VARIATION IN DIET OF THE GRAY BAT (*MYOTIS GRISESCENS*)

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During spring and summer 1991, a total of 1,476 fresh fecal pellets of gray bats, *Myotis grisescens,* was collected at Blowing Wind Cave, Jackson Co., Alabama. Fourteen orders of Insecta, unidentified Insecta, an unknown organism (possibly Insecta), two orders of Arachnida, and hair from gray bats were recovered; in decreasing order, the most common taxa were Lepidoptera, Diptera, and Coleoptera. Food categories exhibited significant variation among sampling sessions, nights within sampling sessions, and hours within sampling sessions. When quantity of each food category in fecal pellets was compared with quantity of potential prey available for consumption, there was no statistically significant correlation. There was significant variation in diet over time, but bats did not select prey in proportion to availability.

Key words: *Myotis grisescens,* gray bat, endangered species, diet, food habits, feces, behavior, Alabama

Bats of the genus *Myotis* consume a variety of insects, including Coleoptera, Diptera, Ephemeroptera, Lepidoptera, Neuroptera, and Trichoptera (Anthony and Kunz, 1977; Belwood and Fenton, 1976; Brack and La Val, 1985; Brigham et al., 1992; Buchler, 1976; Easterla and Whitaker, 1972; Hayward, 1970; Herd and Fenton, 1983; Husar, 1976; Kunz, 1974; Ross, 1967; Shiel et al., 1991; Swift and Racey, 1983; Warner, 1985; Whitaker, 1972; Whitaker et al., 1981). Most previous studies of diets of *Myotis* have been limited by duration of sampling effort and size of samples (e.g., Brigham et al., 1992; Buchler, 1976; Hayward, 1970; Lacki et al., 1995), but Brack and La Val (1985) conducted an intensive study of the diet of the endangered Indiana bat (*Myotis sodalis*) in Missouri, where samples were collected at 2-week intervals from 7 June to 1 August. Their analyses of 1,272 fecal pellets provided insight into variation in diet over time. To better understand foraging requirements of a species, particularly of species that may be threatened or endangered, it is highly desirable to document the full range of variability in dietary components.

Studies of the endangered gray bat (*Myotis grisescens*—Greenwalt, 1976) have emphasized ecology, behavior, growth, and management (e.g., Best and Hudson, 1996; La Val and La Val, 1980; La Val et al., 1977; Stevenson and Tuttle, 1981; Thomas and Best, in press; Tuttle, 1975, 1976*a,* 1976*b,* 1979). *M. grisescens* forages over streams and reservoirs where it consumes night-flying aquatic insects (La Val et al., 1977; Rabinowitz, 1978; Rabinowitz and Tuttle, 1982; Thomas and Best, in press; Tuttle, 1976*b*), but there is a paucity of data on foods consumed by this species (Lacki et al., 1995). Guthrie (1933) reported remains of insects in feces of gray bats, Tuttle (1976*b*) noted remains of at least six species of mayflies (Ephemeroptera) under a roost, Rabinowitz (1978) and Rabinowitz and Tuttle (1982) reported remains of seven orders of insects in fecal pellets, and Lacki et al. (1995) identified nine orders of insects in fecal pellets. Objectives of our research were to use contents of fecal pellets to ascertain what items were ingested by *M. grisescens* at intervals throughout its annual activity period (April to October), to document variation in diet among sampling ses-

sions, nights, and hours of the night, and to compare variation in diet with variation in availability of prey.

Materials and Methods

Blowing Wind and Hambrick caves, located at Guntersville Reservoir in northeastern Alabama, contain the two largest (>100,000 gray bats each) summer colonies of *M. grisescens* (Tuttle, 1976*a*, 1976*b*). A total of 1,476 fresh fecal pellets was collected at Blowing Wind Cave, Jackson Co., Alabama, 19 April–20 September 1991. Two cloth bed sheets were spread on the ground at the lower opening of the cave to collect fecal pellets from bats entering and exiting the cave. The sheets were cleaned and repositioned after each sample was removed. For most samples, 10 fecal pellets were collected during each of the six 1-h or 2-h intervals from 1930 to 0630 h Central Daylight Savings Time (interval 1, 1930–2030 h; 2, 2030–2230 h; 3, 2230–0030 h; 4, 0030–0230 h; 5, 0230–0430 h; 6, 0430–0630 h) for 1–3 nights during each of 11 sampling sessions (session 1, 19–20 April; 2, 3–4 May; 3, 24–25 May; 4, 8–9 June; 5, 25–28 June; 6, 8–12 July; 7, 22–26 July; 8, 5–8 August; 9, 19–22 August; 10, 3–6 September; 11, 17–20 September). Each sample of fecal pellets was placed in a plastic bag and frozen until examined.

In the laboratory, individual fecal pellets were placed in water in a petri dish and warmed on a slide warmer to soften and expand the contents. Then, each pellet was gently teased apart with a probe while viewed at 60× magnification. A sample of the contents of each fecal pellet was added to one drop of 90% ethyl alcohol, which had been placed on a glass microscope slide. A mixture of mounting medium and xylene (75% mounting medium—Permount, Fisher Scientific, Pittsburgh, PA, and 25% xylene) was used to adhere the sample of contents of each fecal pellet to the slide, which was dried on a slide warmer.

