Am. Midl. Nat. 162:43–51

Prey Consumed by Eight Species of Insectivorous Bats from Southern Illinois

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ABSTRACT.—We collected data on the diet of eight species of insectivorous bats (Chiroptera, Vespertilionidae): big brown bats (*Eptesicus fuscus*), red bats (*Lasiurus borealis*), evening bats (*Nycticeius humeralis*), northern myotis (*Myotis septentrionalis*), little brown myotis (*M. lucifugus*), Indiana myotis (*M. sodalis*), southeastern myotis (*M. austroriparius*) and eastern pipistrelles (*Perimyotis subflavus*). Bats were mist netted during the summers of 1999 and 2000 at 41 forest sites throughout southern Illinois. We analyzed prey remains in fecal pellets of 305 individuals to assess diet similarity among species and relationships between bat body mass and prey diversity and hardness. Larger species included big brown bats and evening bats that ate primarily hard-bodied beetles (Coleoptera). These bats had the greatest dietary similarity index value compared with the other chiropterans in the community, and the highest hardness indices of prey consumed. Red bats, second only to *E. fuscus* in mean body mass, ate more soft bodied moths (Lepidoptera) and leaf hoppers (Homoptera) than beetles. Smaller bats, including three species of *Myotis*, consumed the greatest diversity of prey and were generally grouped together in diet similarity indices. Little brown myotis, northern myotis and Indiana myotis fed primarily on moths and beetles. Northern myotis and little brown myotis also fed extensively on spiders, suggesting significant gleaning behavior. Unlike other *Myotis*, the southeastern myotis had a low dietary diversity index and fed primarily on caddisflies (Trichoptera), as did eastern pipistrelles. Pipistrelles and myotines had the lowest hardness indices of prey consumed. Bats in southern Illinois exhibited landscape level (macroscale) feeding patterns consistent with the predicted relationship between body size and hardness of prey consumed, while at the local, site-specific level (microscale) they foraged with extensive overlap among similar-sized species, especially most *Myotis*. Regional differences in diets were minimal within the same assemblage of bat species in southern Indiana.

INTRODUCTION

Close relationships exist between diets of bats and factors such as foraging habitats used, wing morphology, tooth structure, jaw musculature and resultant bite force, characteristics of echolocation calls and hardness of prey consumed (Belwood and Fenton, 1976; Fenton and Morris, 1976). For example, relative to smaller bats, larger bats with more robust skulls and larger teeth should be able to consume prey over a wider range of sizes (Aldridge and Rautenbach, 1987), including more hard-bodied insects such as coleopterans (Aguirre *et al.*, 2003; Freeman, 1981). Also, bats with low aspect ratios and wing loadings, and short, broad based calls, are adapted for slow, maneuverable flight in cluttered habitats (Fenton, 1990;

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Norberg, 1994; Fenton and Bogdanowicz, 2002; Aguirre *et al.*, 2003). Insectivorous bats in tropical communities consist of species that fly rapidly, fly slowly, hover or glean so that flight characteristics of bats may result in partitioning of food resources (Norberg, 1994), although most species combine two or more strategies and communities may contain very similar species.

Temperate communities are much less diverse than in the tropics, often being limited to vespertilionids (as in southern Illinois), where body size ranges from the 30-g hoary bat (*Lasiurus cinereus*) to the 5-g small-footed myotis (*Myotis leibii*, Steffen *et al.*, 2006). Nonetheless, within the genus *Myotis* (Chiroptera, Vespertilionidae), distributed worldwide, feeding modes include aerial hawkers, gleaners, water bats and trawlers (Fenton and Bogdanowicz, 2002). Several of these modes occur in north temperate communities although Black (1974:138) concluded that most north temperate insectivorous bats "could be classified as either moth or beetle strategists." However, a great deal of intraspecific variation in diet may exist because of spatial and temporal differences in prey availability.

Thirteen species of vespertilionid bats occur in southern Illinois. Most are sympatric and commonly captured. We compared prey selection among eight species of insectivorous bats in southern Illinois: big brown bats (*Eptesicus fuscus*), red bats (*Lasiurus borealis*), evening bats (*Nycticeius humeralis*), northern myotis (*Myotis septentrionalis*), little brown myotis (*M. lucifugus*), Indiana myotis (*M. sodalis*), southeastern myotis (*M. austroriparius*) and eastern pipistrelles (*Perimyotis* [formerly *Pipistrellus*] *subflavus*; see Simmons, 2005). Our objectives were to examine relative similarity of diets and diversity of diet relative to body size, and the extent of regional differences within the same assemblage of bat species in west central Indiana. Based on body size, we expected big brown bats and red bats would have the broadest dietary diversity. Regionally, we expected that prey eaten by the guild of bats in southern Illinois and in Vigo County, Indiana, would be similar.

