

**Partitioning of Food Resources by Syntopic Eastern Red (*Lasiurus borealis*),
Seminole (*L. seminolus*) and Evening (*Nycticeius humeralis*) Bats**

ABSTRACT.—We evaluated partitioning of food resources among syntopic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats at the Savannah River Site, South Carolina, from June through August of 1996 and 1997. We compared diets to indices of relative prey availability, which were based on samples of the insect communities in bat foraging habitats and the amounts of time the bats foraged in each habitat. The relative proportions of insect orders consumed differed among the species. We recorded only minor differences between insect consumption and indices of prey availability, as assessed by insect light traps placed within foraging habitats. Our data suggest that Eastern red bats and evening bats altered their prey selection late in the summer.

INTRODUCTION

Limitations of flight, echolocation and vision may constrain the selection of foraging habitats used by some species of bats (Norberg and Rayner, 1987). Complex habitats containing structural clutter may be unsuitable foraging habitats for bats that are less maneuverable because of greater wing loading ratios (Fenton, 1990; Kalcounis and Brigham, 1995) although prey availability may be higher in such habitats (Brigham *et al.*, 1997). Thus, bats may select foraging habitats and prey based on habitat structure as well as prey availability.

Although many researchers have examined the interactions between single species of bats and their prey (*e.g.*, Fenton, 1990; Sample and Whitmore, 1993), only a few have focused on food resource partitioning among several species in a defined area (*e.g.*, Husar, 1976; Saunders and Barclay, 1992). Some studies have reported diet specialization among syntopic species, whereas others have demonstrated that syntopic bats feed opportunistically and may consume the same food (Hickey *et al.*, 1996). However, the methods used to sample prey availability and determine dietary components often influence the conclusions drawn (Whitaker *et al.*, 1999). For example, the placement of insect sampling devices may affect the assessment of prey selection because bats may feed in areas other than where insect traps are placed (Whitaker, 1995). Thus, insect availability must be based on a determination of bat foraging locations and collection at these sites. Further, insect availability must be weighted by the amount of time that each species spends foraging in each habitat (Whitaker, 1995).

We assessed prey consumption and foraging area preference among three syntopic bats species. We radio-tracked syntopic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats to determine foraging habitats of each species, collected insects from sites where the bats foraged and compared fecal sample contents to indices of relative prey availability in each habitat. We hypothesized that eastern red and Seminole bats would forage in more open areas and select different prey than the smaller more maneuverable evening bats.

MATERIALS AND METHODS

This study was conducted on the U.S. Department of Energy's Savannah River Site (SRS), a 780-km² facility in west-central South Carolina. The SRS is located in the Upper Coastal Plain and is bounded by the Savannah River along the southwestern edge. The topography is characterized by gentle rolling ridges, broad flat regions and interspersed stream courses. Bottomland hardwood stands of various widths (<50 to >1000 m) occur along stream courses and may be flooded seasonally during late winter-early spring. Dominant canopy species in bottomland hardwoods include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), laurel oak (*Q. laurifolia*), overcup oak (*Q. lyrata*) and cherrybark oak (*Q. falcata* var. *pagodaefolia*). The bottomland hardwood stands are surrounded by closed-canopy mixed pine (*Pinus* spp.) forests, upland forests, old fields and aquatic habitats. The upland forests include a mix of pines and hardwood species.

We captured bats from mid-June through mid-August of 1996 and 1997 using 15 mist net systems placed in areas of concentrated bat activity such as roads, skidder trails, streams and ponds. All bats were placed in plastic cups for ≤ 1.5 h to collect fecal pellets and were released the same night. Fecal samples were analyzed using methods described by Whitaker (1988) and insect fragments were identified to the ordinal level. We used a modified version of Black's (1972) method to estimate percent volume because lepidopterans often are represented only by scales. We compared summer diets within species to assess differences among the early, middle and late summer periods. Proportional data were transformed using an arcsine square-root transformation and analyzed using an Analysis of Variance (ANOVA) and a Tukey's mean separation test (SAS Institute Inc., 1990).

We determined foraging habitats by radio-tracking bats instrumented with LB-2 radio-transmitters (0.45 g, Holohil Systems Ltd., Ontario, Canada) glued to the back of adult bats with Skin-bond[®] surgical adhesive (Pfizer Hospital Products Group, Inc., Largo, FL). Transmitters had a range of 1.6 km and a battery life of approximately 21 d. The transmitters weighed less than 5% of the body mass of a tagged bat and presumably had a negligible effect on activity (Aldridge and Brigham, 1988).

