

Flight Activity and Food Habits of Three Species of *Myotis* Bats (Chiroptera: Vespertilionidae) in Sympatry

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(Accepted May 5, 2004)

Ya-Fu Lee and Gary F. McCracken (2004) Flight activity and food habits of three species of *Myotis* bats (Chiroptera: Vespertilionidae) in sympatry. *Zoological Studies* 43(3): 589-597. Spatiotemporal distributions in nocturnal flight activities and variations in food resource use among the little brown (*Myotis lucifugus*), northern long-eared (*M. septentrionalis*), and Indiana myotis (*M. sodalis*) were studied in central and northern Indiana where the 3 species occur in sympatry. We netted pairs of these 3 species on the same nights at 4.3% to 8.5% of the total netting sites, while all 3 species were netted on the same night at only 1 site (~1.1%). When each species was captured alone, the mean capture time of the little brown myotis was earlier than those of the Indiana and northern long-eared myotis; but the 3 species did not differ in heights of capture. At sites where paired species were caught, the mean capture time of the Indiana myotis shifted from being no different from, to being earlier than, that of the northern long-eared myotis; and the mean capture height of the Indiana myotis shifted from being no different from, to being higher than, that of the little brown myotis. Based on analyses of feces, the little brown myotis has a more-diverse diet, feeds on more beetles of a smaller size range, and consumes more aquatic insects than do the Indiana and northern long-eared myotis. While the northern long-eared myotis fed primarily on beetles, moths, and dipterans, and took greater quantities of large-sized (4~6 mm and > 6 mm) beetles, moths were the major prey of the Indiana myotis. Variations in diets among these 3 species are consistent with their foraging behavior, are correlated to their temporal activities, and support predictions based on previously reported differences in their mean lengths of the maxillary tooth-row. <http://www.sinica.edu.tw/zool/zoolstud/43.3/589.pdf>

Key words: Activity, Diets, Bats, *Myotis*, Sympatry.

Insectivorous bats in sympatry may show differences in time of foraging (Rydell et al. 1996), habitat use (Herd and Fenton 1983, Saunders and Barclay 1992), or both (Kunz 1973), due to some crucial eco-morphological features or behavioral differences (Norberg and Rayner 1987, Jones and Rydell 1994). They may also differ in types and/or sizes of insects consumed (Barclay 1985); however, it is not known whether this is independent of the patterns observed in the other 2 dimensions. Insects typically have patchy distributions, and their abundances may change from 1 time to another, often with daily weather patterns (Wolda 1988). Thus, spatial and temporal activities of foraging bats often likely correspond with the distribution and abundance of insects (Aldridge and Rautenbach 1987, Rydell et al. 1996).

Throughout much of the north-central Eastern US, the little brown myotis *Myotis lucifugus*, northern long-eared myotis *M. septentrionalis*, and the endangered Indiana myotis *M. sodalis*, co-occur (Hall 1981, Mumford and Whitaker 1982). The 3 species are similar in body size, skull length, and wingspan; but the northern long-eared myotis has a longer ear length than the other 2 species, and a larger mean length of maxillary tooth-row than the Indiana myotis, while the little brown myotis shows greater variation in the latter feature (Hall 1981). The 3 species also have similar wing shapes, low aspect ratios, and wing loadings (Norberg and Rayner 1987). They emit frequency-modulated echolocation calls of short duration, with short inter-pulse intervals, most at energies around 45~55 kHz (Fenton and Bell 1981); but the calls of

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northern long-eared myotis are at a lower intensity (Faure et al. 1993).

Previous studies on these bats found that the little brown myotis tends to forage over water or the ground surface, and occasionally along the tops of trees (Buchler 1976, von Frenchell and Barclay 1987). This species eats dipterans and various other insects with substantial site-to-site variation (e.g., Belwood and Fenton 1976, Anthony and Kunz 1977, Griffith and Gates 1985). The northern long-eared myotis frequently forages under the forest canopy and above shrubs (LaVal et al. 1977), and takes moths and beetles as its major food items (Brack 1983, Griffith and Gates 1985). The Indiana myotis may forage in both riparian and non-riparian habitats (Humphrey et al. 1977, LaVal et al. 1977), and moths, beetles, and caddisflies are its major food items (Brack and LaVal 1985, Kurta and Whitaker 1998). Those results suggest that the observed patterns of food resource use by these bats are associated with their foraging and flight activities. Yet, few studies have investigated the resource use patterns of the 3 species as an assembly in sympatry. Belwood (1979) found no evidence of partitioning among the 3 species, whereas Brack (1983) suggested dietary partitioning of the Indiana myotis with the other 2 species.

