a particular prey item was identified, divided by the total sum of the numbers of pellets that contained each prey item that was identified (McAney et al. 1991). The percent volume of a prey item for each date was averaged over all pellets examined on a given sampling date to provide an index of the proportional contribution of each prey item to the diet of the bats sampled on that date (Whitaker 1988). If a prey item comprised more than 1/2 of the total volume in a sample, we defined it as "predominant". We used the arithmetic mean of the frequency of occurrence and the percent volume to estimate the relative importance of each

prey item in the diet (Bauerova 1986).

Statistical analysis

We restricted our analyses of dietary variation to the ordinal level because fragments of prey, particularly those of soft-bodied insects, were often difficult or impossible to identify to family. Unless otherwise noted, data are presented as the mean ± standard error (SE). All statistical tests were determined at a significance level of $p < 0.05$ using STATISTICA 6.0 for Windows 98 (StatSoft 2001). Data in proportions were arcsine-transformed to meet the normality requirement (Sokal and Rohlf 1994). We used linear regression to evaluate the correlation between the dry mass of the feces and the number of prey items revealed in each pellet; between dietary heterogeneity and the total number of fecal pellets examined in each sample; and between the percent volume and percent frequency of prey orders in the diets of these bats. A multivariate analysis of variance (MANOVA) was used to examine the temporal effects (e.g., year and month) of sampling dates on the variance in the relative proportions of each prey. We also used MANOVA to look for seasonal variations in the bats' diets. For this analysis, we subdivided our samples into 3 seasonal periods: (I) before juvenile volancy, i.e., Apr. to mid-July; (II) after juvenile volancy, i.e., late July to Oct.; and (III) winter, i.e., Nov. to Mar. When significant dietary variations were detected, we conducted post hoc multiple range comparisons by Tukey honest significant difference test (HSD) for unequal sample size to pinpoint the differences. We examined dietary variation of the bats against temporal sampling units only for the 8 prey orders that had the highest important values, because the remaining orders occurred in low frequency, resulted in excessive null data. We also adopted the reciprocal Simpson index, $1/D = 1/\Sigma(P_i^2)$, to assess dietary heterogeneity, where P_i is the relative proportion of particular prey item i (i = 1 to n, n being the total number of prey items) A higher index value indicates a more-diverse diet with a more-even proportional distribution (Krebs 1999). The 95% confidence intervals of dietary heterogeneity indices were estimated using the jackknife technique (Sokal and Rohlf 1994, Magurran 2004).

RESULTS

We examined a total of 248 fecal pellets of Japanese pipistrelles and found 1024 prey items. The number of prey items identified in each pellet varied from 1 to 9 (mean = 4.2 ± 0.1), but 86.3% (213 pellets) contained 3~6 items. No correlation
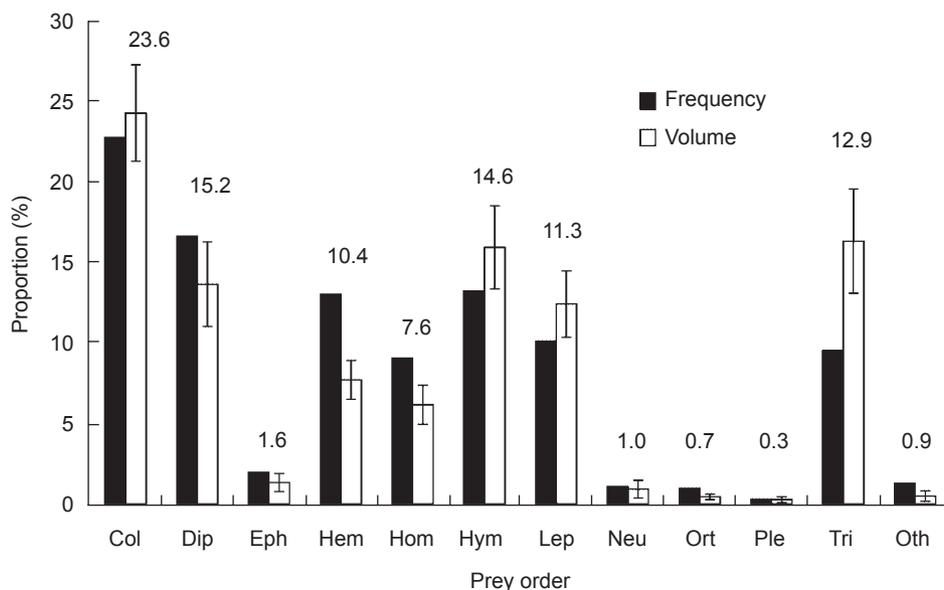