We determined foraging locations using standard two-station simultaneous triangulation (Schmutz and White, 1990). Locations of telemetry stations were recorded using a global positioning system (GPS, Trimble Navigation Limited, Sunnyvale, CA). To estimate locations of foraging bats, we entered the Universal Transverse Mercator (UTM) coordinates of telemetry stations and the azimuths of readings into the program LOCATE (Kie *et al.*, 1996). Because of our close proximity to the tagged bats, error polygons were small (≤ 4 ha). We imported bat locations into PC Arc/Info, Geographical Information Systems (Environmental Systems Research Inst., Inc., Redlands, CA) and superimposed locations onto vegetation maps of the SRS to calculate the proportions of locations within each habitat. We categorized all locations of foraging bats for each species by habitat type across the 2 y of the study to determine proportional use of habitats and to generate a weighted sampling of availability based on light-trap samples. We followed Workman and McLeod (1990) and combined community types that the bats used into four categories: pine forests, upland forests, bottomland forests and aquatic habitats. Pine forests were areas in which pines were the dominant canopy species ($>75\%$) and included plantations of loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*) and slash pine (*P. elliottii*). Upland hardwood forests were defined as areas in which upland hardwood species were the dominant canopy species ($>75\%$). Bottomland hardwood forests incorporated Workman and McLeod's (1990) swamp forests vegetation type along with areas in which bottomland hardwood species dominated the canopy. Water areas were streams, ponds, lakes and Carolina bays.

We used 12-volt black-light insect traps (BioQuip Products, Gardena, CA) to collect insects from the habitats where radio-instrumented bats foraged. A trap was placed in each of 3 replicates of each habitat (bottomlands, pine stands, uplands and aquatic habitats) for 3 nights each week. We retrieved insects after each night and froze them for subsequent analysis. A random subsample, selected based on the sample size from the light trap, was identified and percent occurrence and percent volume was recorded for each insect order. To assess relative prey availability based on habitat use, we multiplied the percentage of time (based on number of telemetry locations) that a bat spent in each habitat type by the proportion (based on percent volume) of each insect order in that habitat type (Whitaker, 1995). Comparisons were conducted at 3.5 week intervals beginning in mid-June and represented early, mid and late summer. If the diet differed from our estimate of insect availability ($P < 0.05$, *t*-test), we assumed prey selection as per Whitaker (1988).

RESULTS

To examine habitat selection, we included telemetry data from 14 Eastern red bats (12F;2M), 8 Seminole bats (4F;4M) and 18 evening bats (14F;4M) for which we had >20 locations per sampling period. To generate sufficient sample sizes we pooled data across the 2 y of the study. We observed minor differences in habitat selectivity among the three species. Eastern red bats rarely foraged over upland hardwood habitats (5%) relying instead on bottomland (55%) and pine (40%) forests. Seminole bats foraged primarily in pine stands (55%), but also frequented bottomlands (35%) and uplands (11%). Evening bats confined most of their activities to pine forests (59%) and bottomlands (37%) and rarely foraged in upland hardwoods.

Insect availability, based on percent volume, varied in the foraging areas of each bat species during the summer. Beetles (Coleoptera) were the most consistently available food in the foraging habitats (Table 1), although Hemiptera and Lepidoptera also were abundant in most locations. Insects from some orders often emerged in irregularly dispersed swarms. Although not always available, these taxa (*e.g.*, Hymenoptera) were locally common and composed a substantial portion of the insect fauna for brief periods.

We examined 417 samples of fecal pellets from 80 bats. Distribution of the fecal samples among the species was 30% Eastern red bat, 9% Seminole bat and 61% evening bat. The food habits of the three bat species differed across sampling periods (Table 1). Coleoptera was the most abundant taxon in the fecal samples of eastern red bats in early and mid-summer, but the bats consumed a greater proportion of Lepidoptera during late summer as beetle availability decreased. During early summer, Seminole bats consumed mostly Hymenoptera by volume, although Coleoptera and Hemiptera were found in samples frequently. During the mid-summer, Seminole bats ingested a large volume of Coleoptera. Evening bats consumed mostly Coleoptera during the first two-thirds of the summer, but their diet consisted of almost equal parts of Hemiptera, Homoptera, Coleoptera and Hymenoptera during the late summer.

Eastern red bats consumed more Coleoptera than Seminole bats ($P = 0.018$) in early summer and fed on Lepidoptera more often than did evening bats, especially in late summer ($P = 0.014$). During mid-summer, evening bats consumed more Hemiptera than did Seminole bats ($P = 0.028$). During late summer, evening bats consumed more Hemiptera than did red bats ($P = 0.024$).

The fecal pellets of Seminole bats contained lower volumes of Coleoptera, Hemiptera and Trichoptera than were indexed to be available by the light-trap samples. Coleoptera, Lepidoptera and Hymenoptera were the primary foods during mid-summer when Hymenoptera were taken in greater proportion than their relative availability. Diptera, Hemiptera and Trichoptera were consumed less frequently than available in mid-summer.

During early summer and mid-summer, evening bat pellets were comprised primarily of Coleoptera, Hymenoptera and Hemiptera. Lepidoptera, Diptera and Trichoptera were consumed less than their relative availability during both these periods. In late summer, evening bat samples were composed of Hemiptera, Homoptera, Coleoptera and Hymenoptera. Coleoptera, Lepidoptera and Diptera were eaten less than their relative availability, whereas Hemiptera and Homoptera were used more than their relative availability in the habitats sampled.