Ten fields on each slide were examined at ≥200× magnification; a square ocular grid (10 squares on a side) divided each field into 100 equal-sized squares. Average percentage composition by volume of each food item based on 10, 100-unit grids was calculated by dividing the number of squares occupied by a food category by the total number of squares with food present for the fecal pellet, then multiplying this number by 100. It was assumed that Acari (chiggers) and hair of *M. grisescens* were not ingested as a source of food, but were taken in during grooming. These nonfood categories were quantified separately from food categories; Acari was recorded as total number of squares occupied in 10, 100-unit grids and bat hair was assigned values of 0 (absent), 1 (≤15 hairs observed on 10, 100-unit grids), and 2 (>15 hairs observed on 10, 100-unit grids).

Identification of remains to taxonomic order was determined, when possible, using keys and descriptions in Whitaker (1988) and Borror et al. (1989) and by comparison of remains with specimens in the Auburn University Entomology Collection. Insects that could not be identified to taxonomic order were included in the category Insecta; structures in this category included fragments of wings, legs, head capsules, and compound eyes. Round, eye-like structures, which appeared to be all from the same type of organism (possibly Insecta) and could not be identified to any taxonomic unit with certainty, were recorded as Unknown 1.

Reliable estimates of the quantity of prey that is available to foraging bats are difficult to obtain (Whitaker, 1994). We attempted to quantify the relative number of prey that potentially was available for consumption by gray bats by collecting a total of 384 samples of potential prey from within 2 km of Blowing Wind Cave. One terrestrial and three aquatic habitats were sampled with a 38-cm diameter, hand-held sweep net at ca. 2-h intervals during seven sampling sessions (25 June–20 September). In obtaining these sweep-net samples, the collector walked through the terrestrial habitat or was riding through aquatic habitats in a canoe; the collector made a total of 50, ca. 3-m wide, figure-8 swings during each sweep-net sample. The terrestrial habitat sampled was an open field adjacent to Guntersville Reservoir (characterized by grasses—*Sorghum*, goldenrod—*Solidago*, and sumac—*Rhus glabra*). There were three aquatic habitats: over water with no aquatic vegetation; over water with emergent Eurasian watermilfoil (*Myriophyllum spicatum*); over water with emergent American lotus (*Nelumbo lutea*). These four habitats were selected because they represented most habitat types available to *M. grisescens* at the reservoir. Contents of each sample of potential prey were identified to taxonomic order by comparison with keys in Whitaker (1988) and Borror et al. (1989). Average

TABLE 1.—*Average percentage composition by volume of food categories and relative abundance of nonfood categories in fecal pellets of* Myotis grisescens *at Blowing Wind Cave, Jackson Co., Alabama, during 11 sampling sessions from April to September 1991 (see Materials and Methods for dates). The number of fecal pellets examined is in parentheses.*

	Sampling session										
Contents of feces	1 (30)	2 (60)	3 (70)	4 (70)	5 (170)	6 (180)	7 (180)	8 (180)	9 (180)	10 (180)	11 (176)
Food category											
Lepidoptera (moths)	30.5	45.6	48.5	57.8	30.0	40.8	32.9	32.4	22.4	27.5	32.5
Diptera (flies)	46.0	25.6	16.0	19.8	13.1	23.0	21.6	18.8	35.4	40.2	31.8
Coleoptera (beetles)	17.9	14.4	24.2	3.8	5.4	13.6	14.3	7.2	5.7	2.8	9.2
Insecta	3.5	6.4	2.3	2.8	9.3	5.6	3.6	12.1	10.3	18.1	12.6
Unknown 1	0.5	0.5	2.8	4.1	30.3	5.2	5.3	17.7	5.3	0.4	0.5
Trichoptera (caddisflies)	0.0	2.7	1.3	3.8	4.2	4.8	13.7	1.7	10.2	4.3	3.4
Hemiptera (bugs)	0.0	1.5	2.0	1.1	0.1	1.9	3.0	1.5	3.3	1.3	3.4
Homoptera (leafhoppers)	0.1	0.3	0.5	0.3	0.5	3.2	2.3	1.7	4.0	2.0	3.4
Hymenoptera (wasps)	1.4	1.1	0.1	0.8	0.2	2.6	2.3	1.7	2.5	2.8	1.9
Ephemeroptera (mayflies)	0.0	0.0	0.0	0.0	5.6	0.0	1.9	3.0	0.0	0.0	0.0
Araneae (spiders)	0.2	2.1	1.7	<0.1	0.7	0.0	0.2	0.2	0.1	0.5	0.3
Neuroptera (lacewings)	0.0	0.0	0.3	0.1	0.1	0.0	0.3	0.0	0.1	0.3	1.1
Plecoptera (stoneflies)	0.0	0.0	0.3	0.0	0.0	<0.1	<0.1	1.7	<0.1	0.0	0.0
Orthoptera (grasshoppers)	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.0	0.1	<0.1	<0.1
Mecoptera (scorpionflies)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	<0.1	0.0	0.0
Thysanoptera (thrips)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	<0.1
Odonata (dragonflies)	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Nonfood category											
Acari (chiggers)	1.3	0.0	0.3	0.0	0.8	0.4	0.8	0.2	0.9	0.1	0.4
Bat hair	0.2	0.2	0.2	0.5	0.3	0.5	0.4	0.3	0.2	0.1	0.1

percentage of individuals of each potential prey item in each sample was calculated by dividing number of individuals of each taxon by total number of individuals in the sample, then multiplying this number by 100. Prey taxa that could not be identified to taxonomic class were listed as unidentified Insecta.