Fig. 1. The diet of Japanese pipistrelles presented by percent frequencies of occurrence and mean volume percentages (± SE) of various types of prey. Col, Coleoptera; Dip, Diptera; Eph, Ephemeroptera; Hem, Hemiptera; Hom, Homoptera; Hym, Hymenoptera; Lep, Lepidoptera; Neu, Neuroptera; Ort, Orthoptera; Ple, Plecoptera; Tri, Trichoptera; and Oth, prey that occurred in feces on fewer than 3 occasions (e.g., termites and spiders) and some unidentified insects. The number at the top of each column is the relative importance (%) of the respective prey.

existed between the dry mass of feces (mean = 10.9 ± 2.2 mg) and the number of prey items found within (r^2 = 0.004, $F_{(1, 195)}$ = 0.004, p = 0.95).

We identified fragments from various arthropods, including 12 insect orders, i.e., beetles, flies, hymenopterans, caddisflies, moths, true bugs, homopterans, mayflies, neuropterans, orthopterans, stoneflies, and termites, as well as spiders. The 1st 6 orders had the highest important values (each above 10%; Fig. 1). These 6 orders accounted for 85.3% of the total frequency of occurrence, and contributed over 90.5% of the volume to the diets of these bats. Homoptera followed and accounted for 9.1% of the frequency and 6.2% of the volume. The remaining prey orders each accounted for less than 2% of the frequency and 1.5% of the volume. Two rarer prey items, stoneflies and termites, were completely absent from the winter samples.

A strong correlation existed between percent volumes and percent frequencies of prey orders in the bats' diet (r^2 = 0.76, $F_{(1, 10)}$ = 56.69, p < 0.001). Discrepancies, measured as the minimum percent difference of the frequency from the volume, appeared only in caddisflies, true bugs, and homopterans. The discrepancy in each of these 3 orders was greater than 15% of their percent frequencies. Caddisflies occupied a greater volume, and the latter 2 accounted for a smaller volume, than suggested by their relative frequencies of occurrence, respectively (Fig. 1). Overall, beetles accounted for the highest volume percentage in 12 samples (44.4%), followed by hymenopterans and caddisflies (each in 5 samples; 18.5%), dipterans (3 samples; 11.1%), and homopterans and moths (each in 1 sample only; 3.7%). Only caddisflies in 2 samples (72.5% and 57.5%) and dipterans in 1 sample (52.3%), however, accounted for greater than half of the total volume and were considered predominant prey items.

