The Foraging Ecology of Some Bats in Indiana

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Introduction

Twelve species of Chiroptera have been reported from Indiana (23), but *Myotis austroriparius* (southeastern myotis) and *Plecotus rafinesquii* (Rafinesque's big-eared bat) are extremely rare. Only 1 colony of *Myotis grisescens* (gray bat) is known from Indiana (7). *Pipistrellus subflavus* (eastern pipstrelle) is relegated to southern Indiana which was not glaciated by the most recent (Wisconsinan) glaciation. *Nycticeius humeralis* (evening bat) is uncommon in Indiana, with only a few nursery colonies containing adult females and young of the year having been located in Indiana (23). *Lasiurus cinereus* (hoary bat) is widely distributed but rarely common at any locale. Males are rare in the state (23). *Lasionycteris noctivagans* (silver-haired bat) is found in Indiana only in spring and autumn as a migrant (23). During the summer, the sexes of *Myotis sodalis* (Indiana bat) are allopatric within the state. *Myotis keenii* (Keen's bat), *Myotis lucifugus* (little brown myotis), *Lasiurus borealis* (red bat), and *Eptesicus fuscus* (big brown bat), occur throughout Indiana.

Several species of bats can frequently be found within the same area or same habitat. This study was undertaken to determine the foods eaten, habitats or parts of habitats used, and times of activity, of each of the 10 species. Results of 2 of these, *M. sodalis* and *M. keenii*, will be reported upon elsewhere.

Materials and Methods

Bat Capture

Bats were captured during the season of reproduction (15 April to 15 August) in wooded upland (14 sites; 89 net nights) and riparian areas (21 sites; 61 net nights) throughout Indiana. Mist nets were "stacked" and run on a rope pulley system to close off all flight space from the forest floor or stream surface up to the canopy. Capture time and height, and the sex, age, and reproductive condition were noted for each bat. Chi-square tests were used to determine randomness of activity during the night (divided into the periods: dusk to 22:00 h/22:00 to 24:00 h/24:00 to 02:00 h/02:00 h to dawn), height of catch, and habitat (riparian/nonriparian) of catch. Heights of capture correspond to the 3 foliage layers (22): shrub ($\leq$ 0.6 m), canopy (usually $>$ 7.6 m, depending of the vegetation), and the understory or subcanopy. Catch per habitat was tested by both catch per net night and by catch per net site. Feces were sometimes collected from bats captured at caves.

Fecal Analysis

The analysis method used was that of Brack and LaVal (5). Briefly, insect parts were identified from the feces, and quantified by an estimate of percent volume. When the diets of 2 or more bats was combined each bat contributed equally to the combined diet. An analysis of variance was conducted on an arcsine-transformation of the date to compare diets among dates of sampling or sample groups. Statistical analyses were completed on Digital Equipment Corporation PDP-11/70 computer systems using a version of SPSS (24) from Northwestern University.

A diet diversity index (DDI) was calculated for each species, and for some species by date, sex, and age of sample. The diversity index used was that of MacArthur (21): $DDI = 1/\sum P_i^2$, where P_1, P_2 ... were the proportions of each insect order in the diet.

Results

Myotis lucifugus

Adult males were captured at caves during the summer but few individuals roosted there. No females or juveniles were caught at caves until late in the season. Only 4 adult males, but 34 adult females and 19 juveniles, were caught outside the cave region. County records were established for Porter, Jasper, Starke, and LaPorte counties.

The catch of *M. lucifugus* was similar in riparian and nonriparian habitat when considering catch per site, but more bats were caught in riparian habitat when considering catch per net night (Table 1). In riparian habitat, catch was concentrated in the understory; in nonriparian habitat, catch was too small to test (Table 2). Catch was distributed evenly throughout the night (Table 3).

Myotis grisescens

Only 7 lactating females and 4 males were netted, all in riparian habitat. Two were caught in the subcanopy layer and 9 in the shrub layer. The catch appeared bimodal with bats captured early and late in the night, but the sample was too small to test. A total of 84 fecal pellets, 48 from females and 36 from males, were analyzed. Males' and females' diets were similar. Trichopterans formed 56.0% of the diet, coleopterans 23.3%, lepidopterans 11.3%, dipterans 5.8%, hymenopterans 1.2%, plecopterans 0.5%, and homopterans 0.7%. Fewer homopterans were eaten by females ($P = 0.040$). The diet diversity index (DDI) was 5.79 for both sexes and 5.18 when combined.