Variation among sampling sessions, nights, and hours (1-h and 2-h blocks), for contents of fecal pellets and samples of potential prey, was assessed using analysis of variance and a Student-Newman-Keuls a posteriori test for multiple comparisons among means. Spearman-rank correlation coefficients were used to compare variation in each taxon between contents of fecal pellets and potential prey (Norušis, 1990; Sokal and Rohlf, 1981; Swift et al., 1985). The level of statistical significance was corrected for multiple comparisons with the sequential Bonferroni adjustment (Rice, 1989); to obtain the corrected α-value, 0.05 was divided by the number of statistical comparisons made in each group of analyses.

RESULTS

Contents of fecal pellets.—Remains of 14 orders of Insecta, unidentified Insecta, eyelike structures from Unknown 1, two orders of Arachnida (Araneae, Acari), and hair from gray bats were recovered (Table 1). The three most common taxa recovered, in decreasing order of presence, were Lepidoptera, Diptera, and Coleoptera. Together these three taxa represented ≥48.5% of the total in each of the sampling sessions. Araneae, Hemiptera, Homoptera, Hymenoptera, Trichoptera, unidentified Insecta, and Unknown 1 also were present regularly. Ephemeroptera, Mecoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, and Thysanoptera occurred sporadically in fecal pellets (Table 1).

Variation among sampling sessions.—Of the 17 food categories listed in Table 1, 12 exhibited significant variation among sam-

TABLE 2.—*Occurrence of items in fecal pellets of* Myotis grisescens *as shown by one-way analysis of variance*[a] *and Student-Newman-Keuls a posteriori test among 11 sampling sessions used to obtain fecal pellets at Blowing Wind Cave, Jackson Co., Alabama, April to September 1991 (see Materials and Methods for dates). Numbers corresponding to sampling sessions are listed above the average percentage occurrence of each food or nonfood category* (d.f. = *10,1465 for all comparisons). Lines beneath averages indicate nonsignificant subsets.*

Contents of feces	*F*-ratio	Results of Student-Newman-Keuls analysis										
Food category												
		2	3	5	10	11	7	8	1	9	4	6
Araneae	3.04[a]	2.1	1.7	0.7	0.5	0.3	0.2	0.2	0.2	0.1	<0.1	0.0
		3	1	2	7	6	11	8	9	5	4	10
Coleoptera	12.02[a]	24.2	17.9	14.4	14.3	13.6	9.2	7.2	5.7	5.4	3.8	2.8
		1	10	9	11	2	6	7	4	8	3	5
Diptera	20.03[a]	46.0	40.2	35.4	31.8	25.6	23.0	21.6	19.8	18.8	16.0	13.1
		5	8	7	1	2	3	4	6	9	10	11
Ephemeroptera	10.59[a]	5.6	3.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		11	9	7	3	6	8	2	10	4	5	1
Hemiptera	3.60[a]	3.4	3.3	3.0	2.0	1.9	1.5	1.5	1.3	1.1	0.1	0.0
		9	11	7	6	10	8	3	5	4	2	1
Homoptera	5.67[a]	4.0	3.4	2.3	2.2	2.0	1.7	0.5	0.5	0.3	0.3	0.1
		4	3	2	6	7	11	8	1	5	10	9
Lepidoptera	9.01[a]	57.8	48.5	45.6	40.8	32.9	32.5	32.4	30.5	30.0	27.5	22.4
		11	3	7	10	5	9	4	1	2	6	8
Neuroptera	4.23[a]	1.1	0.3	0.3	0.3	0.1	0.1	0.1	0.0	0.0	0.0	0.0
		8	3	6	7	9	1	2	4	5	10	11
Plecoptera	3.75[a]	1.7	0.3	<0.1	<0.1	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
		7	9	6	10	5	4	11	2	8	3	1
Trichoptera	9.72[a]	13.7	10.2	4.8	4.3	4.2	3.8	3.4	2.7	1.7	1.3	0.0
		10	11	8	9	5	2	6	7	1	4	3
Insecta	16.95[a]	18.1	12.6	12.1	10.3	9.3	6.4	5.6	3.6	3.5	2.8	2.3
		5	8	9	7	6	4	3	11	2	1	10
Unknown 1	41.67[a]	30.3	17.7	5.3	5.3	5.2	4.1	2.8	0.5	0.5	0.5	0.4
Nonfood category												
		6	4	7	5	8	2	9	3	1	11	10
Bat hair	9.67[a]	0.5	0.5	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.1	0.1

[a] Significant differences based on sequential Bonferroni minimum table-wide significance level set at 0.0026 for a table of 19 tests.

pling sessions (Table 2). The largest difference among sessions (F-value = 41.67) was for Unknown 1; most items in this category occurred during sampling sessions 5 and 8 (25–28 June, 5–8 August) when 30.3 and 17.7%, respectively, of items recovered from fecal pellets were remains of this unidentified organism. Other than in sampling sessions 5 and 8, Unknown 1 in the remaining sampling sessions was represented by ≤5.3% of contents. Coleoptera, Diptera, Ephemeroptera, Lepidoptera, Trichoptera,

and unidentified Insecta had F-values >9, indicating they also were more variable than remaining food categories. Of these six categories, Ephemeroptera was the only one that occurred sporadically. No consistent chronological patterns relative to changes in occurrence of any food category could be discerned.