Our study examines temporal-height distributions of flight activity and documents food resource uses of the 3 species in sympatry. Previous studies showed differences in foraging and flight activities of these bats in the spatial dimension. We predicted that these closely related and similar species of bats in sympatry should differ in their use of space (e.g., sites or heights), but not in time, because summer nights are short, and the abundance of nocturnal insects may decline greatly over time (Kunz 1973). Second, we tested the hypothesis that these bats should have different patterns of food resource use independent of the abundance of insects. The sizes of insects taken by bats may be correlated with their cranial-dental morphology (Freeman 1981). With this in mind, we predicted that the northern long-eared myotis should eat a greater quantity of larger-sized insects than does the Indiana myotis, because of its larger jaw length.

MATERIALS AND METHODS

Fieldwork took place during 3 June ~1 Aug. 1991 and 8 June ~14 Aug. 1992, in central and

northern Indiana. Selective logging and agricultural clearing have much reduced non-riparian forests in Indiana, with limited riparian woody areas relatively less impacted in the central region (Mumford and Whitaker 1982). In total, we sampled 94 sites in riparian forests in 40 counties (2.4 ± 0.4 sites/county), where 74 creeks of 20 major river systems are distributed. Major woody plants in our sites include species of *Quercus* (Fagaceae), *Carya* (Juglandaceae), *Acer* (Aceraceae), and *Ulmus* (Ulmaceae).

Mist netting and fecal sample collection

We set up mist nets in forest corridors over streams to catch bats. Each night, we connected together 4 nets of equal length vertically using string, and raised the top of the top net to 10 m above the water surface. From 19:30 to 02:00 h, we checked the nets at intervals of 10~15 min. We determined species, age (adult vs. juvenile), sex, and reproductive status; measured forearm length and body mass; and recorded the time and height of capture for each bat. Each bat was kept in a separate cloth bag for ~2 h to collect feces, and then was released. Fecal samples were stored for later analysis. Our procedures were consistent with the guidelines for the capture, handling, and care of mammals (American Society of Mammalogists 1998).

Dietary analysis

Dietary analysis followed the procedure of Whitaker (1988). We treated the collective pellets from a single bat as 1 sample for examination. Prey items were identified to the lowest possible taxonomic level, mostly orders. We identified some insects to the family level, but many fragments belonging to soft-bodied insects (e.g., moths, caddisflies, mayflies, and stoneflies) were only identifiable to orders due to the efficient mastication by bats. As a result, dietary data are presented as the frequency of occurrence (%) and percent volume of each order identified. We acknowledge the likelihood of underestimating the presence of soft-bodied insects in the samples (Robinson and Stebbings 1993). We also measured the lengths of beetles' femora found in each pellet, and compared them with those of beetles collected in the field to estimate the range of body sizes of beetles consumed by the bats (Bayne and Brigham 1995). The estimated body sizes of beetles were categorized into four classes: ≤ 2 , > 2 to

≤ 4 , > 4 to ≤ 6 , and > 6 mm. The femora of other insect orders were either too few or too fragmented to provide reliable measurements for estimates of body size.

Insect composition and abundance

We used sticky traps to approximate relative abundance and taxonomic diversity of flying insects in the field at sites adjacent to our mist nets. This non-attractant trap consisted of 4 wooden panels (45 x 40 cm) assembled in a cross, with a piece of paperboard (35 x 28 cm) hung on the top edge of alternating sides of each panel. Tangle-trap Adhesive glue (BioQuip, Gardena, CA, USA) was spread over the out-facing side of each paperboard. Each night, we set up 2 traps, 1 on each side of the stream bank, and at heights of 3 and 10 m, respectively. One trap was upstream, and the other downstream, approximately 30~50 m from the mist nets. The paperboards of each trap were replaced hourly from sunset until the bat netting ended. Each paperboard was then covered with a sheet of plastic wrap and stored for later analysis.

We added additional Universal Black Light Traps (2851U, BioQuip) to the sampling protocol in the middle of the 1991 field season, and light traps were used exclusively in 1992, because sticky traps had a comparatively lower success in sampling insects. We set up 2 light traps each night in the same manner as sticky traps, but they were at least 150 m apart and each was 70~80 m from the mist nets. We also checked the light traps hourly, collected the insects, and stored them in 70% ethanol. Insect samples were categorized by date, height, and time of collection. We identified insects to order and to family when possible. We also determined the size of all insects from sticky traps, and randomly selected sub-samples of insects from light traps (5% of the total), by measuring body length excluding antennae and wings. Insects larger than 20 mm were rarely collected, and were excluded because they are considered too large for small *Myotis* species to catch and handle (Barclay and Brigham 1994).