Lasiurus borealis

A total of 85 individuals were caught; 6 unsexed, unaged bats escaped from nets before they could be removed. Four bats were caught at caves; 2 adult males and 2 juveniles. The adult male (N = 22) and female (N = 21) catch was nearly equal. *Lasiurus borealis* was caught at more sites than any other species (Table 1). Catch was equal in riparian and nonriparian habitat when considered by net site, but greater in riparian habitat when considered by net night (Table 1). In riparian habitats the catch was greatest in the subcanopy layer but equal in the subcanopy and canopy layers in nonriparian habitat (Table 2). On 2 occasions, pastures dotted with small trees contained large numbers of *L. borealis* foraging several times the height of existing vegetation. This bas was most frequently caught during the dusk and dawn periods, representing a bimodal activity period (Table 3).

TABLE 1. Bat catch by net night and by catch site in riparian (R) and nonriparian (NR) habitats. Statistics are based on 150 net nights (61 riparian, 89 nonriparian) at 35 catch sites (21 riparian, 14 nonriparian).

Species	Total Catch		Number of Bats Caught				Number of Sites Where Caught			
	Bats/Net Night	Proportion of Sites	R	NR	X^2	P	R	NR	X^2	P
M. lucifugus	0.3867	.4000	50	8	49.843	0.000	10	4	0.762	0.383
M. grisescens	0.0733	.1143	11	0	16.047	0.000	4	0		
L. borealis	0.6133	.8000	56	36	15.557	0.000	18	10	0.214	0.643
L. cinereus	0.1200	.2857	4	14	2.539	0.111	4	6	1.667	0.197
E. fuscus	1.7133	.7714	110	147	0.484	0.487	14	13	0.747	0.388
P. subflavus	0.0733	.1429	11	0	16.047	0.000	5	0		
N. humeralis	0.0333	.0286	0	5			0	1		
L. noctivagans	0.0133	.0286	0	2			0	1		

TABLE 2. Bat catch at shrub (1), subcanopy (2), and canopy (3) levels in riparian, nonriparian, and both habitats combined.

Species	Riparian					Nonriparian					Combined	
	1	2	3	X^2	P	1	2	3	X^2	P	X^2	P
M. lucifugus	5	40	3	54.125	0.000	0	5	3			55.750	0.000
M. grisescens	9	2	0			0	0	0				
L. borealis	4	31	11	25.609	0.000	0	16	16	16.000	0.000	35.615	0.000
L. cinereus	0	3	2			0	6	7	6.615	0.037	9.000	0.011
E. fuscus	7	55	13	54.720	0.000	1	95	34	104.969	0.000	157.532	0.000
P. subflavus	0	9	2			0	0	0				
N. humeralis	0	0	0			0	0	5				
L. noctivagans	0	1	0			0	1	2				

Feces, totaling 318 pellets, from 59 bats were analyzed. Coleoptera (42.5%) and Lepidoptera (37.5%) were the major prey. Insects of the orders Diptera and Homoptera were each 4.3% of the diet, Plecoptera 2.1%, Neuroptera 1.8%, Hymenoptera 0.9%, and Trichoptera 0.5% of the diet. The following families of Coleoptera were identified in the feces: Scarabaeidae 10 times, Elateridae 8 times, Silphidae 3 times, and Carabidae once. Curculionidae remains were identified 3 times; 2 of these were the Asiatic oak weevil, *Cyrtepistomus castaneus*. The diets of males, females, and juveniles were similar. There was no difference between the diets from bats captured in different years. Dietary variation of bats captured at widely separated localities was also low, although consumption of Neuroptera varied ($P = 0.011$). DDI's varied between 2.00 and 6.13. The overall DDI was 5.07.

Lasiurus cinereus

Five adults (1 male), 12 juveniles, and 1 unsexed unaged bat were caught. County records were established for Porter, Steuben, and Noble counties. The adult male is only the second known from the state. There was no difference between the numbers of bats caught in riparian and nonriparian habitats, either by site or by net night (Table 1). In nonriparian habitat catch was divided between the canopy and subcanopy; riparian catch was too small to test (Table 2). Bats were caught throughout the night (Table 3).