Variation among nights within sampling sessions.—Variation in contents of fecal pellets was assessed among 3 nights for each of seven sampling sessions (sessions 5–11, 25 June–20 September). There was no significant difference among nights for any food category in sampling sessions 5, 6, 9, or 10. In sampling session 7, significantly more Coleoptera (F = 6.89; average = 23.3%) was present 25–26 July than 23–24 and 22–23 July (13.6 and 6.1%, respectively), more Ephemeroptera (F = 6.53; average = 5.8%) was present 22–23 July than 23–24 and 25–26 July (0% for both nights), and more Unknown 1 (F = 8.57; average = 11.2%) was present 22–23 July than 25–26 and 23–24 July (3.0 and 1.6%, respectively). In sampling session 8, significantly more Diptera (F = 11.03) was present 7–8 and 5–6 August (26.3 and 22.2%, respectively), than 6–7 August (7.9%), more Ephemeroptera (F = 7.28; average = 6.6%) was present 6–7 August than 7–8 and 5–6 August (2.4 and 0%, respectively), and more Unknown 1 (F = 19.51) was present 5–6 and 6–7 August (27.3 and 25.2%, respectively) than 7–8 August (0.8%). In sampling session 11, significantly more Coleoptera (F = 6.69) was present 17–18 and 18–19 September (average = 12.9 and 12.2%, respectively) than 19–20 September (2.2%), more Hemiptera (F = 15.32) was present 18–19 September (average = 7.4%) than 17–18 and 19–20 September (2.3 and 0.1%, respectively), and more Lepidoptera (F = 38.19) was present 19–20 September (54.6%) than on the previous 2 nights (25.1 and 19.4%, respectively). Thus, nine of 91 comparisons (10%) indicated significant differences among nights within sampling sessions.

Variation among hours within sampling sessions.—To ascertain the degree of variation among hours (1-h and 2-h blocks), we analyzed data from the 3 nights combined within each of sampling sessions 5–11. When all 91 comparisons were considered together, the sequential Bonferroni minimum significance level was 0.0006 (Table 3). At this significance level, 25 of 91 comparisons (25%) exhibited significant differences among hours. Four food categories (Diptera, Lepidoptera, unidentified Insecta, Unknown 1) accounted for 18 significant comparisons (72%), with Coleoptera, Ephemeroptera, Hemiptera, Homoptera, and Trichoptera each representing one significant difference among hours (Table 3).

Greatest differences among hours (F-values >27) were for the five significant comparisons of Lepidoptera (Table 3); these five comparisons showed that *M. grisescens* had significantly more Lepidoptera in fecal pellets at 1930–2030 h than at other times. Three of these comparisons also indicated that, although it was significantly less than for 1930–2030 h, Lepidoptera was present in significantly greater quantities at 2030–2230 h than during the remainder of the night. Except for Lepidoptera, 1930–2030 h often was the hour with the least amount of other food categories listed in Table 3.

Variation in presence of Acari.—Acari was detected in fecal pellets in nine of 11 sampling sessions (Table 1). There was no significant difference among sampling sessions, nights, or hours within sampling sessions in incidence of Acari. No chronological pattern in abundance of this taxon was detected.

Variation in presence of bat hair.—Hair of *M. grisescens* was present in fecal pellets collected during every sampling session (Table 1); there was significant variation in quantity of hair among sampling sessions (Table 2). Although not statistically well-differentiated, there was a tendency for more bat hair to be present during sampling sessions 4–7 (8 June–26 July) than in ear-

TABLE 3.—*Occurrence of food items at different hours of the night, as shown by selected results of one-way analysis of variance*[a] *and Student-Newman-Keuls a posteriori test among hours of collection of fecal pellets of* Myotis grisescens *at Blowing Wind Cave, Jackson Co., Alabama, April to September 1991. Results are presented for Coleoptera, Diptera, Lepidoptera, and other food categories that exhibited significant variation among hours. Hourly sampling intervals (1-h and 2-h blocks) are listed above average percentage occurrence by volume of each food category represented in fecal pellets (see Materials and Methods for times). Lines beneath averages indicate nonsignificant subsets.*

Sampling session	Food category	*d.f.*	*F*-ratio	Results of Student-Newman-Keuls analysis					
5				4	3	2	6	5	1
	Coleoptera	5,164	4.49	14.4	10.8	4.1	2.5	2.1	0.0
				4	6	3	5	2	1
	Diptera	5,164	3.42	19.8	18.8	14.3	12.7	12.5	0.8
				1	2	3	4	5	6
	Lepidoptera	5,164	27.60[a]	81.7	35.8	17.9	14.8	13.3	12.4
				5	6	3	2	4	1
	Insecta	5,164	4.62[a]	15.6	11.2	9.6	9.4	8.7	1.2
				5	6	3	2	4	1
	Unknown 1	5,164	6.42[a]	50.1	46.0	27.9	22.6	21.8	12.7
6				3	6	4	5	2	1
	Coleoptera	5,174	5.30[a]	25.5	20.2	16.3	13.9	3.4	2.1
				5	4	6	3	2	1
	Diptera	5,174	16.02[a]	36.7	34.1	31.0	27.9	7.2	0.9
				3	6	5	4	1	2
	Homoptera	5,174	5.99[a]	9.1	2.6	0.7	0.5	0.4	0.0
				1	2	5	6	4	3
	Lepidoptera	5,174	77.61[a]	93.2	79.0	24.9	18.7	14.8	14.1
				4	6	3	5	2	1
	Insecta	5,174	7.21[a]	15.3	6.5	6.2	2.9	1.3	1.3
7				3	5	6	4	2	1
	Coleoptera	5,174	3.91	28.6	18.2	14.0	13.0	11.4	0.8
				6	3	5	4	2	1
	Diptera	5,174	11.52[a]	39.7	29.7	28.1	14.0	13.3	4.9
				1	2	6	4	5	3
	Lepidoptera	5,174	39.12[a]	90.5	33.7	21.0	19.1	18.7	14.4
				4	2	6	3	5	1
	Trichoptera	5,174	13.39[a]	37.5	25.7	6.7	6.3	6.3	0.0
				5	6	3	1	2	4
	Unknown 1	5,174	9.64[a]	19.1	7.1	3.4	1.0	0.9	0.1