Data analysis

Unless otherwise noted, data are presented as the mean \pm standard error (SE). Statistical tests were conducted using STATISTICA 6.0 for

Windows 98 (StatSoft, Tulsa, OK, USA), at a significance level of 0.05. We used R x C G-tests for the contingency tables (bat species vs. time or height intervals) to examine the independence of bat captures over time (minutes relative to sunset) and height (meters above ground). The same test was used on the relative abundance of insect samples among orders and body sizes between light and sticky traps at sites where both traps were used, and for the contingency tables (bat species vs. type or size classes of prey) to examine the independence of consumption of prey type or prey size by bats. We used analysis of variance (ANOVA) and subsequent Fisher's LSD multiple range tests to compare the temporal and height distributions of bat captures for each species when netted alone, and for paired species when netted at the same site on the same night, respectively. We used an *F*-test to compare the variance of numbers of insects and insect orders collected per site at the 2 heights between the 2 traps. We also conducted the reciprocal Simpson's index, $1/\sum(p_i^2)$, to assess dietary diversity (Krebs 1989), where p_i is the relative proportion of prey item i . Dietary variations among species were examined by multiple analysis of variance (MANOVA; Rao's *R* value) and subsequently Fisher's LSD tests if necessary. Proportional data were arcsine-transformed to meet the normality assumption and to reduce heterogeneity (Sokal and Rohlf 1994).

We measured the relative preference for major prey types in the diets of the 3 *Myotis* species by correlating the rank orders of major prey types in the diets against the rank orders of the relative abundance of different prey types, as assessed by the insect traps; and statistically tested this using Snedecor's *F* value (Johnson 1980). We made comparisons for each site where both dietary data and trapping data were available. We acknowledge the potential bias associated with the nature of light traps (Kunz 1988), and bats' diets were measured against 2 independent sets of trapping data, from light traps and from non-attractant sticky traps. The orders of insects in both the bats' diet and the trap samples were lumped into 4 major groups, due to the occurrence of "0" data in those less-prevalent insect orders (Johnson 1980). The 4 groups included beetles, moths, soft-bodied insects (e.g., caddisflies, dipterans, mayflies, and stoneflies; CDM), and insects with a medium-hard exoskeleton (e.g., true bugs, homopterans, hymenopterans, and orthopterans; BHH).

RESULTS

Temporal and height distributions of bat captures

We caught a total of 177 little brown myotis at 34 sites (36.2% of the total sites) in 19 counties (47.5% of the counties sampled), 37 Indiana myotis at 22 sites (23.4%) in 15 counties (37.5%), and 24 northern long-eared myotis at 14 sites (14.9%) in 8 counties (20%). Of these, 116 little brown (65.5%), 27 Indiana (73%), and 23 northern long-eared myotis (95.8%), were from central Indiana. Over the 2 summers, we netted pairs of these 3 species on the same nights at 18 sites in 10 counties, or 19% of the mist-netting sites. We netted the little brown with Indiana myotis on the same nights at 8 sites (8.5%), and each species with the northern long-eared myotis at 6 (6.4%) and 4 sites (4.3%), respectively. All 3 species were captured on the same night at only 1 site, where we netted 1 northern long-eared, 2 Indiana, and 33 little brown myotis. The latter had a higher capture frequency (48.6%) and mean capture (1.9

± 0.5 bats/site; $F_{(2, 282)} = 9.5$, $p < 0.001$) than both the Indiana (31.4%; 0.4 ± 0.1 bats/site) and northern long-eared myotis (20.0%; 0.3 ± 0.1 bats/site).