Twelve feces were collected from an adult female who had eaten only hymenopteran insects. Diets of 8 juvenile bats, determined from 37 fecal pellets, varied widely. Six had eaten diets containing more than 90% coleopterans. The remainder of their diets

TABLE 3. Bat catch per species during four periods between dusk and dawn.

Species	Sunset to 22:00 h	22:00 h to 24:00 h	24:00 h to 02:00 h	02:00 h to Sunrise	X^2	P
M. lucifugus	18	19	16	9	3.935	0.269
M. grisescens	3	2	0	6		
L. borealis	34	18	10	20	14.585	0.002
L. cinereus	2	8	3	5	4.667	0.198
E. fuscus	112	69	22	42	74.233	0.000
P. subflavus	4	2	4	1		
N. humeralis	0	3	1	1		
L. noctivagans	1	1	0	2		

were lepidopterans. Two bats ate predominantly lepidopterans (83.6 and 96.3%) but both also consumed some coleopterans (3.8 and 15.0%). Carabidae (Order: Coleoptera) were identified 6 times. Individual bats also ate insects belonging to the orders: Diptera (5.0%), Homoptera (1.3%), and Orthoptera (1.0%). The DDI was 2.42.

Eptesicus fuscus

This bat is common statewide and was most frequently caught (Table 1). Four nursery colonies were located, 1 each in Shelby, Hamilton, St. Joseph, and Miami counties. At the caves, a few males could be caught as they came to night roost. Sometimes 1 or more bats would use the same roost spot night after night, beneath which was a notable feces accumulation. The catch of *E. fuscus* was similar in riparian and nonriparian habitats (Table 1), and in both habitats the catch was largest in the subcanopy layer (Table 2). Most bats were caught in the 2 periods from dusk to 24:00 h, with the smallest catch from 24:00 to 02:00 h (Table 3).

Pipistrellus subflavus

Males were captured at caves during summer sampling; females and juveniles were not. Only 11 individuals (5 females) were netted away from caves, all in riparian habitat. Two males caught over the Salamonie River, Wabash County represent both the northern most Indiana record and a county record. The sample was too small to test, but most captures were in the understory (Table 2). The catch appeared distributed throughout the night.

Feces were analyzed from 23 bats. The diet contained 33.0% dipterans (both Chironomidae and Muscidae were each identified once), 19.7% trichopterans, 14.1% coleopterans (Elateridae was identified 9 times; Curculionidae, 2 of which were Asiatic oak weevils, 8 times; Scarabaeidae 6 times; and Silphidae 3 times), 13.6% lepidopterans, 12.0% homopterans, 3.0% hymenopterans, 2.6% neuropterans, and 0.1% plecopterans. The DDI of males and females were similar; the combined DDI was 6.68.

Nycticeius humeralis

Two females and 3 juveniles, were caught in 1980 in a Montgomery County upland woodlot; all were caught in the canopy layer after 22:00 h. The females ate 69.6% coleopterans, 29.1% lepidopterans, and 1.2% homopterans, while the juveniles at 68.9% coleopterans, 9.2% dipterans, 14.9% homopterans, 5.3% trichopterans, 1.5% hymenopterans, and 0.2% hemipterans. The combined DDI was 5.26.

Lasionyceteris notivagans

Two adult males were caught in Miami County on 3 June 1981 from the canopy layer of an upland woodlot. A third male was caught in Tippecanoe County on 18 June 1983 from the subcanopy of riparian habitat. Thus all 3 represent later springs records than previously recorded in Indiana, i.e., 28 May (23). A juvenile was caught on 8 September 1981 from the subcanopy of an upland woodlot. These four captures were scattered throughout the night (Table 3).

Feces were collected only from adult males. All ate dipterans (55.2%), neuropterans (22.1%), and lepidopterans (9.3%); one individual had also eaten insects belonging to the Coleoptera, Trichoptera, and Hymenoptera. The DDI was 4.80.

Discussion

Myotis lucifugus has frequently been found foraging low over pond and stream surfaces (13, 9, 2, 1, 10), and food habits studies have further substantiated this behavior (9, 2, 1). In the present study, *M. lucifugus* frequented subcanopy riparian habitat, and was active throughout the night. In Iowa (16) the species was active early but almost totally inactive the latter half of the night.

