

Summer Food Habits of *Myotis leibii* in the Central Appalachians Ecoregion and Comparison to Similar Studies

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ABSTRACT

Food habits of *Myotis leibii*, Eastern Small-footed Myotis, were studied during summer in the Central Appalachians Ecoregion. Moths were 70.0% of the diet by volume and were in 97.7% of samples (percent frequency). Beetles, flies, and spiders comprised much of the remaining diet. Percent volume and percent frequency metrics produce similar results. These data and past studies indicate this bat eats a relatively low-diversity diet centered on terrestrial-based arthropod prey across a broad geographical area, irrespective of season, sex, or age. The presence of spiders in the diet may indicate gleaning.

INTRODUCTION

The range of *Myotis leibii* (Eastern Small-footed Myotis), extends from northern New England through New York, south along the Appalachian Mountains to North Carolina and westward through Tennessee and northern Georgia, Alabama, and Mississippi (Whitaker and Hamilton 1998). Throughout its wide distribution, it has typically been considered uncommon (Barbour and Davis 1969; Best and Jennings 1997; Johnson et al. 2011, 2012) and the advent of the fungal disease white-nose syndrome (WNS) has further reduced both winter (Frick et al. 2015; Powers et al. 2015) and summer (Francl et al. 2012; Moosman et al. 2013) populations. Food habit studies are limited to sample sizes of 4 (McDowell-Griffith 1983), 39 (Moosman et al. 2007), 44

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go hand-in-hand. *Myotis leibii* forages more in deciduous forests than in large open areas, often near ridge tops (Johnson et al. 2009) where they roost in rock outcrops (Johnson et al. 2011).

The three previous food habits studies all identified moths (order Lepidoptera) as the most abundant diet component by both percent volume and percent frequency, while beetles (order Coleoptera) and flies (order Diptera) ranked second and third in both measures but not always in the same order of abundance across studies. Within studies, ranking between percent volume and percent frequency sometimes differed. Ants (order Hymenoptera), lacewings (order Neuroptera), booklice (order Psocoptera), and leafhoppers (order Homoptera) were ranked fourth or fifth most abundant in at least one study by either percent volume or percent frequency. Spiders were part of the diet in two of the three studies, and while Moosman et al. (2007) ranked them fourth in percent volume and fifth in percent frequency, Johnson et al. (2012) ranked them last (of eight) using both metrics.

Our paper adds to the knowledge of food habits of *M. leibii* from part of the Central Appalachians Ecoregion (Omernik and Griffith 2014) where Virginia, West Virginia, and Kentucky meet. We compare findings, expressed as percent volume and percent frequency of taxa of arthropod prey in the diet, with similar studies. Percent volume is widely used to determine proportions of arthropod taxa in the diet of a group, whereas percent frequency is less widely used to determine how broadly taxa are consumed by individuals of that group (Whitaker 1988). We use a ranking system to compare percent volume and percent frequency across all taxa, for this and previous studies, whereas this comparison is typically limited to individual taxa. This comparison furthers understanding of how the two metrics of diet relate. We use an index of diet diversity as a simple indication of a specialized or generalized diet to compare among our study sites, and among this and previous studies.

MATERIALS AND METHODS

Study Area

Studies were completed in the Central Appalachians ecoregion (Omernik and Griffith 2014), or Allegheny Plateau Physiographic Province, where Virginia, West Virginia, and Kentucky meet. Geologic strata are sedimentary, and the terrain is characterized by high elevation, high relief, and a well-dissected dendritic drainage. The region's naturally rugged terrain is enhanced by extensive bituminous coal mining (surface and sub-surface). While cliff faces and talus rock slopes provide natural roosting habitat for *M. leibii* (Johnson et al. 2011), old above ground mine works such as high walls, and old subsurface mines provide cracks and fissures for roosting. The area has a continental climate with warm to hot summers and cold winters. This is part of Braun's (1950) mixed mesophytic forest region while Dyer (2006) includes it in the Appalachian Oak Section of the Mesophytic Forest.