Capture of the little brown myotis peaked in the first 2 h after sunset, and then decreased through the night; however, captures of both the Indiana and northern long-eared myotis peaked in the 2 h interval before midnight ($G = 8.10$, d.f. = 4, $p < 0.1$; Fig. 1a). At sites where each species was netted alone, captures of the little brown myotis showed an earlier peak, and had an earlier mean capture time ($F_{(2, 89)} = 4.15$, $p < 0.02$) than did both the Indiana (Fisher's LSD: $p < 0.05$) and northern long-eared myotis (Fisher's LSD: $p < 0.05$; Fig. 2a). When paired species were netted at the same site on the same night, the mean capture time of the little brown myotis was still earlier than that of the Indiana myotis ($F_{(1, 38)} = 4.65$, $p < 0.05$), but did not differ from that of the northern long-eared myotis ($F_{(1, 52)} = 1.97$, $p > 0.1$). When the latter 2 species were netted at the same site, however, the mean capture time of the Indiana myotis was earlier ($F_{(1, 13)} = 4.70$, $p < 0.05$) than that of the northern long-eared myotis (Fig. 2b).

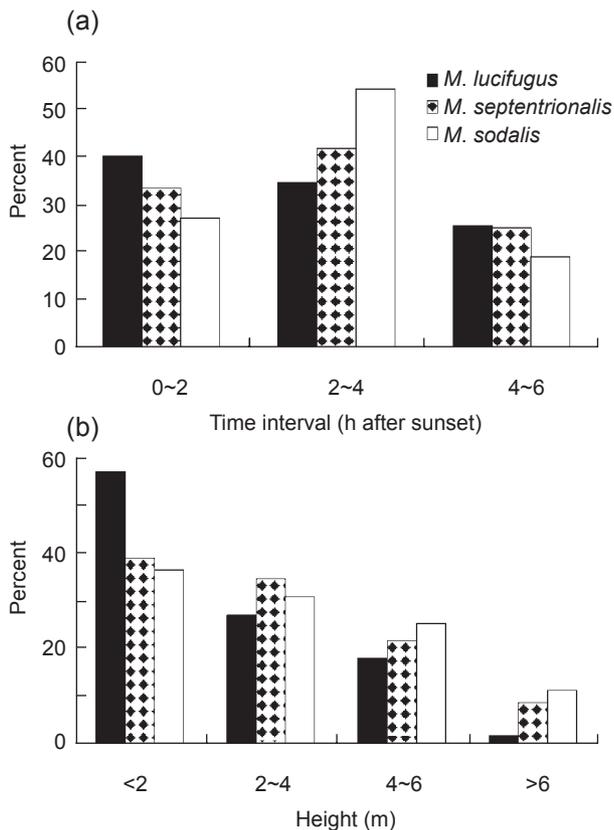


Fig. 1. Temporal (a) and height (b) distributions of bat captures of *Myotis lucifugus* ($n = 177$), *M. septentrionalis* ($n = 24$), and *M. sodalis* ($n = 37$).

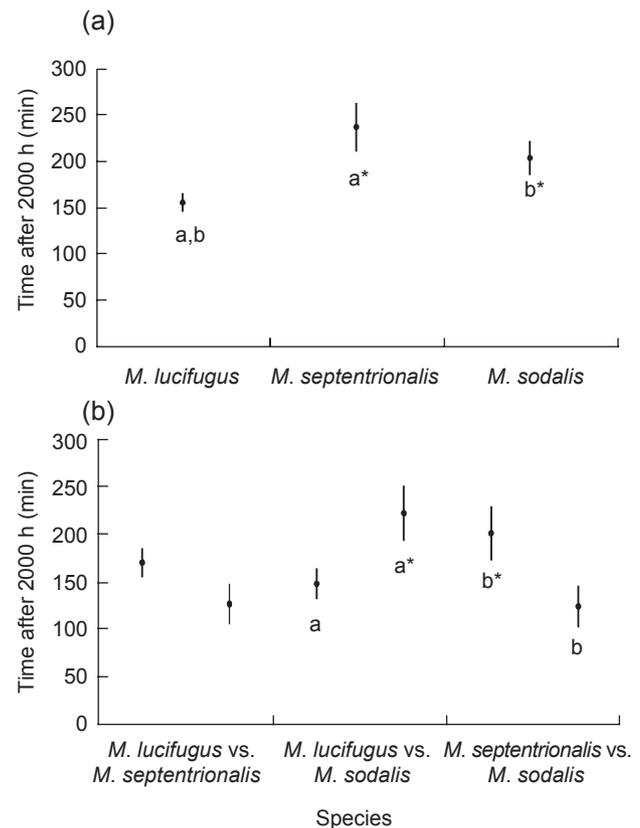


Fig. 2. Mean capture times (min \pm SE) of the 3 *Myotis* species when (a) each species was netted alone, and (b) paired species were netted at the same site. Data points with the same letter (i.e., a or b) indicate pair comparisons where a significant difference was found (* $P < 0.05$).