TABLE 3.—*Continued.*

Sampling session	Food category	*d.f.*	*F*-ratio	Results of Student-Newman-Keuls analysis					
8									
				3	4	2	6	5	1
	Coleoptera	5,174	3.28	17.1	9.5	6.6	4.7	4.2	1.2
				6	3	4	5	2	1
	Diptera	5,174	9.68[a]	31.7	30.4	25.0	12.8	11.2	1.7
				5	6	1	2	3	4
	Ephemeroptera	5,174	11.87[a]	13.6	4.5	0.0	0.0	0.0	0.0
				1	2	3	4	5	6
	Lepidoptera	5,174	32.31[a]	85.0	50.1	17.9	16.1	12.9	12.5
				5	6	4	3	1	2
	Insecta	5,174	7.22[a]	22.0	20.8	12.2	8.1	5.7	4.0
9									
				3	6	4	2	5	1
	Coleoptera	5,174	1.95	10.0	9.1	7.2	4.3	2.9	0.7
				5	4	6	2	3	1
	Diptera	5,174	9.00[a]	46.1	44.8	41.1	36.2	31.9	12.4
				3	2	4	5	6	1
	Hemiptera	5,174	4.66[a]	7.7	4.5	3.2	2.9	1.8	0.0
				1	2	3	6	5	4
	Lepidoptera	5,174	29.86[a]	67.2	21.4	18.5	10.5	8.5	8.2
				5	6	4	2	1	3
	Unknown 1	5,174	15.83[a]	21.7	9.2	0.8	0.2	0.0	0.0
10									
				3	5	6	4	2	1
	Coleoptera	5,174	1.39	5.8	2.9	2.8	2.6	1.7	0.8
				5	3	4	2	6	1
	Diptera	5,174	3.60	48.4	45.2	44.9	44.0	30.4	28.3
				1	4	2	5	6	3
	Lepidoptera	5,174	1.87	38.0	29.6	27.4	27.0	24.0	19.1
				6	1	2	5	4	3
	Insecta	5,174	5.44[a]	28.3	26.7	20.6	11.8	10.6	10.5
11									
				6	5	4	3	1	2
	Coleoptera	5,170	4.28	18.2	14.3	10.3	8.3	2.2	1.2
				1	2	3	4	6	5
	Diptera	5,170	4.56[a]	45.0	41.7	35.1	28.7	22.0	19.8
				4	5	6	3	2	1
	Lepidoptera	5,170	2.13	38.5	37.2	36.9	31.6	31.0	18.0
				1	2	3	5	6	4
	Insecta	5,170	6.50[a]	28.8	13.7	10.1	8.7	8.5	8.1

[a] Significant differences based on sequential Bonferroni minimum table-wide significance level set at 0.0006 for a table of 91 tests.

TABLE 4.—*Presence of bat hairs in fecal pellets of* Myotis grisescens *at different times of the night, as shown by one-way analysis of variance*[a] *and Student-Newman-Keuls a posteriori test of presence of bat hair among hours of collection at Blowing Wind Cave, Jackson Co., Alabama, April to September 1991. Hourly sampling intervals (1-h and 2-h blocks) are listed above the average incidence of bat hair in fecal pellets (see Materials and Methods for times). Lines beneath averages indicate nonsignificant subsets.*

Sampling session	*d.f.*	*F*-ratio	Results of Student-Newman-Keuls analysis					
			1	2	4	5	6	3
5	5,164	40.66[a]	1.4	0.3	0.1	0.1	<0.1	0.0
			1	2	4	6	5	3
6	5,174	49.02[a]	1.5	1.3	0.2	0.1	0.1	0.1
			1	2	4	3	5	6
7	5,174	19.78[a]	1.4	0.5	0.5	0.1	0.1	0.1
			1	2	4	3	5	6
8	5,174	42.61[a]	1.2	0.4	0.1	0.1	0.0	0.0
			1	4	5	3	2	6
9	5,174	33.95[a]	1.0	0.2	0.1	<0.1	0.0	0.0
			1	4	2	5	3	6
10	5,174	3.45[a]	0.3	0.1	0.1	0.1	0.0	0.0
			1	4	5	2	3	6
11	5,170	0.37	0.2	0.2	0.2	0.1	0.1	0.1

[a] Significant differences based on sequential Bonferroni minimum table-wide significance level set at 0.0071 for a table of seven tests.

lier or later sampling sessions. Comparisons within sampling sessions 5–11 revealed no significant differences in presence of hair among nights.