Field Studies

Bats were captured 15 May to 15 August 2000 and 2001, in Wise County in western Virginia and adjacent counties in southern West Virginia and eastern Kentucky. Mist nets were placed in concave (open) corridors such as roads and utility rights-of-way through upland woodlands, typically with a mature oak-hickory component. In high relief terrain, pools of drinking water are uncommon, so nets were often placed near water-filled road ruts (Kiser and MacGregor 2004; Johnson et al. 2011, 2012); reproductive female *M. leibii* often roost close to water sources (Johnson et al. 2011). Netting followed protocol of the U.S. Fish and Wildlife Service for the endangered *Myotis sodalis* (Indiana Myotis) at that time (current version at USFWS 2020). The protocol required mist nets extend from ground to canopy, usually requiring two to three vertical tiers of nets and two nights of netting with two nets sets (four net nights) for each 100 ha of suitable habitat sampled.

When bats were removed from the net, morphometric measurements, sex, age, and reproductive condition were recorded. *M. leibii* were placed in individual cloth bags for 10–20 minutes to collect fecal samples. Feces were placed in catalogued containers, air-dried, and transported to the laboratory. Bat capture and handling followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Fecal Analyses

Guano samples were obtained from 43 bats: 23 from western Virginia, 15 from eastern Kentucky, and 5 from southern West Virginia (Table 1). In the laboratory, pellets from a single bat were placed on a petri dish and wetted with an ethanol and water mixture and teased apart. Insect remains were identified using a dissecting microscope, and percent volume was estimated visually for each arthropod taxon (insects and spiders). Insects were identified to the lowest taxon possible, usually order and sometimes family. The volume of remains of each taxon in the diet of a bat was expressed as a percent of that bat's total diet. When diets of individuals were combined, guano from each bat was treated as a single unit regardless of the number of pellets, so each bat contributed equally to the combined group diet, avoiding bias from samples weighted by numbers of pellets. Data were summarized by percent volume (volume of each food/total volume x 100) and percent frequency, the percentage of bats in a sample eating arthropods of a particular taxon (Whitaker 1988).

For each sample (by state and combined), a diet diversity index (DDI) was calculated: $DDI = 1/\sum P_i^2$ (MacArthur 1972), where P_i is the proportional occurrence of an arthropod taxon (seven insect orders plus spiders) in a sample. This index is a quick estimate of the number of equally represented taxa in the diet, which provides an easy indication of a specialized or generalized diet but does not identify taxa.

Bats of all ages and sexes were pooled by state because of small sample sizes. Analysis of variance (ANOVA) was used to compare arthropod taxa among pooled state samples. Analyses of percent volume uses arcsine-transformed data to stabilize variance and normalize proportional data in biological studies (Sokal and Rolf 1981) and is frequently employed in bat dietary analyses

(Humphrey et al. 1983; Brack and LaVal 1985, 2006; Dalton et al. 1986; Whitaker 1988; Sample and Whitmore 1993; Brack and Whitaker 2001; Moosman et al. 2007; Rakotoarivelo et al. 2007).

Percent volume and percent frequency are frequently used metrics of bat diets. Although often compared within individual taxon, there is no standard comparison across the many taxa that comprise a diet. We made this comparison by ranking taxa by percent volume and percent frequency, most to least common, and subtracting the rank for percent frequency from rank for percent volume. This produced a zero, positive, or negative number, indicating ranks were the same, or that percent frequency ranked lower or higher than percent volume, with numerals indicating the number of levels of rank change.

Comparison to Similar Studies

We compared the combined sample for the Central Appalachians Ecoregion to similarly pooled samples of previous studies (Johnson and Gates 2007; Moosman et al. 2007; Johnson et al. 2012). Comparisons include (1) ANOVAs on percent volume and percent frequency of all arthropod taxa, (2) ANOVAs on the four most common taxa (moths, beetles, flies, and spiders) because DDI in each study was between four and five, (3) percent volume versus percent frequency, and (4) DDIs. We graphically display (compare) percent volume and percent frequency of the four most common taxa from this and previous studies.