METHODS

We mist netted bats from 18 May–18 Aug. 1999 and 12 May–20 Jul. 2000 at 41 forest sites throughout 109,267 ha Shawnee National Forest in southern Illinois. The forest extends from approximately 37°17′ to 37°83′ latitude and approximately 89°67′ to 88°08′ longitude. Sites were dominated by oak (*Quercus* sp.) and hickory (*Carya* sp.) overstory. Mist netting followed the Indiana Bat Protocol (USFWS, 1999) with net sets placed over water sources or near edge habitats, as well as in interior forest (Carroll *et al.*, 2002; Feldhamer *et al.*, 2001). We recorded species, gender, age (juvenile or adult), body mass and reproductive condition for each individual. Each bat was placed in a plastic cup for about 10 min to collect fecal pellets. Pellets from each bat were kept in sealed vials until analyzed. Analyses of prey remains in fecal pellets were to the ordinal or family level as described by Whitaker (1988, 2004). Pellets were covered with ethanol in a Petri dish, teased apart and examined with a dissecting microscope at a magnification of 30×. Results represent average percentage volume for each prey taxon based on visual estimates. We retain the taxon Homoptera (Triplehorn and Johnson, 2005) to facilitate comparison with previous studies of bat feeding habits and to differentiate homopterans from true bugs (Hemiptera). We followed guidelines of the American Society of Mammalogists for handling animals and the Institutional Animal Care and Use Committee at Southern Illinois University approved all protocols.

We used percentage volumes for each prey taxon to calculate a similarity index (Whitaker, 2004) for each pair of bat species. Diet similarities were determined as: $SI = 2 (\Sigma W)/ A + B$, where W was the lesser of the two values of each food group (insect order or arachnids) for each pair, and A and B were the percentage volume totals for the species pair (which did not always equal 200 because of rounding error and trace food components [<0.1%] that were not tallied). Clustering of similarity index values for bat communities was generated by use of the unweighted pair group method with arithmetic averages (UPGMA). We calculated a feeding diversity index for each bat species using the Shannon-Weiner Index as $DI = e^H$ with $H = -\Sigma p_i \ln p_i$ where p_i was the proportion of each prey species in the diet. We derived a Hardness Index for the diet of each species of bat using percentage volume (p_i) of each prey order consumed and the associated hardness value (HV) from 5 (hardest) to 1 (softest) for each order (Freeman, 1981) as $\Sigma [p_i \times HV]$. Statistical tests were calculated using the program JMP IN 4.0.2 (SAS Institute, Inc,) with $\alpha = 0.05$.

RESULTS

Eptesicus fuscus.—As expected for a "beetle strategist," big brown bats fed primarily on coleopterans (72.2% by volume), with 22 of 24 individuals sampled (91.7% frequency) taking beetles. Ground beetles (Carabidae) comprised the bulk of coleopterans consumed both years, followed by diving beetles (Dytiscidae) and scarabs (Scarabaeidae). The two individuals that did not feed on coleopterans primarily ate other hard-bodied insects, specifically stink bugs (Hemiptera: Pentatomidae) and ichneumons (Hymenoptera: Ichneumonidae). The only other major food group (17.1%) for big brown bats was hemipterans. No lepidopterans were in pellets collected from the 24 *E. fuscus* (Table 1). Consistent with the predominance of coleopterans in their diet, big brown bats had the lowest feeding diversity index (Table 2) of the eight bat species.

Lasiurus borealis.—Unlike big brown bats, lepidopterans formed the largest component (39.1%) of the diet of red bats. Homopterans (27.1%) also were common, with leafhoppers (Cicadellidae) accounting for all of this order. Coleopterans (primarily scarab beetles) made up 23.1% of the diet. All other groups comprised <5% of the diet (Table 1). The remains of spiders (Araneae) were found in two of the 48 red bats (4.2%) sampled.