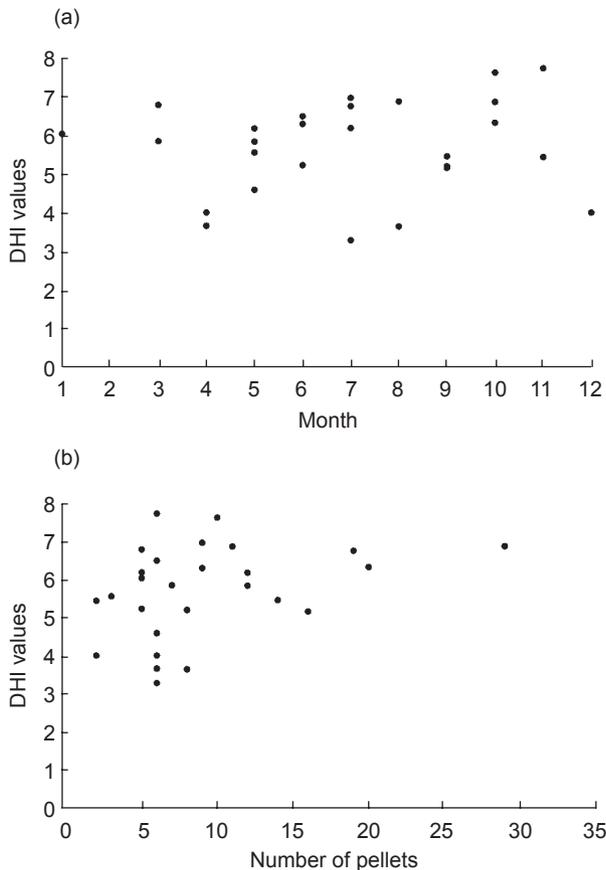The dietary heterogeneity index (DHI) of

Fig. 2. Distribution (a) of the dietary heterogeneity index (DHI) values of Japanese pipistrelles over the sampled months; and the relationship (b) between DHI values and the number of fecal pellets examined for the monthly fecal samples.
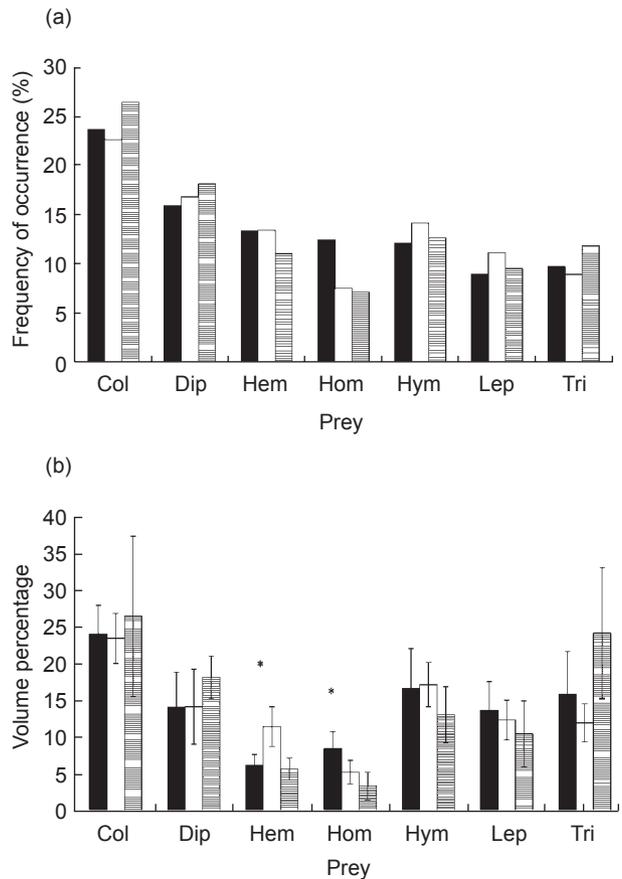
Fig. 3. Distribution of (a) frequencies of occurrence, and (b) volume percentages (± SE), of the 7 major prey orders in the diets of Japanese pipistrelles in Taiwan over the 3 seasonal periods: (■) Apr. to mid-July − before juvenile volancy; (□) late-July to Oct. − after juvenile volancy; and (▨) Nov. to Mar.

Japanese pipistrelles over the study period was 9.25, but it varied among samples, and we observed no apparent seasonal trends ($r^2 = 0.02$, $F_{(1, 25)} = 0.39$, $p = 0.54$; Fig. 2a). DHI values were strongly correlated to the numbers of food types identified ($r^2 = 0.79$, $F_{(1, 25)} = 92.98$, $p < 0.001$), but showed virtually no correlation to the number of pellets examined in each sample ($r^2 = 0.12$, $F_{(1, 25)} = 3.32$, $p = 0.08$; Fig. 2b). Overall DHI values and 95% confidence intervals appeared to be a little higher after mid-summer, i.e., 9.43 (8.17-11.05) between late-July and Oct. (after juvenile volancy) and 9.39 (8.41-11.39) from Nov. to Mar., compared to 8.67 (7.52-10.18) during the period of Apr. to mid-July (before juvenile volancy).