The heights of bat captures also tended to be non-random. The lowest 2 m above water accounted for 50% of the overall captures; captures declined with increasing height, and this was consistent for all 3 species ($G = 11.32$, d.f. = 6, $p < 0.1$; Fig. 1b). Where each species was netted alone, mean capture heights of the 3 species did not differ ($F_{(2, 86)} = 0.03$, $p > 0.9$; Fig. 3a). When the little brown and Indiana myotis were netted at the same site on the same night, significantly more of the former were netted at lower heights (1~3 m), while most of the Indiana myotis were netted at 4~7 m ($F_{(1, 38)} = 45.23$, $p < 0.001$). Capture heights of the little brown and northern long-eared myotis ($F_{(1, 52)} = 0.47$, $p > 0.4$), when caught at the same site, did not differ, and this was also the case for the northern long-eared and Indiana myotis ($F_{(1, 13)} = 0.02$, $p > 0.9$; Fig. 3b).

Insect abundances

Light and sticky traps collected the same 11 insect orders: beetles, flies, mayflies, true bugs, homopterans, hymenopterans, moths, neuropter-

ans, orthopterans, stoneflies, and caddisflies, as well as spiders. Light traps, however, collected more insect orders/site (3 m: 8.6 ± 0.6 orders, 10 m: 8.4 ± 0.5 orders; $F_{(1, 24)} = 50.83$, $p < 0.001$) and more insects/site (3 m: 1898 ± 880 individuals, 10 m: 617.1 ± 147.7 individuals; $F_{(1, 24)} = 7.66$, $p < 0.01$) than did sticky traps (3 m: 3.1 ± 0.9 orders, 22 ± 7.5 individuals; 10 m: 4.0 ± 0.7 orders, 24.1 ± 7.0 individuals). The 2 traps also differed in relative abundances ($G = 1102.70$, d.f. = 6, $p < 0.001$) and size distributions ($G = 450.28$, d.f. = 4, $p < 0.001$) of the insects collected.

Food resource use

Diets of the 3 species of bats contained the same 10 insect orders, and the distributions of the relative frequencies of these insects did not deviate from randomness ($G = 23.42$, d.f. = 18, $p > 0.4$). Beetles were the most-prevalent and abun-

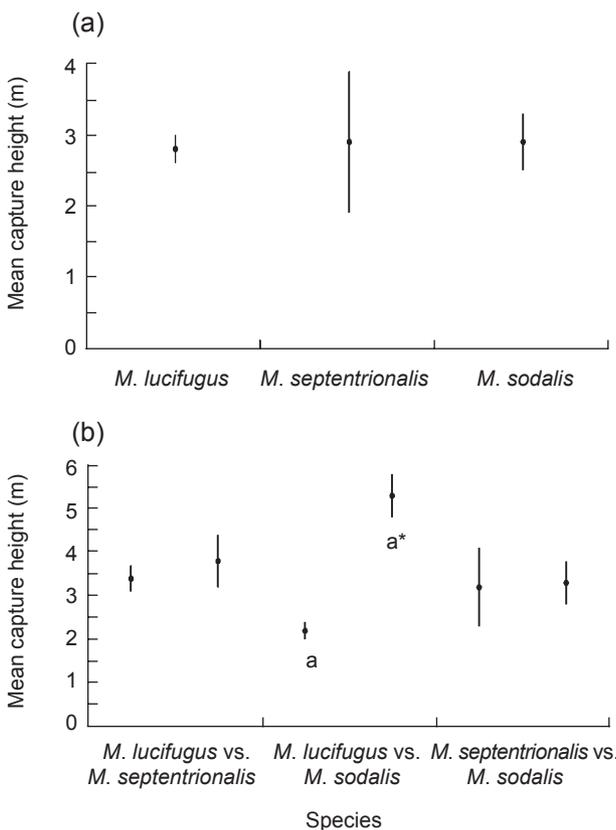


Fig. 3. Mean capture heights (m \pm SE) of the 3 *Myotis* species when (a) each species was netted alone, and (b) paired species were netted at the same site. Data points with the same letter (i.e., a or b) indicate pair comparisons where a significant difference was found (* $P < 0.05$).