Nycticeius humeralis.—Evening bats (n = 20) were similar to big brown bats in that ground beetles (coleopterans) comprised the bulk of the diet (52.8%). Hemipterans also were common (13.0%). Again like big brown bats, evening bats took no lepidopterans. Unlike *Eptesicus fuscus*, homopterans–specifically leafhoppers–were a major dietary item (21.0%).

Perimyotis subflavus.—Trichopterans (caddisflies) formed the bulk of the diet (55.7%) of 67 eastern pipistrelles, followed by coleopterans (21.5%) and Hymenoptera (11.8%; ants, Formicidae). The dietary similarity index of *P. subflavus* was closer to that of *Myotis austroriparius* than to other *Myotis* (Table 3, Fig. 1C). The hardness index for *P. subflavus* was very close to the indices for *M. septentrionalis* and *M. lucifugus* (Table 2).

Myotis species.—We treated these bats together because of the similarities in their morphological features, dietary habits of all but the southeastern bat (Table 1), and resultant similarity indices (Fig. 1, Table 3). Relatively diverse diets were found in all the *Myotis* sampled, especially little brown myotis, northern myotis and Indiana myotis. These three species fed primarily on lepidopterans and coleopterans. Southeastern myotis were the exception. They had a lower diversity index (3.26) compared to the mean of 5.68 for the other three *Myotis* species. The diet of southeastern myotis was 59.0% trichopterans. Caddisflies also were common in the myotine diets, but in *M. lucifugus*, *M. septentrionalis* and *M. sodalis* they represented less than half the volume found in *M. austroriparius*. Also, southeastern myotis, like Indiana myotis, ate relatively few arachnids, whereas spiders were a common prey for northern myotis (15.6%) and little brown myotis (14.3%).

TABLE 1.—Percentage volume of prey remains for insects (to order and family) and spiders from 305 bats of eight species from southern Illinois. Sample sizes are in parentheses. Overall total percentage for each species of bat may not equal 100. Number [1–5] following ordinal names of prey is the hardness value of that taxon from Freeman (1981), with 5 = hardest

	BAT SPECIES[a]							
PREY GROUP	EPFU (n = 24)	LABO (n = 48)	NYHU (n = 20)	MYAU (n = 10)	MYLU (n = 8)	MYSO (n = 12)	MYSE (n = 116)	PESU (n = 67)
COLEOPTERA [5]	72.2	23.1	52.8	1.0	20.7	18.3	19.3	21.5
Carabidae	41.7	2.0	40.0		10.7	13.8	0.8	
Chrysomelidae							2.1	
Curculionidae	1.9	0.5	3.0				0.6	
Dytiscidae	16.2		2.0					
Elateridae	3.3	0.5	2.8		3.6			
Scarabaeidae	8.5	14.5	2.0		3.6	2.9	2.9	3.4
DIPTERA [1]	0.5	2.7	0.8	11.5	8.6	2.9	7.9	6.6
HEMIPTERA [4]	17.1	1.0	13.1	14.0		6.7	1.9	0.1
Coreidae	1.0		2.5					
Lygaeidae		0.6	2.8	0.5		3.8	0.1	
Miridae				10.0				
Pentatomidae	16.1		7.8					
HOMOPTERA [2]	2.1	27.1	21.0		7.1	10.4		1.9
Cicadellidae		27.1	20.8		7.1	10.4		1.9
Diaspididae	2.1		0.2					
HYMENOPTERA [4]	4.6	1.3	2.0			4.6	0.1	11.8
Formicidae		1.3	0.8			0.8		11.8
Ichneumonidae	4.6		1.2			3.8	0.1	
LEPIDOPTERA [2]		39.1		14.0	27.1	42.5	31.8	1.4
NEUROPTERA [1]	0.1	0.2	2.8			0.4		
Hemerobiidae	0.1	0.2				0.4		
ORTHOPTERA [3]							0.2	
TRICHOPTERA [1]	3.3	4.3	7.0	59.0	22.1	14.2	21.8	55.7
ARANEAE [2]		0.4		0.5	14.3		15.6	
OVERALL TOTALS	99.9	99.2	99.5	100.0	99.9	100.0	98.6	99.0

[a] abbreviations: EPFU = *Eptesicus fuscus*, big brown bat; LABO = *Lasiurus borealis*, red bat; NYHU = *Nycticeius humeralis*, evening bat; MYAU = *Myotis austroriparius*, southeastern myotis; MYLU = *Myotis lucifugus*, little brown myotis; MYSO = *Myotis sodalis*, Indiana myotis; MYSE = *Myotis septentrionalis*, northern myotis; PESU = *Perimyotis subflavus*, eastern pipistrelle