The ranking patterns of the frequency of occurrence among prey orders during the 3 seasonal periods were similar (I and II: $r^2 = 0.88$, $F_{(1, 9)} = 68.4$, $p < 0.001$; I and III: $r^2 = 0.87$, $F_{(1, 9)} = 54.8$, $p < 0.001$; and II and III: $r^2 = 0.94$, $F_{(1, 9)} = 124.7$, $p < 0.001$); except that relative to the other major prey orders, true bugs after Oct. and homopterans after mid-July appeared less frequently, while beetles, dipterans, hymenopterans, moths, and caddisflies appeared more frequently in the bats' feces (Fig. 3a). The volume percentages of the diets of the bats also correlated to each other among the 3 seasonal periods (I and II: $r^2 = 0.87$, $F_{(1, 9)} = 58.8$, $p < 0.001$; I and III: $r^2 = 0.77$, $F_{(1, 9)} = 30.7$, $p < 0.001$; and II and III: $r^2 = 0.64$, $F_{(1, 9)} = 15.4$, $p < 0.005$).

Diets of bats differed among the 3 seasonal periods for the 7 major prey orders that had the highest important values, e.g., beetles, flies, hymenopterans, caddisflies, moths, true bugs, and homopterans (MANOVA Rao's $R_{(14, 470)} = 2.15$, $p < 0.01$), but not between years (Rao's $R_{(7, 235)} = 1.67$, $p = 0.12$). A factor x factor effect (Rao's $R_{(14, 470)} = 2.79$, $p < 0.001$), however, was also observed. Among the major prey orders, bats appeared to have consumed higher proportions of homopterans (HSD: $p < 0.001$) in the 1st period than in the 3rd period, but to have consumed higher proportions of true bugs (HSD: $p < 0.05$) in the 2nd period than in either the 1st or 3rd periods (Fig. 3b); whereas, higher proportions of hymenopterans were consistently taken in the 1st sampling year (HSD: $p < 0.05$).

DISCUSSION

Our results indicate a fairly broad diet (i.e., 12 insect orders) in Japanese pipistrelles in Taiwan, which is more diverse than previously reported (e.g., 4 insect orders in Funakoshi and Uchida 1978 and 6 orders in Yang 1996). Both Funakoshi and Uchida (1978) and Yang (1996) confined their studies to the typically defined non-hibernating period of insectivorous bats. Instead, we reported the diet of Japanese pipistrelles through an entire yearly cycle. The diets of these bats in the 3 seasonal periods were generally similar, with only minor variation. Certain rarer prey items, such as stoneflies and termites, were not found in the winter samples. The observed diverse diet of these bats, thus, is not likely an exclusive consequence of including winter samples. Spatial variations in the diets of this species over its geographic range may warrant further studies.

A similarly diverse diet was found in common pipistrelles in Ireland (12 orders in Sullivan et al. 1993) and eastern pipistrelles (*P. subflavus*) of North America (10 orders in Griffith and Gates 1985). Whitaker et al. (1999) identified 8 orders and 12 families of insects in the diet of Indian pygmy pipistrelles (*P. mimus*). Barlow (1997), and earlier Sullivan et al. (1993), Hoare (1991), and Swift et al. (1985), showed that nematocerans (Diptera) comprised the most frequently taken food item (from nearly 60% to 90%) of common pipistrelles in Europe, followed by caddisflies. In particular, the latter 2 studies found that nematocerans and caddisflies were also the 2 most-abundant insects collected in the field (~80%), and suggested a non-selective diet for this species.

In contrast to common pipistrelles, Japanese pipistrelles eat a variety of insects with relatively even distributions in the frequency of occurrence and volume percentage among prey orders. Their diet was comprised of 6 major insect orders each valued above 10% by relative importance; and none of these insects, except beetles, accounted for more than 20% either by percent volume or frequency of occurrence. Caddisflies and flies were not as important in the diet of Japanese pipistrelles in Taiwan as they are to common pipistrelles. This dietary pattern is more similar to that of Indian pygmy pipistrelles (Whitaker et al. 1999) and eastern pipistrelles (Griffith and Gates 1985), except that caddisflies occurred much less frequently in the Indian pygmy pipistrelle diet, and were not found at all in the diet of eastern pipistrelles.