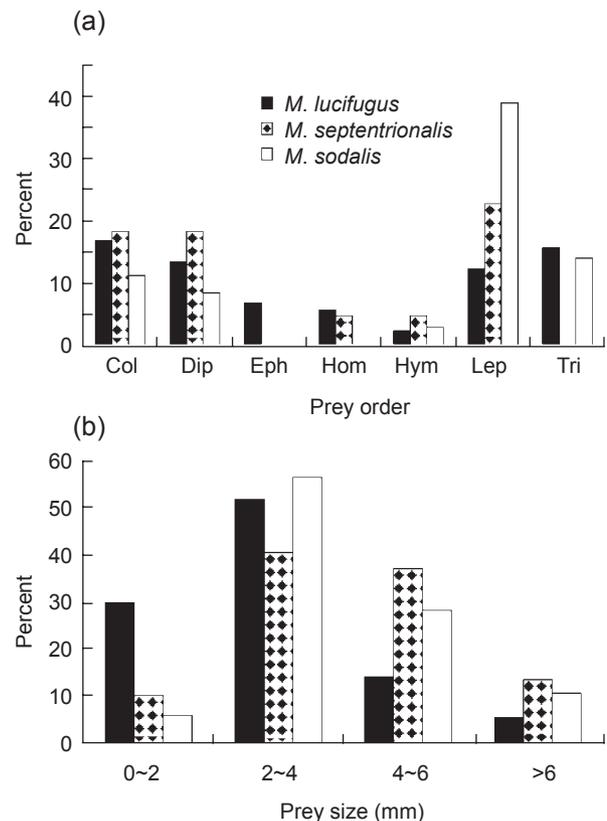


Fig. 4. (a) Different proportions of individual bats in *Myotis lucifugus* ($n = 90$), *M. septentrionalis* ($n = 22$), and *M. sodalis* ($n = 36$), which took each insect order as the predominant prey (defined as accounting for $> 50\%$ in a bat's diet) in their diets. (b) Distribution of estimated body sizes (mm) of beetles consumed by *Myotis lucifugus* ($n = 129$), *M. septentrionalis* ($n = 30$), and *M. sodalis* ($n = 86$).

dant prey in all 3 species' diets, except for being second to moths in proportion in the diet of the Indiana myotis. Moths, flies, and caddisflies each were among the 3 most-prevalent or abundant prey in diets of at least 2 species. Homoptera and Hymenoptera accounted for > 10% in frequency and > 5% in volume in all 3 species, and often followed the above 3 orders in both measurements. Despite these results, the diets of the 3 bats differed in relative proportions (Rao's $R_{(22, 268)} = 1.79$, $p < 0.02$) and in the rank orders of the relative importance of some insects, and in the diversity indices calculated (Table 1).

Among species, the Indiana myotis consumed significantly more moths than did the little brown myotis (Rao's $R_{(22, 268)} = 1.79$, $p < 0.02$; Fisher's LSD: $p < 0.001$). Mayflies accounted for a considerable amount in the diet of the little brown myotis, and surpassed that in the Indiana myotis' diet (Fisher's LSD: $p < 0.02$). The northern long-eared myotis consumed a higher proportion of orthopterans (Fisher's LSD: $p < 0.01$) than did either of the other 2 species. The remaining orders all accounted for < 5% in frequencies and < 2% in propor-

tions. The dietary diversity was higher in the little brown myotis than in the other 2 species (Table 1).

Individually, the proportion of the northern long-eared myotis that took beetles, flies, and hymenopterans as the dominant prey (defined as accounting for > 50% in a bat's diet) was higher than those of the other 2 species, while a higher proportion of the Indiana myotis took moths as the dominant prey. In contrast, a higher proportion of the little brown myotis took caddisflies and homopterans as the dominant prey compared to the other bats; and it was the only species that took mayflies as its dominant prey (Fig. 4a). The diet of the northern long-eared myotis did not differ between bats that were netted alone and those netted with either of the other 2 species (Rao's $R_{(20, 18)} = 1.73$, $p > 0.1$), and this was also the case for the Indiana myotis (Rao's $R_{(20, 44)} = 0.66$, $p > 0.8$). Diets of the little brown myotis, when netted alone, showed a lower proportion of flies than did when netted with the northern long-eared myotis (Rao's $R_{(22, 142)} = 2.06$, $p < 0.01$; Fisher's LSD: $p < 0.001$). Its diet also contained a lower proportion of flies (Fisher's LSD: $p < 0.05$) but a

Table 1. Relative frequency, relative proportions, and the relative importance (RI) of each prey order in the diets of (a) *Myotis lucifugus*, (b) *M. septentrionalis*, and (c) *M. sodalis*. Letters following a prey item indicate a significantly higher value in proportion to the bat species associated with the 1st letter than bat species associated with letters after the dash, in paired comparisons. Sample sizes (n = bats) are in parentheses