Chemiluminescently tagged *M. grisescens* in Missouri foraged largely in riparious areas, just over the water surface (18). The habitat and height of captures in the present study concur with those findings, as does the diet with that in Missouri (20), emphasizing aquatic based prey.

Foraging by *L. borealis* has been reported mainly from high over trees and pastures (19, 18). Prey reported previously (26, 27, 28, 8) and herein have been largely terrestrial. Inconsistent with this, more bats per net night were caught in riparian habitats. One logical explanation for this discrepancy is that riparian captures, mostly in the subcanopy, represent use of this space as a travel lane. As in Iowa (16), activity was greatest during early evening.

Although homopterans were frequently a small part of the *L. borealis* diet, Whitaker (28) and Brack *et al.* (8) found they sometimes constitute major parts of the diet. Whitaker (28) also found larger percentages of Orthoptera in the diet. However, similarities to past studies (26, 27, 28, 8), and comparisons among sex, age, and temporal subgroups of this study indicate a relatively stable diet composed largely of terrestrial prey.

It is probable that *L. cinereus*, like *L. borealis*, frequents waterways primarily as travel lanes. This is supported by present and past food habit studies (3, 4, 27, 28, 30, 8), and past foraging observations (18, 11, 30, 23). *L. cinereus* has been referred to as a moth specialist (3, 4), although a variety of other prey has been reported (27, 28, 30, 8). The species has a robust jaw and a skull morphology suitable for eating hard-bodied insects (12). In this study, most prey were hard-bodied; most individuals' diets contained small percentages of soft-bodied (Lepidoptera) prey. Two bats ate predominantly lepidopteran prey. In British Columbia (11) and Iowa (16) *L. cinereus* was active late at night, temporally separating the foraging of the 2 *Lasierus* species.

Typically, the diet of *E. fuscus* contains large proportions of hard-bodied insects, especially coleopterans (14, 25, 3, 4, 28). Since aquatic insect species are predominantly soft-bodied, it appears that *E. fuscus* uses open understory waterways for travel and feeds predominantly in uplands. Although catch was greatest in the understory, *E. fuscus* also uses the canopy and higher air spaces while foraging (25, 11). In Iowa (16) and British Columbia (11), as in Indiana, *E. fuscus* foraged predominantly early in the evening.

Whitaker (28) reported a diet for *P. subflavus* similar to that reported here, with a wide diversity of prey items, including terrestrial and aquatic species. In Missouri, trichopterans predominated in the diet (20), and luminescently tagged bats foraged over or near streams (18). Data from the present study complement those findings; all captures were in the subcanopy and canopy of riparian habitat.

Limited observations (18, 23) indicate that *N. humeralis* frequents tree crowns of open and early successional wooded pastures and floodplains. This bat has a cranial and jaw morphology of intermediate robustness, appropriate for some types of hard-bodied prey (12), and has been reported to eat largely Coleoptera, Homoptera, Hymenoptera, and Hemiptera, as well as Lepidoptera and Diptera (27, 28). Though again limited, the data collected on this species encourages a similar interpretation.

In general, *L. noctivagans* forages in or near woodlands adjacent to streams or bodies of water (17), and has post dusk and predawn feeding periods (16, 15). Past dietary samples are small but include representatives of the Lepidoptera, Hemiptera, Coleoptera, Diptera, Trichoptera, and Isoptera (28, 29, 15). Similarly, small dietary samples in this study contained neuropterans, and lepidopterans as major components.

In summary, 3 of the species of bats studies rely heavily upon a riparian environment. *M. grisescens* foraged low over water, *M. lucifugus* was caught in the understory, and *P. subflavus* foraged around the riparian canopy and understory. The 2 *Myotis* species eat aquatic prey. *Lasiurus borealis, L. cinereus*, and *E. fuscus* frequent the

riparian understory but do not forage there. They likely used it as a travel lane. *E. fuscus* feeds on coleopterans and is frequently caught in the upland understory, while both lasurines feed around and above woodland canopy. Because of a lack of data in this and other studies, the foraging ecology of *N. humeralis* and *L. noctivagans* cannot be accurately characterized.

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