Differences in the diet between Japanese pipistrelles and those other species may be attributed to the compositions and variations in insect availabilities at the various sites where those studies were conducted. Pipistrelles forage in various

types of habitats, such as the edge of woods (Schnitzler et al. 2003), over water surfaces (Racey et al. 1998), and around streetlamps (Blake et al. 1994). Our study site was located at the border of hilly terrain which leads toward the Central Mountain Range of Taiwan; at the site itself, a mixture of habitats exists, including woodlands, croplands, aquatic environments (streams, drains for irrigation, and wet paddy fields), and human residences with streetlights. While dipterans and trichopterans are often found in aquatic habitats, woodlands and croplands usually support abundant populations of beetles, moths, true bugs, and homopterans; and streetlights often attract diverse arthropods (Anthony and Kunz 1977, Lee and McCracken 2002). This factor of diverse habitats may also explain the dietary variation observed in Japanese pipistrelles in Taiwan.

While limited overall variation in insect availability may restrict the dietary diversity of bats, as evidenced in common pipistrelles (Swift et al. 1985), declines in insect abundance over time may lead to a more-diverse diet. We did not systematically survey insect compositions, relative abundances, or variations over time in this study, and thus cannot verify this speculation. Previously, Yang (1996) reported a general correspondence between the diet of Japanese pipistrelles and the insect abundance assessed during Apr. and Oct. in a coastal village of south-central Taiwan principally surrounded by cultivated areas. Our data indicated no apparent seasonal pattern in DHI values, although a rising trend in DHI values and respective 95% confidence intervals after mid-summer was observed. Further studies are needed to incorporate both food habits of the bats and prey abundances over the entire time frame in subtropical and tropical Asia in order to test the increasingly accepted view that most aerial hawking insectivorous bats (e.g., pipistrelles) are opportunistic foragers (Fenton 1990, Jones and Rydell 2003).

REFERENCES

Anthony ELP, TH Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology **58:** 775-768.

Barclay RMR. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasiurus noctivagans*) bats and the consequences for prey selection. Can. J. Zool. **63:** 2507-2515.

Bauerova Z. 1986. Contribution to the trophic bionomics of *Myotis emarginatus*. Folia Zool. **35:** 305-310.

Barlow KE. 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. J. Zool. (Lond.) **243:** 597-609.

Belwood JJ, MB Fenton. 1976. Variation in the diet of *Myotis lucifugus*. Can. J. Zool. **54:** 1674-1678.

Blake D, AM Hutson, PA Racey, J Rydell, JR Speakman. 1994. Use of lamplit roads by foraging bats in southern England. J. Zool. (Lond.) **234:** 453-462.

Borror DJ, CA Triplehorn, NF Johnson. 1989. An introduction to the study of insects. Orlando, FL: Harcourt Brace.

Churchill SK. 1994. Diet, prey selection and foraging behaviour of the orange horse-shoe bat, *Rhinonycteris aurantius*. Wildlife Res. **21:** 115-130.

Corbet GB, JE Hill. 1992. The mammals of the Indomalayan region: a systematic review. Oxford, UK: Oxford Univ. Press.

Eckrich M, G Neuweiler. 1988. Food habits of sympatric insectivorous bats *Rhinolophus rouxi* and *Hipposideros lankadiva* from Sri Lanka. J. Zool. (Lond.) **215:** 729-737.

Fenton MB. 1990. The foraging behaviour and ecology of animal-eating bats. Can. J. Zool. **68:** 411-422.

Fenton MB, DW Thomas. 1980. Dry season overlap in activity patterns, habitat use and prey selection by some African insectivorous bats. Biotropica **12:** 81-90.

Funakoshi K, TA Uchida. 1978. Studies on the physiological and ecological adaptation of temperate insectivorous bats: III. Annual activity of the Japanese house-dwelling bat, *Pipistrellus abramus*. J. Fac. Agr. Kyshu Univ. **23:** 95-115.

Funakoshi K, TA Uchida. 1982. Age composition of summer colonies in the Japanese house-dwelling bat, *Pipistrellus abramus*. J. Fac. Agr. Kyshu Univ. **27:** 55-64.

Griffith LA, JE Gates. 1985. Food habits of cave-dwelling bats in the central Appalachians. J. Mammal. **66:** 451-460.

Hoare LR. 1991. The diet of *Pipistrellus pipistrellus* during the pre-hibernal period. J. Zool. (Lond.) **225:** 665-670.

Huang W, X Huang. 1982. The seasonal activity of *Pipistrellus abramus* in relation to environmental factors. Acta Therio. Sinica **2:** 143-155.

Jones G. 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? J. Anim. Ecol. **59:** 587-602.

