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PE-48

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Diet of the Endangered Indiana Bat (Myotis sodalis) on the Northern Edge of Its Range

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ABSTRACT.—Dietary preferences of Indiana bats were determined by analyzing 382 fecal pellets collected beneath roost trees in southern Michigan, over parts of 3 yr. Although terrestrial insects (Lepidoptera and Coleoptera) usually dominated the diet of Indiana bats in more southern states, those in Michigan consumed mostly insects associated with aquatic environments. Indiana bats in Michigan ate primarily Trichoptera (55.1% of volume) and Diptera (25.5%), followed by Lepidoptera (14.2%) and Coleoptera (1.4%). Consumption of Diptera was highest during lactation (48.2%), whereas consumption of Lepidoptera was least during this time (7.7%). Although most insectivorous bats do not prey on mosquitoes (Culicidae), these insects were a consistent component of the diet of Indiana bats and were eaten most heavily during pregnancy (6.6%).

INTRODUCTION

Knowledge of the diet can provide fundamental insights into the ecology and behavior of an animal, and dietary information is essential for proper management of any species. For example, the type of food predicts an animal's basal metabolic rate, which, in turn, determines aspects of the animal's population ecology and home-range size (McNab, 1980). In addition, knowledge of the diet may reveal where, when, how, and how often an animal forages. Understanding the foods eaten by an endangered species is particularly important, because a population's decline may be related to the diet; for example, lack of suitable prey (MacKenzie and Oxford, 1995) or exposure to pollutants obtained through contaminated prey (Clark, 1981, 1996; Wiemeyer *et al.,* 1984; Clawson and Clark, 1989; McLachlan and Arnold, 1996) have been implicated in the decline of many species.

The Indiana bat (*Myotis sodalis*) is a small, 7–10 g, insectivorous species that ranges throughout much of the eastern United States (Thomson, 1982). At one time, 90% of the known population hibernated in only three caves and one mine (Brady *et al.,* 1983). Because of large declines in population size and the apparent lack of critical habitat in winter, the species was declared endangered in the United States in 1967. The primary focus of the original recovery plan for this species (Brady *et al.,* 1983) was to prevent disturbance to hibernating bats, yet despite current protection of all major hibernacula, the species continues to decline. The magnitude of the problem, however, varies across the species' range, with some areas showing little, if any, decline in population, while others report alarming losses. The population in Missouri, for example, has decreased by 80% over the last 13 yr (Indiana Bat Recovery Team, 1996; Clawson, 1987).

The continued decline of the Indiana bat, despite protection in winter, suggests that there also are problems during spring and summer when females gather in maternity colonies and actively forage. However, the only available information on diet of this species during the maternity season is from unpublished thesis research in Indiana (Belwood, 1979; Brack,

PE-48

1983; Lee, 1992). Because many aspects of the roosting ecology and behavior of Indiana bats in northern areas differ from those observed in more southern states (Kurta *et al.,* 1993, 1996), it is essential that the diet of this endangered species be examined in all parts of its range (Indiana Bat Recovery Team, 1996). The purpose of the present report is to document the diet of Indiana bats at the most northern maternity colony known for the species and to summarize and make comparisons with unpublished studies from more southern locations.

METHODS

Study animals.—We determined diet by examining fecal pellets collected from a maternity colony of Indiana bats that roosted under the exfoliating bark of dead trees, near Vermontville, Eaton Co., Michigan (Kurta *et al.,* 1993, 1996). These bats used at least 23 trees over 3 yr and as many as 18 different trees in 1 yr; no tree was continually used throughout any year. We did not know where these bats foraged, but it was not in the immediate vicinity of the roosts; radiotagged individuals left the roosting area every night, and some individuals were captured up to 2 km from their dayroost. This population of Indiana bats consisted of 20–25 adult females, most of which gave birth to a single young in late June (Kurta *et al.,* 1993, 1996).

Fecal analysis.—To obtain feces, we placed a nylon screen on wooden supports below the preferred entrance/exit of six of the most commonly used roost trees. Maximum distance between roosts from which we collected feces was less than 150 m. Overall, we collected 27 samples, containing 2 to 125 pellets each; 18 samples were from 6 June to 17 July 1993, six were from 22 July to 28 August 1994, and three from 2 to 10 June 1995. After collection, pellets were dried and stored in vials, and later, up to 30 pellets from any one sample were randomly selected and examined under a dissecting microscope; examination of 30 pellets is sufficient to document all major dietary items in a sample of the feces of insectivorous bats (Whitaker, 1999). Insect remains were identified to order, and occasionally family, and the percent-volume of each taxon in each pellet was estimated visually (Whitaker, 1988). Differences among samples from bats in different reproductive conditions were examined using Kruskal-Wallis tests, followed by Bonferroni-adjusted Wilcoxon tests for multiple comparisons (SAS Institute, 1990).

RESULTS

A total of 382 pellets were examined. Indiana bats in Michigan ate mainly Trichoptera (caddisflies; 55.1% of volume) and Diptera (true flies; 25.5%), followed by Lepidoptera (moths; 14.2%) and Coleoptera (beetles; 1.4%—Table 1). The remaining 3.8% consisted of six other insect orders, as well as spiders (Araneae). On occasion, we were able to identify the foods to lower taxa (Table 1). Numerically, the most important of these were the dipteran families Chironomidae (midges; 4.1%) and Culicidae (mosquitoes; 2.7%). Although mosquitoes are not an important food for most species of bats (Whitaker and Lawhead, 1992), these small insects were consistently present in the diet of Indiana bats in Michigan, appearing in 22 of 27 collections.