When hours within sampling sessions 5–11 were compared, there were significant differences among hours in all but sampling session 11 (Table 4). For all sampling sessions, fecal pellets obtained during 1930–2030 h, the first session of the evening, contained the most bat hair, and this hour was significantly different from all other hours in four of the seven sampling sessions. We believe presence of bat hair in fecal pellets resulted from incidental ingestion during grooming.

Availability of potential prey.—One order of Arachnida (Araneae), 10 orders of Insecta, and unidentified Insecta were represented in our sweep-net samples (Table 5). Results of analysis of variance revealed that Diptera and unidentified Insecta varied significantly among sampling sessions: more Diptera was present in samples taken during sessions 8 (5–8 August; 63.2%) and 10 (3–6 September; 65.9%) than in samples taken during session 11 (17–20 September; 30.3%); more unidentified Insecta (5.2%) was recorded in sampling session 5 (25–28 June) than in the six other sessions (Table 5). When variation among hours within sampling sessions 5–11 was analyzed, there was no significant difference within any category of potential prey.

Comparison of potentially available prey with food categories represented in fecal pellets.—Average percentage by volume of each food category in fecal pellets during each sampling hour (1-h and 2-h blocks) was compared with average percentage of individuals of the respective prey category that potentially was available for consumption by *M. grisescens*. There was no significant correlation.

Because it usually takes ca. 0.5–2 h for most ingesta to pass through the digestive

TABLE 5.—*Potential prey available to bats as shown by one-way analysis of variance[a] and Student-Newman-Keuls a posteriori test among sessions 5–11 for samples at Guntersville Reservoir, Jackson Co., Alabama, April to September 1991. Sampling sessions (see Materials and Methods for dates) are listed above the average percentage of individuals of prey taxa collected in each sampling session* (d.f. = *6,377 for all comparisons*). *Lines beneath averages indicate nonsignificant subsets.*

Availability of prey	*F*-ratio	Results of Student-Newman-Keuls analysis						
		10	8	5	9	6	7	11
Diptera	3.50[a]	65.9	63.2	53.6	50.9	49.1	43.6	30.3
		7	8	11	9	10	6	5
Lepidoptera	2.86	9.1	3.3	2.9	2.0	1.0	1.0	0.3
		8	5	9	7	10	6	11
Ephemeroptera	1.66	5.7	4.1	4.0	2.0	0.7	0.6	0.0
		5	7	6	9	8	10	11
Araneae	3.22	7.5	3.4	2.8	1.3	0.9	0.2	<0.1
		10	8	7	6	9	5	11
Trichoptera	3.05	6.5	1.6	1.2	1.1	0.6	0.4	0.1
		6	8	5	7	9	10	11
Coleoptera	2.29	4.0	2.1	1.5	0.8	0.0	0.0	0.0
		5	6	8	7	9	10	11
Homoptera	1.07	2.3	2.0	1.5	1.4	0.5	0.1	0.0
Unidentified		5	11	7	9	10	8	6
Insecta	10.20[a]	5.2	1.0	0.3	0.2	0.2	0.1	0.0
		9	7	6	8	5	11	10
Odonata	1.26	2.8	1.6	1.0	0.6	0.3	0.1	<0.1
		8	5	9	6	7	10	11
Hemiptera	2.39	1.0	0.3	0.2	0.0	0.0	0.0	0.0
		5	6	8	7	9	10	11
Hymenoptera	2.12	0.6	0.1	<0.1	0.0	0.0	0.0	0.0
		9	5	6	7	8	10	11
Neuroptera	0.90	0.8	0.0	0.0	0.0	0.0	0.0	0.0

[a] Significant differences based on sequential Bonferroni minimum table-wide significance level set at 0.0042 for a table of 12 tests.

tract of similar vespertilionid bats (Anthony and Kunz, 1977; Buchler, 1975; Kunz and Whitaker, 1983; Whitaker, 1988), we also compared contents of fecal pellets with quantity of potential prey that was available ca. 1–2 h prior to the time fecal pellets were collected. There was no significant correlation in these comparisons.

The third comparison of occurrence of food categories in fecal pellets and availability of potential prey was among sampling sessions 5–11. Again, there was no significant correlation among these comparisons.

Because there was no significant correlation between quantity of each food category in fecal pellets and availability of potential prey, we examined data in Tables 2 and 5 and looked for patterns of variation within sampling sessions 5–11. For Coleoptera, Diptera, and Lepidoptera there were strong indications that these categories were not being selected in proportion to availability. *M. grisescens* had a greater amount of Coleoptera and Lepidoptera represented in fecal pellets during each of the seven sampling sessions than was present in samples of potentially available prey. Conversely, Diptera was taken less frequently than available, except during sampling session

11 (17–20 September). Gray bats did not select prey in proportion to availability.

Discussion

Whitaker et al. (1996) recently suggested that interpretations of food habits may be biased unless samples from all nightly feeding bouts are included in analyses. Our samples, which were obtained throughout >20 nights, revealed that gray bats took a wider variety of prey items than previously reported (e.g., Lacki et al., 1995; Rabinowitz, 1978; Rabinowitz and Tuttle, 1982). Although we had anticipated variation in diet over time, as has been shown in other species of *Myotis* (e.g., Brack and La Val, 1985; Herd and Fenton, 1983; Shiel et al., 1991; Swift and Racey, 1983; Warner, 1985; Zinn and Humphrey, 1981), we had not anticipated the significant differences shown among sampling sessions and hours within sampling sessions. We expected that availability of prey would change through time, and that this change would be reflected in dietary components. Perhaps availability of prey in habitats where gray bats forage is related to the sporadic emergences and resultant swarms of potential prey. These emergences provide a temporary abundance of food represented by a few taxa at any time, but a number of taxa become available at intervals during the night, month, and annual activity season.