DISCUSSION

We detected only minor differences in habitat use among the three bat species. However, our consolidation of the complex habitat at our study site into three forest types may have masked variation in selection of foraging habitat by the three species. Nevertheless, we did find differences in prey availability when we calculated indices of relative prey availability based on the percent of time that the bats spent in each habitat type.

Although many insectivorous bats are regarded as diet generalists, the species we examined exhibited some selectivity throughout the summer despite the fact that our classification only identified insects to the ordinal level. The bulk of the diets of these species consisted of the most common prey items and some less common prey taxa were rarely represented in fecal samples. Although prey selectivity may be a factor in the foraging strategy of these bats, prey density also influences prey choice. Foraging location is an important component of prey availability. Selection of foraging location can affect diet composition as much as prey selection within that area. Some taxa, such as flying ants (Hymenoptera), may be locally common at times in some habitats and they are used extensively when present.

Eastern red bats demonstrated little prey selectivity in our study and the composition of prey eaten did not differ from other reports on the food habits of this species (Feldhamer *et al.*, 1995; Whitaker, 1972; Whitaker *et al.*, 1997). Until recently, there were few reports of Seminole bat food habits and most were based on single samples (Zinn, 1977). Carter *et al.* (1998) examined 24 fecal samples from coastal Georgia and reported that Seminole bats fed primarily on Coleoptera, Lepidoptera and Hymenoptera and used Homoptera and Diptera less than their relative availability in the habitat. We found that Hymenoptera (primarily flying ants) also composed a large proportion of the diet and, when found, represented a large proportion of the sample.

TABLE 1.—Percent occurrence (Occ.) and percent volume (Vol.) of insect orders recovered from fecal samples of three bat species, compared to an index of the insect taxa available (Avl.) by volume in the environment at the Savannah River Site, South Carolina, June through August 1996 and 1997. Significance levels are provided when percent volume in fecal samples differs from percent available ($P < 0.05$, t -test)

	<i>Lasiurus borealis</i>				<i>Lasiurus seminolus</i>				<i>Nycticeius humeralis</i>			
	Occ.	Vol.	Avl.	P	Occ.	Vol.	Avl.	P	Occ.	Vol.	Avl.	P
Early summer												
Coleoptera	100	74	59	ns ¹	80	30	58	ns	97	51	58	ns
Hemiptera	56	10	19	ns	80	8	20	0.04	69	16	19	ns
Lepidoptera	44	5	8	ns	40	9	8	ns	59	5	8	0.04
Homoptera	33	3	0	ns	20	10	0	ns	31	3	1	ns
Diptera	0	0	4	ns	0	0	3	ns	3	1	3	0.01
Hymenoptera	33	8	2	ns	60	43	2	ns	69	23	2	ns
Trichoptera	0	0	7	0.04	0	0	7	0.05	16	1	8	0.05
Neuroptera	0	0	0	ns	0	0	0	ns	0	0	0	ns
Middle summer												
Coleoptera	80	38	48	ns	100	46	52	ns	100	45	49	ns
Hemiptera	80	13	9	ns	43	3	11	0.01	89	15	10	ns
Lepidoptera	50	16	21	ns	71	22	17	ns	78	6	19	0.02
Homoptera	70	10	2	ns	43	6	3	ns	67	13	2	ns
Diptera	0	0	9	0.01	0	0	6	0.01	0	0	8	0.01
Hymenoptera	70	24	3	ns	86	19	3	0.04	67	20	3	ns
Trichoptera	0	0	6	0.01	14	4	7	ns	11	1	7	0.01
Neuroptera	0	0	2	ns	0	0	1	ns	0	0	2	ns
Late summer												
Coleoptera	75	21	33	ns					100	21	49	0.01
Hemiptera	25	6	5	ns					100	29	6	0.01
Lepidoptera	100	63	41	ns					75	5	25	0.01
Homoptera	50	10	5	ns					100	24	6	0.02
Diptera	0	0	10	0.01					0	0	6	0.01
Hymenoptera	0	0	1	0.02					50	18	2	ns
Trichoptera	0	0	5	0.01					25	2	5	ns
Neuroptera	0	0	1	ns					25	1	0	ns

¹ ns = not significant

Typically, Coleoptera are the most important food resource for evening bats, but Hymenoptera, Hemiptera and Homoptera also are eaten frequently (Feldhamer *et al.*, 1995; Whitaker, 1972; Zinn, 1977). However, like Carter *et al.* (1998), we found that evening bats consumed fewer Coleoptera than available, especially during late summer. Lepidoptera, although important prey for many species, apparently are used little by evening bats. Evening bats may be prevented from eating large moths because of difficulties capturing and handling bulky insects.

Although our telemetry data suggested only minor differences in foraging habitats among these species, the food habits analyses indicated a degree of prey selectivity. The partitioning of resources we observed may have been due to temporal differences in nocturnal foraging activity, although our data do not allow this assessment. Alternately, selection of foraging locations within habitats, or habitat selection at a finer scale than we were capable of assessing may have contributed to differences in prey selection. Nevertheless, our results demonstrate some prey selection among the three species as well as changes in prey selection over relatively brief time periods.

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