Prey [§]	(a) ($n = 89$)			(b) ($n = 22$)			(c) ($n = 36$)		
	Freq.	Prop.	RI*	Freq.	Prop.	RI	Freq.	Prop.	RI
Col	20.8	23.6±2.8	22.2	22.0	28.8±6.4	25.4	21.1	20.7±3.8	20.9
Dip	18.4	15.6±2.4	17.0	20.0	20.5±6.4	20.2	16.8	11.9±3.7	14.4
Eph ^{a-c}	6.2	7.5±2.0	6.9	5.0	3.5±1.9	4.2	1.2	0.5±0.4	0.9
Hem	5.4	1.8±0.6	3.6	2.0	0.2±0.1	1.1	3.7	0.7±0.3	2.2
Hom	16.2	11.1±1.9	13.6	10.0	5.7±2.8	7.8	14.3	6.5±1.5	10.4
Hym	10.8	6.6±1.4	8.7	14.0	7.8±2.7	10.9	9.9	4.7±1.9	7.3
Lep ^{c-a}	9.2	15.2±2.8	12.2	15.0	25.7±6.7	20.3	18.0	37.1±5.5	27.5
Neu	1.1	0.2±0.1	0.6	2.0	0.5±0.5	1.3	1.9	0.2±0.1	1.0
Ort ^{b-a,c}	0.8	<0.05	0.4	2.0	0.4±0.3	1.2	0.6	<0.05	0.3
Tri	9.7	18.3±2.9	14.0	8.0	7.1±2.4	7.5	11.8	17.7±4.5	14.8
Oth ⁺	1.4	0.1±0.1	0.8	0.0	0.0	0.0	0.6	<0.05	0.3
Total	100	100	100	100	100	100	100	100	100
DHI [†]		6.28			4.85			4.31	

[§] Col, Coleoptera; Dip, Diptera; Eph, Ephemeroptera; Hem, Hemiptera; Hom, Homoptera; Hym, Hymenoptera; Lep, Lepidoptera; Neu, Neuroptera; Ort, Orthoptera; Tri, Trichoptera; Oth, other.

* Relative importance (%) = (relative frequency + relative proportion)/2.

[†] Including araneids and unidentifiable fragments.

[‡] Dietary heterogeneity index = $1 / \sum (p_i^2)$, where p_i is the relative proportion of prey item i (i.e., each prey taxon) (Krebs 1989).

higher proportion of moths than it did when it was netted with the Indiana myotis (Fisher's LSD: $p < 0.05$). The estimated body sizes of beetles taken, based on 245 femora found in the bats' feces, ranged from ≤ 2 to ~ 10 mm, and most beetles taken by the 3 species were between > 2 and ≤ 4 mm (51.4%). The little brown myotis took more beetles of ≤ 2 mm and fewer beetles of > 4 mm in size than did the other 2 species. In contrast, higher proportions of the northern long-eared myotis took beetles of larger sizes (> 4 mm; $G = 29.67$, d.f. = 6, $p < 0.001$; Fig. 4b).

Compared to the insect abundances assessed by both sticky (Snedecor's $F_{(3, 13)} = 7.14$, $p < 0.005$) and light traps (Snedecor's $F_{(3, 13)} = 10.99$, $p < 0.001$), the Indiana myotis had a greater preference for moths, followed by beetles and the BHH group, and the least preference for the CDM group. The diet of the northern long-eared myotis showed the same pattern of prey preference as that of the Indiana myotis (Snedecor's $F_{(3, 17)} = 5.8$, $p < 0.005$). When compared with collections from the sticky traps, the little brown myotis had a greater preference for the BHH group, followed by moths and beetles, with the CDM group the least preferred (Snedecor's $F_{(3, 44)} = 9.28$, $p < 0.001$). Compared with the prey abundance assessed by the light traps, its diet still showed a greater preference for the BHH group, but it preferred the CDM group over moths and beetles (Snedecor's $F_{(3, 31)} = 16$, $p < 0.001$).