A recent study by Barclay and Brigham (1994) indicated that insectivorous bats may not be as selective in what they eat as has been shown in laboratory trials. Under controlled laboratory conditions, insectivorous bats used echolocation to make detailed discriminations among targets. However, bats did not make such discriminations under natural conditions. Barclay and Brigham (1994) reported that insectivorous bats, in the field, attacked any moving target of an appropriate size and appeared not to make fine-detailed discriminations based on shape and texture of target that occurred in the laboratory. This lack of discrimination may be due to rapid flight of bats and the short range at which prey can be detected by echolocation. Bats have only a fraction of a second between detection and capture of prey, possibly not enough time to distinguish among prey (Barclay and Brigham, 1994). Thus, diet of insectivorous bats should change over time if diet is determined by what prey items are encountered; i.e., as long as prey items are of proper size, shape, texture, etc. Herein, we have demonstrated that *M. grisescens* consumes a wide variety of taxa of prey during its annual activity period (Table 1), and that components of the diet are significantly different over short periods of time (Tables 2 and 3). As might be predicted from observations by Barclay and Brigham (1994), our findings could indicate that *M. grisescens* encountered a variety of acceptable taxa of food that varied in abundance and distribution throughout the season of activity of the bats, and that components of the diet varied accordingly. However, our data on prey that potentially were available for consumption by bats rarely varied significantly through time (Table 5).

Fenton and Morris (1976) suggested that most insectivorous bats would eventually be shown to be opportunistic feeders. As pointed out by Jones (1990), opportunistic foraging suggests that a strong positive correlation should occur between incidence of a particular prey in the diet, and its abundance in the environment. For selective foraging, a similar comparison should result in no correlation, or even a negative correlation between dietary incorporation and abundance of less-preferred prey (Anthony and Kunz, 1977; Jones, 1990). Because there was no significant correlation between contents of fecal pellets and availability of potential prey, we believe the population of *M. grisescens* we studied was selective in what it consumed. Our data indicated that the three primary components of the diet (Lepidoptera, Coleoptera, and Diptera) were not consumed in proportion to their availability at Guntersville Reservoir. Gray bats were opportunistic in the sense that they

probably took advantage of emergences of these taxa, and also because they consumed a variety of other taxa in small quantities.

Araneae has been reported in small quantities in the diet of *Myotis evotis* and *Myotis volans* in eastern Oregon; both of these species are common inhabitants of forested areas (Whitaker et al., 1981). In northern Alabama, spiders often dispersed from hatching sites by ballooning, and spiders frequently were suspended in open areas that made them susceptible to capture by *M. grisescens*. Although a regular component of the diet in our study, spiders were never present in large quantities (Table 1).

Previously, Acari was recovered in small quantities from fecal pellets of *M. volans* from eastern Oregon (Whitaker et al., 1981) and from fecal pellets of *M. grisescens* from Tennessee (Rabinowitz and Tuttle, 1982). Because ectoparasites may be ingested during grooming (Marshall, 1982), we believe that the chiggers we found in fecal pellets were incidentally ingested. Kunz (1974) also noted small percentages of acarines (Mesostigmata) in stomachs of *Myotis velifer* from Kansas. It also is possible that these acarines crawled onto fecal pellets during the $\leq$2 h when fecal pellets were on collecting cloths at the lower opening of Blowing Wind Cave (J. O. Whitaker, Jr., pers. comm.).

The significantly greater amount of bat hair in fecal pellets defecated during the evening exit from the roost probably is related to grooming behavior of gray bats. Other species of bats are known to groom extensively before beginning their nightly forays (Kunz, 1982; Nellis and Ehle, 1977), and this probably also is true for *M. grisescens*. When cleaning pelage and other structures, hair is ingested incidentally. Because there usually was significantly less hair present in fecal pellets later in the night, gray bats may spend little time grooming during the nighttime hours. In general, there was more hair present in fecal pellets from early June to early August than earlier or later in the activity season of gray bats (Table 2). June–August is the time of parturition and lactation, and the time when young become volant. Perhaps these reproductive activities increase the need to groom, or this period is when annual molting of pelage occurs.

Buchler (1975) demonstrated that food moves quickly through the digestive tract of *Myotis lucifugus*. Because this probably is true for *M. grisescens* as well, we believe the samples of fecal pellets we collected usually represented food ingested within ca. 1–2 h prior to defecation. The exception would be samples collected during emergence of bats from the roost at dusk. Contents of fecal pellets voided on emergence might be more representative of what was ingested just before entry into the roost that morning. We were not able to test this statistically, but there usually were more Lepidoptera (in five of seven sampling sessions) in samples of potential prey collected after midnight than before midnight. Perhaps, it took longer for scales and other body parts of Lepidoptera to pass through the digestive tract of the bats, and these remains were not defecated until the evening emergence. This might account for the high incidence of this taxon in fecal pellets obtained early in the evening when Lepidoptera rarely was present in sweep-net samples.