Jones G, J Rydell. 2003. Attack and defense: interactions between echolocating bats and their insect prey. *In* TH Kunz, MB Fenton, eds. Bat ecology. Chicago, IL: Univ. of Chicago Press, pp. 301-345.

Ke WY. 1995. Reproductive cycle of the house bat, *Pipistrellus abramus*, in Pingtung County, southern Taiwan. Master's thesis, Tung-Hai Univ., Taichung, Taiwan.

Koopman KF. 1993. Order Chiroptera. *In* DE Wilson, DM

Reeder, eds. Mammal species of the world: a taxonomic and geographic reference. Washington, DC: Smithsonian Institution Press, pp. 137-241.

Krebs CJ. 1999. Ecological methodology. New York: Addison Wesley Longman.

Lee LL. 1995. A preliminary study on the reproductive pattern of *Pipistrellus abramus* in northern Taiwan. Acta Zool. Taiwanica **6:** 61-66.

Lee YF, GF McCracken. 2002. Foraging activity and resource use of Brazilian free-tailed bats *Tadarida brasiliensis* (Molossidae). Ecoscience **9:** 306-313.

Lee YF, GF McCracken. 2004. Flight activity and food habits of three species of *Myotis* bats (Chiroptera: Vespertilionidae) in sympatry. Zool. Stud. **43:** 589-597.

Lu DJ. 1988. Activity patterns of the house bat, *Pipistrellus abramus*, in Chu-tung. Master's thesis, National Taiwan Univ., Taipei, Taiwan.

Magurran AE. 2004. Measuring biological diversity. Malden, MD: Blackwell Science.

McAney CM, C Shiel, C Sullivan, J Fairley. 1991. The analysis of bat droppings. London: The Mammal Soc. Press.

Racey PA, SM Swift, J Rydell, L Brodie. 1998. Bats and insects over two Scottish rivers with contrasting nitrate status. Anim. Conserv. **1:** 195-202.

Ross A. 1967. Ecological aspects of food habits of insectivorous bats. West. Found. Vert. Zool. **1:** 205-263.

Rydell J. 1992. Exploitation of insects around streetlamps by bats in Sweden. Funct. Ecol. **6:** 744-750.

Schnitzler HU, CF Moss, A Denzinger. 2003. From spatial orientation to food acquisition in echolocating bats. Trends Ecol. Evol. **18:** 386-394.

Shiel CB, PL Duverge, P Smiddy, JS Fairley. 1998. Analysis of the diet of Leisler's bat (*Nyctalus leisleri*) in Ireland with some comparative analysis from England and Germany. J. Zool. (Lond.) **246:** 417-425.

Simmons NB. 2005. Order Chiroptera. *In* DE Wilson and DM Reeder, eds. Mammal species of the World: a taxonomic and geographic reference. Washington, DC: Smithsonian Institution Press (in press)

Sokal RR, FJ Rohlf. 1994. Biometry. New York WH Freeman.

StatSoft. 2001. STATISTICA 6.0. Tulsa, OK.

Sullivan CM, CB Shiel, CM McAney, JS Fairley. 1993. Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentoni* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. J. Zool. (Lond.) **231:** 656-663.

Swift SM, RA Racey, MI Avery. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertillionidae) during pregnancy and lactation. II. Diet. J. Anim. Ecol. **54:** 217-225.

Uchida TA, T Mori, SW Son. 1988. Delayed capacitation of sperm in the Japanese house bat, *Pipistrellus abramus*. J. Mammal. Soc. Jpn. **13:** 1-10.

Whitaker JO Jr. 1988. Food habits analysis of insectivorous bats. *In* TH Kunz, ed. Ecology and behavioral methods for the study of bats. Washington, DC: Smithsonian Institution Press, pp. 171-189.

Whitaker JO Jr, SS Issac, G Marimuthu, TH Kunz. 1999. Seasonal variation in the diet of the Indian pygmy bat, *Pipistrellus mimus*, in southern India. J. Mammal. **80:** 60-70.

Yang SH. 1996. Activity pattern and food habits of *Myotis formosus watasei* and *Pipistrellus abramus* in Yunlin. Master's thesis, National Taiwan Univ., Taipei, Taiwan.