RESULTS

Food Habits in the Central Appalachians Ecoregion

We identified arthropod remains in feces to seven orders of insects plus spiders; some insect remains were identified to 10 families. Moths, the most important food (Table 1), were in the diet of all but one individual bat. Beetles were second most important in the diet. Remains of scarab beetles (family Scarabaeidae) were in five samples from Virginia, four from Kentucky, and one from West Virginia, while remains of leaf beetles (family Chrysomelidae) were in two samples from Virginia and one sample from Kentucky. Flies were the third most common food; remains of crane flies (family Tipulidae) were in feces of two bats from Virginia. Leafhoppers (family Cicadellidae, order Homoptera) were a relatively small part of the diet by volume but were in samples from all three states and 34.9% of all samples. Spiders were in samples from each state and 18 of 43 bats (Table 1).

Location (state) had no significant impact on percent volume ($F_{(2,24)} = .068$, $p = .934$) or percent frequency ($F_{(2,24)} = .014$, $p = .985$) of arthropod taxonomic groups in the diets. As such, data were pooled across the ecoregion (Table 1). The DDI was 5.06 for the pooled sample and 4.57 to 5.20 within states (Table 1). Rankings of taxa in the diet, most to least common, were similar for percent volume and percent frequency (Table 2). In individual states, only three taxa varied by more than one rank (Table 2), and when combined, the rank of two taxa each varied by a single rank.

TABLE 1. Foods (arthropod taxa) of *M. leibii* from the Central Appalachians Ecoregion by percent volume (Vol.), percent frequency (Freq.), and number of occurrences in the sample (No.). The Diet Diversity Index (DDI) provides an estimate of the number of equally represented taxa in the diet.

Arthropod Taxon	Virginia			Kentucky			West Virginia			TOTAL		
	N = 23			N = 15			N = 5			N = 43		
	Vol.	Freq.	No.	Vol.	Freq.	No.	Vol.	Freq.	No.	Vol.	Freq.	No.
Lepidoptera	58.5	95.7	22	80.3	100.0	15	90.0	100.0	5	70.0	97.7	42
Coleoptera (no ID)	13.2	65.2	15	6.0	60.1	9	1.0	40.0	2	9.5	61.0	26
No ID	6.2	34.8		1.3	26.7		0.4	20.0		3.8	27.9	
Scarabaeidae	5.3	21.7		3.0	26.7		0.6	20.0		4.2	25.6	
Chrysomelidae	1.7	8.7		1.7	6.7		0.0	0.0		1.5	7.5	
Diptera (no ID)	11.7	52.2	12	4.1	66.7	10	1.0	60.0	3	7.5	58.2	25
No ID	11.0	43.5		4.1	66.7		1.0	60.0		7.2	53.5	
Tipulidae	0.7	8.7		0.0	0.0		0.0	0.0		0.3	4.7	
Hymenoptera	1.7	4.3	1	0.4	13.4	2	0.4	20.0	1	1.2	9.3	4
Formicidae	1.7	4.3		0.3	6.7		0.4	20.0		1.1	7.0	
Ichneumonidae	0.0	0.0		0.1	6.7		0.0	0.0		0.1	2.3	

Neuroptera: Hemerobiidae	0.4	4.3	1	0.0	0.0	0	0.0	0.0	0	<0.0	2.3	1
Hemiptera	1.2	21.6	5	0.0	0.0	0	0.0	0.0	0	0.6	11.6	5
Pentatomidae	0.6	13.0		0.0	0.0		0.0	0.0		0.3	7.0	
Lygaeidae	0.2	4.3		0.0	0.0		0.0	0.0		0.1	2.3	
Reduviidae	0.4	4.3		0.0	0.0		0.0	0.0		0.2	2.3	
Homoptera: Cicadellidae	6.9	34.8	8	4.7	40.0	6	0.4	20.0	1	5.4	34.9	15
No ID insect	0.0	0.0		0.2	6.7		0.2	20.0		0.1	4.7	
Araneae	6.3	39.1	9	4.2	33.3	5	7.0	80.0	4	5.7	41.9	18
Total Occurrences			73			47			16			136
DDI			5.20			4.69			4.57			5.06

TABLE 2. Diet by percent volume and percent frequency are compared for states and total in the current and three similar studies. Taxa were ranked most to least common and for each taxon, rank for percent frequency is subtracted from rank for percent volume. This produces a zero when ranks are the same, or a positive or negative number, indicating the number or ranks percent volume is higher or lower (respectively) than percent frequency. When two or more taxa ranks are equal, comparisons between percent volume and percent frequency are shown with a slash (/).