Body mass and diet.—Mean body masses of *Eptesicus fuscus*, *Lasiurus borealis*, and *Nycticeius humeralis* were significantly different than the other five species (Table 2). Dietary diversity indices were highest in three of the four *Myotis* species and lowest in *E. fuscus* (Table 2). There was no significant relationship between mean body mass of bats and dietary diversity ($F = 3.63$, $df = 7$, $P < 0.106$). However, as expected, the hardness index was highest in *E. fuscus*—2.8 times greater than in *M. austroriparius* (Table 2). There was a significant positive relationship between body mass of bats and the associated hardness index of their diet ($F = 11.67$, $df = 7$, $P < 0.014$).

TABLE 2.—Mean body mass, feeding diversity index and hardness index of prey consumed for eight species of bats from southern Illinois. Sample sizes (for mean body mass) are in parentheses. Body masses of species with the same letter are not significantly different at P < 0.05

	EPFU[a] (n = 29)	LABO (n = 74)	NYHU (n = 20)	MYAU (n = 10)	MYLU (n = 13)	MYSO (n = 14)	MYSE (n = 166)	PESU (n = 71)
Mean body mass ± SD	19.50 ± 3.10 A	11.96 ± 2.83 B	10.45 ± 1.71 C	8.75 ± 0.89 CD	7.92 ± 1.55 DE	6.71 ± 0.75 DE	6.61 ± 0.91 EF	6.14 ± 1.18 F
Diversity Index (e^H)	2.47	4.17	3.79	3.26	5.42	6.63	5.00	3.41
Hardness Index[b]	4.59	2.64	3.77	1.62	2.32	2.61	2.29	2.24

[a] abbreviations as in Table 1

[b] See text for calculation. Higher values signify a diet of harder items necessitating greater bite force

DISCUSSION

We found a significant relationship between mean body mass of bats in southern Illinois and prey hardness. The diet of the largest, heaviest bat in our community, *Eptesicus fuscus*, was skewed significantly toward beetles with a marked lack of soft-bodied prey. Smaller bats, although consuming a broad range of prey, took more soft foods. Although Whitaker (2004:462) found "... no apparent relationship between size of bat and food," when we reanalyzed his data (his Table 3) from Vigo County, Indiana, using the prey hardness values of Freeman (1981), there was a significant positive relationship between body mass of bats and hardness of the prey ($F = 9.05$, $df = 6$, $P < 0.03$), similar to that in southern Illinois.

We also expected larger bats would consume a greater variety of prey (Aldridge and Rautenbach, 1987), but we found no relationship. This may have been because the bat community in southern Illinois represents a relatively limited group morphologically and ecologically compared to the broader species diversity found in tropical bat communities. Also, the diversity index did not adequately reflect the range of prey sizes consumed. Finally,

TABLE 3.—Matrix of similarity indices for diets of eight species of bats from southern Illinois collected during summers of 1999 and 2000 (unshaded). Matrix of similarity indices (shaded) for seven species of bats from Vigo County, Indiana (Whitaker, 2004). The southeastern myotis (MYAU) was not collected in the Indiana study

	EPFU	LABO	MYAU	MYLU	MYSE	MYSO	NYHU	PESU
EPFU[a]		0.588	0.188	0.267	0.252	0.356	0.741	0.321
LABO	0.196		0.234	0.626	0.604	0.776	0.520	0.336
MYAU	*	*		0.462	0.474	0.388	0.219	0.651
MYLU	0.228	0.411	*		0.909	0.696	0.357	0.529
MYSE	0.356	0.444	*	0.818		0.696	0.294	0.498
MYSO	0.318	0.389	*	0.838	0.893		0.457	0.436
NYHU	0.739	0.315	*	0.290	0.418	0.379		0.336

[a] abbreviations as in Table 1.