A criticism of analyses of fecal pellets to determine dietary components is that remains of the same insect may appear in fecal pellets voided from 0.5 to 32 h after consumption; in *Eptesicus serotinus*, scales from two moths were contained in 59 fecal pellets, and fragments from three beetles were in 28 fecal pellets (Robinson and Stebbings, 1993). Another criticism is that soft-bodied insects, i.e., small or recently emerged forms, may be digested and rendered unrecognizable, thus potentially contributing to underestimates of the number and kinds of insects actually eaten (Belwood and Fenton, 1976; Rabinowitz and Tuttle, 1982). However, tests conducted by Kunz and Whitaker (1983) demonstrated that analyses of fecal pellets can yield rea-

sonable estimates of foods eaten by insectivorous bats. In addition, Whitaker et al. (1981) reported relatively good agreement between contents of stomachs and feces of bats from eastern Oregon. Our analysis of fecal pellets revealed a variety of small and recently emerged insects, indicating that many of these food items were well represented. Because we examined a large number of fecal pellets from a large number of bats over a long span of time, we believe the data presented herein is a reasonable estimate of what taxa are consumed by gray bats in northern Alabama.

Prior to the study by Lacki et al. (1995), there were no quantitative data on foods consumed by *M. grisescens*. Although they examined only 58 fecal pellets, Lacki et al. (1995) demonstrated that gray bats consumed nine orders of insects in Kentucky. In addition, their samples (of 24, 2, 23, and 9 fecal pellets from May, June, July, and August, respectively) indicated variation in diet among months. The predominant order of insects in the diet of *M. grisescens* in Kentucky was Coleoptera, but Diptera, Lepidoptera, and Trichoptera also were consumed in appreciable amounts. Conspicuously absent from samples collected by Lacki et al. (1995) was Ephemeroptera. Previously, Rabinowitz (1978), Rabinowitz and Tuttle (1982), and Tuttle (1976*b*) reported that Ephemeroptera was an important component of the diet of *M. grisescens*. Their assertion was supported by observations of *M. grisescens* feeding in swarms of Ephemeroptera, but they discovered few remains of mayflies in fecal pellets of bats. To investigate why mayflies were underrepresented in fecal pellets, Rabinowitz and Tuttle (1982) fed gray bats a diet containing Ephemeroptera and then examined the fecal pellets. They determined that mayflies ingested by gray bats rarely were identifiable in fecal pellets, except when wings were eaten. They concluded that body parts of mayflies, other than the usually discarded wings, were largely digested and rendered unidentifiable in the feces. Likewise, Belwood and Fenton (1976) fed mayflies to captive *M. lucifugus* and ascertained that no recognizable trace of ephemeropterans emerged from the digestive tract. However, other studies have been able to detect remains of mayflies in feces of *M. lucifugus* (Anthony and Kunz, 1977; Buchler, 1976) and *Pipistrellus pipistrellus* (Swift et al., 1985). On several occasions, we observed *M. grisescens* foraging at sites where there were swarms of emerging mayflies. Although our quantitative data do not support our qualitative observations of the frequency of Ephemeroptera in the diet, we are confident that gray bats regularly consume mayflies, that many of these are completely digested (at least when only the body of the mayfly is ingested without its wings), and that the actual incidence of Ephemeroptera in the diet of *M. grisescens* is greater than quantified by us or by previous investigators. Our speculation also is supported by the presence of only pieces of wings of mayflies in fecal pellets where this taxon was detected.

Subadults usually consume a wider variety of prey than adults (Anthony and Kunz, 1977; Belwood and Fenton, 1976). Perhaps subadults are unable to differentiate among prey types as effectively as adults. If subadult gray bats were less selective in what they consumed than were adults, we would expect to see a greater variety of prey consumed during sampling sessions after young at nearby Hambrick Cave became volant and began to roost in Blowing Wind Cave, than during the time only adults were foraging. In addition, as females entered hibernation in September the proportion of subadults in the active population would increase. However, we observed no increase in diversity of diet in September. An interesting topic for future study would be variability in diet between subadults and adults before and after adult females enter hibernation in September. Because differences in diet between sexes have been demonstrated in other species of *Myotis* (Husar, 1976) and because gray bats generally segregate by

sex into maternity and non-maternity (primarily adult males and yearlings of both sexes) colonies (Tuttle, 1976*a*), it also might be informative to examine dietary differences between sexes of *M. grisescens*.

Our study and that of Lacki et al. (1995) demonstrate significant variation in diet of *M. grisescens* over time, but contrary to conclusions of Lacki et al. (1995), we have shown that gray bats are selective regarding the most common food categories they consume. It would be informative to conduct multi-year studies at the same study site to examine the degree of variation in diet of gray bats among years, and to examine multiple sites during the same year to quantify geographic variation in diet, e.g., as has been done for *Eptesicus fuscus* (Whitaker, 1995), *Eptesicus nilssoni* (Rydell, 1986, 1989), *Nycteris grandis* (Fenton et al., 1990, 1993), and *Rhinolophus hipposideros* (McAney and Fairley, 1989). We believe the degree of variability that would be elucidated in long-term or multi-site studies would demonstrate that our findings, those of Lacki et al. (1995), and those of previous researchers (Rabinowitz, 1978; Rabinowitz and Tuttle, 1982; Tuttle, 1976*b*) are in concordance and are indicative of the large amount of variability in diet of this endangered species.

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