	This study				Johnson et al.	Moosman et al.	Johnson and
	VA	KY	WV	Total	(2012)	(2007)	Gates (2007)
Lepidoptera	0	0	0	0	0	0	0
Coleoptera	0	-1	-1/0	0	0	0	0
Diptera	0	3	0/+1	0	0	0	0
Hymenoptera	-1/-2	0	-1	-1	0	0	0
Neuroptera	+1/0	0	0	0	1	0	0
Hemiptera	1	0	0	1	-1	1	0
Homoptera	-1	-1	-1	0	0	0	0
Orthoptera	0	0	0	0	0	0	0
Psocoptera	0	0	0	0	0	0	0
Trichoptera	0	0	0	0	0	0	0
No ID insect	0	0	+2/0	0	0	0	0
Araneae	1	-1	0	0	0	-1	0

TABLE 3. A comparison of arthropod prey in fecal samples by percent volume (Vol.) and percent frequency (Freq.), number of occurrences in the sample (No.), and diet diversity (DDI) in this and three similar studies.

	Current study			Johnson et al. (2012)			Moosman et al. (2007)			Johnson and Gates (2007)		
	N = 43			N = 77			N = 39			N = 44		
	Vol.	Freq.	No.	Vol.	Freq.	No.	Vol.	Freq.	No.	Vol.	Freq.	No.
Lepidoptera	70	97.7	42	41.8	100	77	46.2	85	33	58.5	98	43
Coleoptera	9.5	61.0	26	30.4	97	65	19.1	56	22	5.5	46	20
Diptera	7.5	58.2	25	16.7	82	63	18.6	46	18	24.7	66	29
Hymenoptera	1.2	9.3	4	0.7	9	7	0.1	3	1	5.4	27	12
Neuroptera	<0.0	2.3	1	2.3	32	25	0	0	0	1.6	7	3
Hemiptera ¹	0.6	11.6	5	3.3	29	22	5.2	21	8	1.0	5	2
Homoptera	5.4	34.9	15	0	0	0	<0.1	3	1	1.0	5	2
Orthoptera	0	0	0	0	0	0	0.1	3	1	0	0	0
Psocoptera	0	0	0	0	0	0	0	0	0	3.4	16	7
Trichoptera	0	0	0	1.8	16	12	2.0	8	3	0	0	0
Araneae	5.7	41.9	18	0.01	0.01	0	6.4	10	4	0	0	0
Occurrences			136			271			91			118
DDI			5.06			4.76			4.16			4.22

¹Moosman et al. (2007) determined taxa of Hemiptera and Homoptera differently than the other studies

Comparison to Similar Studies

Prey by percent volume and percent frequency is similar among this and three previous studies (Table 3). ANOVA failed to identify a significant difference among studies by either percent volume ($F_{(3,40)} = .006, p > .99$) or percent frequency ($F_{(3,40)} = .255, p = .86$). Differences in ranking taxa by percent volume versus percent frequency among our combined sample and previous studies were infrequent, and never more than a single ranking (Table 2).

Diet diversity indices were also similar among studies. The DDI for this study was 5.06 and ranged from 4.16 to 4.76 for previous studies (Table 3). Because DDI were between four and five, the four most common taxa in the diet of our study were compared across studies by both percent volume and percent frequency (Fig.1). ANOVA failed to identify a significant difference among studies in the four common taxa by percent volume ($F_{(3,12)} = .036, p = .99$) or percent frequency ($F_{(3,12)} = .281, p = .84$).