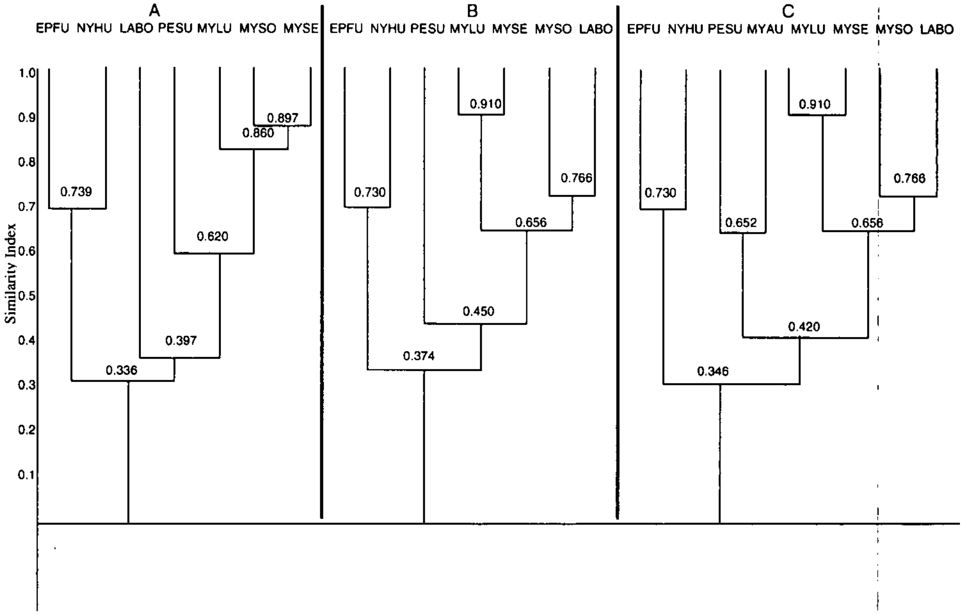

FIG. 1.—Dendrogram of dietary relationships of bats. Larger values indicate greater similarity. A. Data from Vigo County, IN, from Whitaker (2004). B. Data from the current study excluding southeastern myotis (*M. austroriparius*) for comparison with Whitaker (2004). C. Data from the current study including southeastern myotis. Abbreviations for bat species as in Table 1

seasonal variability among sex and age groups of bats and their reproductive condition (Brack and LaVal, 2006), as well as considering only the ordinal level of prey for analyses could mask relationships. If we could identify insect remains to genus and species, there might well be greater differences in diet among the eight species of bats studied.

Other than *M. austroriparius*, the species of bats that we caught in southern Illinois were the same seven species Whitaker (2004) reported from Vigo County, Indiana—approximately 320 km from the center of our sites. Whether we exclude (Fig. 1B) or include (Fig. 1C) *M. austroriparius* from our data set the feeding relationships of the two bat communities were similar. Big brown bats and evening bats grouped closely with similarity indices essentially the same from both study areas (Table 3). Numerous studies since Hamilton (1933) have documented coleopterans as the primary food of big brown bats (Black, 1974; Griffith and Gates, 1985; Whitaker, 1995; Carter *et al.*, 2003; Whitaker and Barnard, 2005) as well as evening bats (Whitaker and Clem, 1992; Feldhamer *et al.*, 1995; Carter *et al.*, 2004). The major difference in southern Illinois relative to Vigo County was the close association of red bats with Indiana bats. Both *Lasiurus borealis* and *M. sodalis* had over 70% of their diets composed of lepidopterans, homopterans, and coleopterans (Table 1). Again, these prey items are well documented in the diet of red bats (Black, 1972; Feldhamer *et al.*, 1995; Hickey *et al.*, 1996; Carter *et al.*, 2003, 2004). Kunz (1973) suggested that red bats consumed a less diverse range of insect taxa than did sympatric *Myotis* species or big brown bats. However, the diversity index of red bats in our study was higher than either big brown bats or evening bats. As noted, lepidopterans were most common in the diet of red bats, as they were in Indiana (Whitaker, 2004).

Eastern pipistrelles were similar to southeastern myotis in their consumption of caddisflies, suggesting both species fed predominately over water (Jones and Manning, 1989). Fujita and

Kunz (1984) reported the diet of eastern pipistrelles included ground beetles, leafhoppers, mosquitos, midges (Diptera: Chironomidae), ants and moths. We found several of these taxa were eaten as well. We determined *Perimyotis subflavus* ate relatively soft prey as expected. We could not determine size of prey consumed; however, as one of the smallest species of bat in Illinois, they would be expected to eat smaller items (Ross, 1967).