DISCUSSION

Our data, consistent with those of Mumford and Whitaker (1982), indicate that the little brown myotis is distributed throughout north-central Indiana in summer, and is the most common *Myotis* in the region. Our captures of the less-common Indiana and northern long-eared myotis came mostly from the central 1/3 of Indiana, and the 2 species co-occurred less frequently than either species with the little brown myotis. Murray et al. (1999) suggested no evidence that either the Indiana or northern long-eared myotis are more difficult to catch than the apparently more-common little brown myotis. The latter species roosts in both trees and man-made structures (Fenton and Barclay 1980); the Indiana myotis exclusively, and the northern long-eared myotis mostly, roosts in trees during the summer (Callahan et al. 1997, Foster and Kurta 1999). The lower capture rate of the Indiana and northern long-eared myotis, and

their more restricted occurrences in central Indiana, may be due to the lower availability of suitable roosting and foraging sites in the northern quarter of the state (Mumford and Whitaker 1982).

Captures data of the little brown myotis differed by time, but not by height, versus the other 2 species when each was netted alone. When they occurred at the same site on the same night, however, both times and heights of bat captures differed between co-occurring species. This is counter to what we predicted for their flight activities. The Indiana myotis displayed shifts both temporally, when netted with northern long-eared bats, and in height distributions, when netted with the little brown myotis, at the same sites. A shift to earlier times in the evening, as the Indiana myotis displayed, would be energetically advantageous to the bats, because of the higher insect abundance near dusk (Kunz 1973), and thus should be selected for. This also suggests, within our sampling scope, a flexible flight behavior of the Indiana myotis in accordance with the absence or presence of other potentially interacting species of bats. Mist netting might not perfectly reveal activity patterns of bats (but see Kunz and Brock 1975), and a drawback of this study is that we did not use ultrasound detectors to confirm the observed pattern. The latter technique, however, would still be biased in assessing activities of bats that use low-intensity calls (i.e., the northern long-eared myotis; Murray et al. 1999).

The overall diets of the 3 species contained the same insect orders, but the relative proportions differed for certain insect orders. The little brown myotis ate more mayflies, and the Indiana myotis ate more moths, than did the other bats. The diet of the northern long-eared myotis contained relatively more orthopterans than did the other 2 species, which may be correlated to their gleaning ability (Faure et al. 1993). The 3 species also differed in the percentages of individual bats that took different insects as dominant prey, and in the rank orders of relative importance of these insects in the bats' diets. The little brown myotis had a broader diet than both the northern long-eared and Indiana myotis, and the latter 2 species appeared to have a greater preference for moths. These results are compatible with a majority of earlier studies on food habits of these bats (Fenton and Barclay 1980, Griffith and Gates 1985, Kurta and Whitaker 1998).

The types and proportions of specific types of insects eaten are very likely to be associated with call features, eco-morphology, and foraging tactics

of bats (Fenton 1985). For instance, the low intensity echolocation calls of the northern long-eared myotis are relatively inaudible to moths (Faure et al. 1993), and thus may increase their success in hunting moths. The temporal distributions in captures of the Indiana and northern long-eared myotis are consistent with the fact that moths typically have higher abundances and activities later in the night than other nocturnal insects, notably beetles, flies, and true bugs, which often show peak activities shortly after dusk (Anthony and Kunz 1977, Rydell 1992), and which may at least in part explain the higher consumption of, and apparent diet preference for, moths by the 2 species.

All the 3 species took beetles of 2~10 mm in size, which is similar to the prey size range reported for the little brown myotis in New Hampshire (3~10 mm, Anthony and Kunz 1977). Yet, the northern long-eared myotis ate a higher percent of larger beetles than did the Indiana myotis, and also than did the little brown myotis. This confirms our prediction based on previously reported differences in the mean length of maxillary tooth-row of these bats; although, the greater proportion of smaller-sized beetles taken by the little brown myotis was unexpected. The mean size of beetles collected in the field (4.6 mm) was smaller than some other insects taken as major prey of these bats, e.g., moths (8.2 mm), caddisflies (5.2 mm), and mayflies (5.8 mm) (Lee, unpubl. data). Because our estimates were based solely on beetles, the actual prey size range of the 3 bats may be larger than observed. Nonetheless, our results support the cranial-dental morphology (e.g., jaw length) being correlated with the sizes of insects taken by bats.

Acknowledgments: We thank USFWS, Indiana DNR, 3D/Environmental Services, Inc., and the University of Tennessee for financial and logistic support; V. Brack Jr, K. Tyrell, H. Luh, and Y.-M. Kuo for advice and assistance; and G. Sexton, C. Hobson, A. King, and P. Clem for assistance with fieldwork. Two anonymous reviewers kindly improved this manuscript.

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