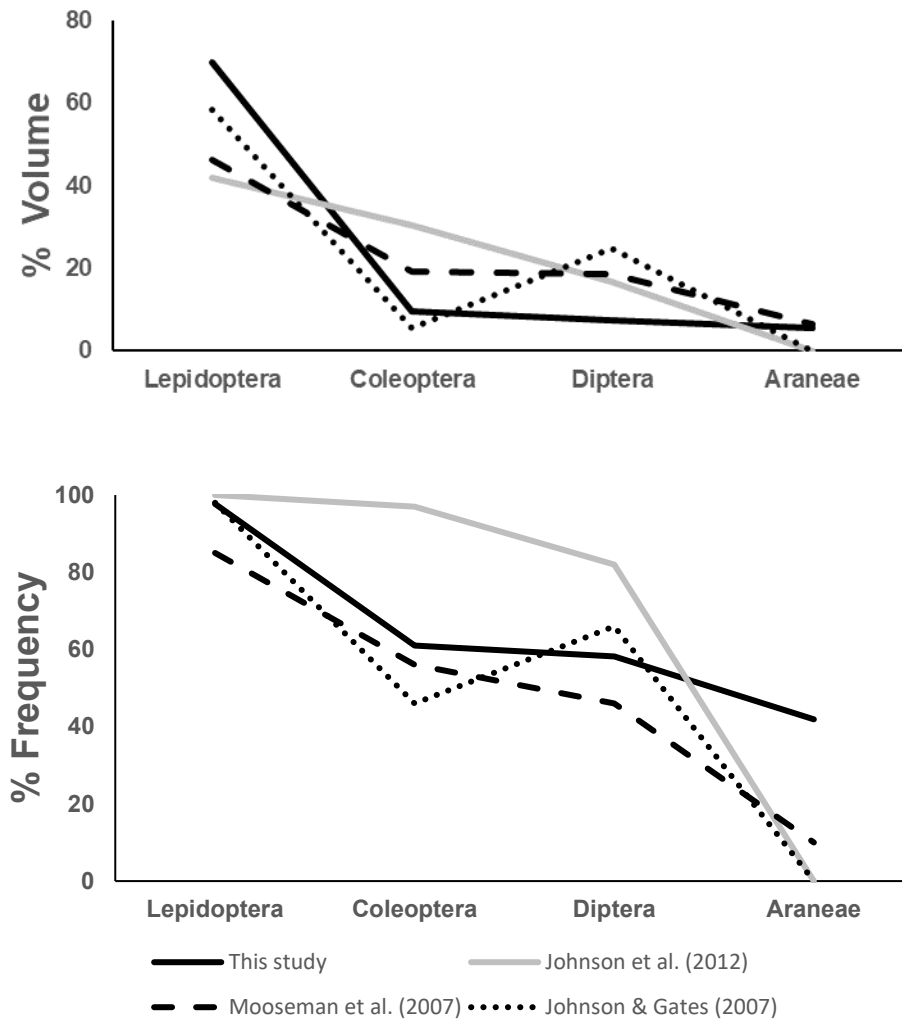


Fig. 1. A comparison of the four major taxa of arthropod prey identified in fecal samples from *M. leibii* in this and three similar studies by percent volume and percent frequency.

DISCUSSION

Summer fecal samples were obtained from bats netted in upland woods, typically with a mature oak hickory component, and prey eaten were more indicative of a terrestrial upland habitat than an aquatic habitat (Brack and LaVal 1985; Clare et al. 2011). It is not surprising that we did not detect differences among locations. Many species of insectivorous bats are generalists over time and space, and often, though not always, consume prey in general proportion to availability within habitats where they forage (Anthony and Kunz 1977; Brack and LaVal 1985, 2006; Sample and Whitmore 1993; Kurta and Whitaker 1998; Murray and Kurta 2002; Rakotoarivelo et al. 2007; Clare et al. 2011). Our data indicate *M. leibii* is a moth-beetle-fly-spider generalist, with an emphasis on moths. This bat flies slow and close (0.3 – 3 m) to the ground (Davis et al. 1965; Barbour and Davis 1969; Neuhauser 1971; van Zyll de Jong 1985), suggestive of a gleaning strategy.

Like past studies in western Maryland May–October (McDowell-Griffith 1983), New Hampshire May–September (Moosman et al. 2007), the Central Appalachians Ecoregion of southeastern West Virginia during autumn swarming (Johnson and Gates. 2007), and the Ridge and Valley Ecoregion in West Virginia spring–autumn (Johnson et al. 2012), the dominant food was moths. Similarly, in all these studies beetles and flies were second and third most common foods, although not always in the same order. Also, as in previous studies, insects from several additional orders comprised the remainder of the diet, although each contributed a small amount. Collectively, these data support the conclusion that this bat is a generalist, feeding in an upland, terrestrial-based habitat.