The diet of most myotines in southern Illinois clustered closely. In Indiana, Whitaker (2004) also noted close similarities in the diet of *Myotis sodalis, M. septentrionalis* and *M. lucifugus* to Illinois samples, although Griffith and Gates (1985) found little diet similarity between males of the latter two species in Maryland. Lee and McCracken (2004) found temporal and spatial shifts in feeding behavior associated with syntopic *M. septentrionalis, M. sodalis* and *M. lucifugus* not found at locations where a single species occurred. Unlike our study, however, *M. sodalis* throughout their range usually include a significant percentage of dipterans in their diet (Kurta and Whitaker, 1998; Murray and Kurta, 2002; Tuttle *et al.*, 2006). Lack of dipterans in our study may reflect the relative availability of other prey items. As noted, the diet of southeastern myotis was closer to that of the eastern pipistrelle than to any of the other species of *Myotis* (Table 3, Fig. 1C), with over half the diet of both species comprised of caddisflies (Table 1). Many bats apparently prefer caddisflies, which are soft-bodied and usually are intermittently available (Whitaker, 2004). Although only *M. lucifugus* ate caddisflies in Vigo County, in southern Illinois they formed a large percentage of the diet of *M. septentrionalis, M. sodalis, M. lucifugus, M. austroriparius* and *Perimyotis subflavus.* Based on a limited sampling period, Zinn and Humphrey (1981) considered *M. austroriparius* in northern Florida to be a generalist feeder, but with a preference for coleopterans and lepidopterans, followed by dipterans (mosquitos). Intraspecific variation and generality of feeding habits of *Myotis* (Belwood and Fenton, 1976; Fenton and Morris, 1976) and other species at the local, site-specific level (microscale) is exemplified by the almost complete lack of coleopterans consumed by southeastern myotis on our study sites. Fenton and Barclay (1980:4) characterized *M. lucifugus* as "... catholic in the food they eat ..." with size (3–10 mm in length) being the primary determinant of selectivity (Anthony and Kunz, 1977). We suggest that this descriptor applies to the adaptable or generalist feeding patterns of most *Myotis* in our study — consuming most of the main prey groups available.

Another reflection of generalist feeding by many temperate insectivorous bats was the gleaning behavior evident in consumption of spiders by *Myotis septentrionalis* (15.6%) and *M. lucifugus* (14.3%) in our study. Ratcliffe and Dawson (2003) demonstrated experimentally that these species both aerial hawk and glean prey. Although bats could consume some spiders aerially as the latter disperse via ballooning, foraging on arachnids clearly involves a large component of gleaning behavior. Gleaning also may be occurring with other prey such as moths, especially in vespertilionids adapted for slow, maneuverable flight, often within cluttered understory (Fenton, 1990; Norberg, 1994). Northern myotis especially seem adapted to gleaning given that Carroll *et al.* (2002) mist netted significantly more in interior forest than along edge habitats in southern Illinois. Also, the echolocation calls of *M. septentrionalis* are better adapted to gleaning than those of *M. lucifugus* (Faure *et al.*, 1993). Whitaker (2004) found only 2.0% spiders by volume in *M. septentrionalis* from Vigo County, and none in *M. lucifugus* or *M. sodalis,* but suggested that all three species could be gleaning. Gleaning also was suggested for *M. lucifugus* in a colony near Fairbanks, Alaska, in which spiders comprised 16.8% of the food items in 100 pellets (Whitaker and Lawhead, 1992). Although most of the species in our study could not be shown directly to be gleaners, they are probably capable of facultative gleaning depending on spatial and temporal changes in prey availability.

We found bats in southern Illinois exhibited overall feeding patterns consistent with previously described macroscale relationships of body size and hardness of prey consumed. At the microscale level, bats appeared to forage generally with extensive overlap among similar-sized species. In addition to morphological features and varying prey availability, a greater diversity of prey consumed by some bat species probably reflects more diverse foraging habitats and behavior. Given the extensive facultative gleaning in *Myotis lucifugus* and *M. septentrionalis* found in our study, and considering the low aspect ratio and wing loading of many southern Illinois bat species, we suspect gleaning–within the limits imposed by size and hardness of prey—potentially is more widespread than has been previously documented.

Acknowledgments.—The United States Forest Service funded this project. We thank personnel of Shawnee National Forest for their support and encouragement, particularly S. Widowski. Additional support was received from the Department of Zoology at Southern Illinois University, Carbondale. We thank C. Krajewski for assistance generating the dendrograms. We also thank the numerous individuals who helped with mist netting.

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SUBMITTED 24 APRIL 2008 ACCEPTED 2 JULY 2008