The DDI values were similar across areas of our study and across all studies. This index does not identify taxa consumed but does provide a comparison of a specialized or generalized diet. For example, DDI of *M. sodalis* and *M. grisescens* (Gray Myotis) both decrease from spring when food is least abundant to late summer when food is most abundant (Brack and LaVal 1985, 2006), and the diet of reproductive female *M. lucifugus* (Little Brown Myotis) is less diverse in summer (Anthony and Kunz 1977), when food is more abundant. Similarly, young less-skilled bats may have a lower DDI when concentrating on easily caught prey (Brack and LaVal 2006), and many species sharing a geographic area eat a common or superabundant prey (Storm and Whitaker 2008; Levin et al. 2009; Clare et al. 2011; Blazek et al. 2021), which can lower the DDI.

We report the highest percent frequency of spider consumption, total and in each state (33.3–80.0%), to date for *M. leibii*, previously reported at 10.0% (Moosman et al. 2007) and 1.3% (Johnson et al. 2012). Bats may catch spiders by gleaning the surface of vegetation or the ground, or in the air where spiders are ballooning or are suspended on a web. The presence of crickets (family Gryllidae, order Orthoptera) in the diet (Moosman et al. 2007) supports the role of a gleaner. Many species of bats that are not gleaning specialists glean occasionally or under specific situations. For example, *M. lucifugus* is an aerial-hawing strategist (Anthony and Kunz 1977), but in Alaska 16.8% of the diet by volume is spiders (Whitaker and Lawhead 1992), in Ontario 7.6% of prey species identified using DNA is spiders (Clare et al. 2011), and in British Columbia, up to 8% of fecal samples contain spiders (Burles et al. 2008). Many species that glean also eat large quantities of moths. In western Indiana, spiders were in 25.4% and moths 69.8% of stomachs of

M. septentrionalis (Northern Long-eared Myotis) (Brack and Whitaker 2001), and in British Columbia > 70% of fecal samples from *M. keenii* (Keen's Myotis) contained moths and spiders. *Corynorhinus townsendii virginianus* (Virginia Big-eared Bat), another species that gleans and forages in Appalachian uplands, eats a high proportion of moths (Dalton et al. 1986; Sample and Whitmore 1993).

Based on standardized techniques (Whitaker 1988), many studies, including *M. leibii*, use percent volume and percent frequency to characterize consumption of taxa as a large proportion of diets versus widespread consumption among individuals. However, while comparison across the many taxa in a diet is difficult, ranking showed the two techniques provided similar results.

Our data support and broaden understanding of food habits of *M. leibii*, a species uncommon throughout its broad distribution. Across a broad geography and irrespective of season, sex, or age, this bat eats a relatively low-diversity diet centered on terrestrial-based insects, predominately moths, beetles, and flies. In addition, spiders are frequently consumed, which may reflect a greater use of a gleaning strategy than previously appreciated. These results highlight a need to better understand the foraging behavior and habitat of this bat.

A great deal remains to be learned about *M. leibii* and post-WNS (white-nose syndrome), it will be more difficult. WNS will likely forever change abundances and distributions of species of cave-hibernating bats in the eastern United States during winter (Frick et al. 2015; Powers et al. 2015) and summer (Dzal et al. 2010; Francl et al. 2012; Moosman et al. 2013; Reynolds et al. 2016). Species less impacted by WNS (Powers et al. 2016; Cheng et al. 2021) may have an advantage while loss or extreme rarity of a species may facilitate ecological release (Bolnick et al. 2010) of competitors, changing diets or habitats (Morningstar et al. 2019; Nocera et al. 2019; Mayberry et al. 2020). Changes resulting from WNS may allow species absent or at the periphery of their ranges, for example *M. grisescens*, to expand into the area (Powers et al. 2016), creating a new and different competition dynamic. These changes may make pre-WNS data helpful for understanding impacts of WNS and help put post-WNS studies in perspective.

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