The most extensive samples were from 1993, and the last date of collection in that year (17 July) coincided with the earliest date that we encountered volant juveniles (Kurta *et al.,* 1996). Assuming 3–4 wk from birth to first foraging flight, as in *Myotis lucifugus* (Buchler, 1980; Fujita, 1986), parturition by Indiana bats began ca. 19–26 June. Consequently, we divided the sample from 1993 into three groups, representing pregnancy (6–17 June, 94 pellets), a transition from late pregnancy to early lactation (19–30 June, 100 pellets), and lactation (2–17 July, 39 pellets). We analyzed the data for the four most common orders

PE-48

TABLE 1.—Percent-volume of foods eaten by Indiana bats in Michigan based on analysis of fecal pellets. When separate families are listed, their percent-volume is included in the value indicated for the whole order. Values for orders within columns do not add to 100 because of rounding errors

	Percent-volume			
Taxon	1993 (n = 233)	1994 (n = 101)	1995 (n = 48)	Total (n = 382)
Trichoptera	47.7	71.4	56.5	55.1
Diptera (all families)	31.8	15.0	17.0	25.5
Chironomidae	2.6	7.8	2.7	4.1
Culicidae	4.2	0.6	0.4	2.7
Tipulidae	0.3	0	1.6	0.4
Dolichopidae	0.02	0	0	0.01
Lepidoptera	16.6	8.8	14.8	14.3
Coleoptera (all families)	0.7	1.5	4.8	1.4
Scarabaeidae	0.9	0	2.0	0.3
Curculionidae	0.3	0	0	0.02
Dytiscidae	0	0.5	0	0.1
Hymenoptera (all families)	1.3	0.5	1.3	1.1
Ichneumonidae	1.3	0.1	1.2	1.0
Formicidae	0	0.2	0	0.07
Neuroptera (Hemerobiidae)	0.2	0.9	4.6	0.9
Araneae	1.0	0.3	0	0.7
Unidentified insects	0.2	0.7	0.7	0.4
Hemiptera (all families)	0.3	0.05	0.3	0.3
Lygaeidae	0.06	0	0	0.04
Homoptera (all families)	0.2	0.4	0	0.2
Cicadellidae	0.2	0.4	0	0.2
Aphididae	0	0.1	0	0.04
Plecoptera	0	0	0.4	0.05
Ephemeroptera	0.04	0	0	0.03
Total for orders	100.04	99.6	100.4	100

and found no significant differences among the three groups for Trichoptera or Coleoptera (Table 2). However, the percent-volume of Lepidoptera was highest in pregnancy and transition and lowest in lactation, whereas all Diptera combined were greater in lactation than in pregnancy or transition. Chironomid flies did not vary across reproductive conditions, but mosquitoes were consumed in highest amounts during pregnancy.

DISCUSSION

To date, there have been four unpublished surveys of the diet of Indiana bats (Fig. 1); each of these was similar to the present study in that each reported the percent-volume of various foods, based on analysis of fecal samples that were collected from May or June through August. Brack and Laval (1985), for example, examined fecal pellets from 140 male Indiana bats, captured as they entered a cave in Missouri, and found 83% Lepidoptera and 7% Coleoptera. Brack and Laval (1985) also indicated that the diet did not vary across the night; they compared the composition of pellets from individuals captured during the postsunset foraging period and those captured during predawn foraging and found no significant differences. In another study, Belwood (1979) analyzed pellets from individual females and juveniles and also pellets collected beneath a maternity roost in southern In-

PE-48

TABLE 2.—Mean percent-volume of the most common foods eaten by Indiana bats in Michigan during pregnancy, transition from pregnancy to lactation, and lactation, in 1993. The indicated probability is for differences among the three groups as indicated by Kruskal-Wallis tests, each with 2 deg freedom. For each taxon, means with different superscripts were significantly different based on Bonferoni-adjusted Wilcoxon tests (alpha = 0.025); actual probabilities for significant Wilcoxon tests were all ≤0.01

	Percent-volume				
Taxon	Pregnancy (n = 94)	Transition (n = 100)	Lactation (n = 39)	χ^2	P
Trichoptera	55.6[a]	43.6[a]	39.4[a]	3.94	0.14
Diptera	22.4[a]	34.3[a]	48.2[b]	17.02	0.002
Chironomidae	1.2[a]	3.6[a]	3.1[a]	1.84	0.40
Culicidae	6.6[a]	2.9[b]	1.5[b]	10.94	0.004
Lepidoptera	16.0[a]	20.7[a]	7.7[b]	9.24	0.01
Coleoptera	0.9[a]	0.5[a]	0.5[a]	0.85	0.65

diana; she reported 57% Lepidoptera, 18% Diptera, and 9% Coleoptera. Similarly, Brack (1983), working at sites throughout Indiana over 3 yr, found Lepidoptera (48%) and Coleoptera (24%) to be major components of the diet, followed by Diptera (8.5%) and Trichoptera (9.8%); although the exact proportions differed, moths and beetles predominated in samples taken from mist-netted individuals of each sex and age (adult vs. juvenile), and these insects also were the most common taxa in pellets collected from beneath a maternity roost. Lepidoptera dominated the diet in every year of his study (Brack, 1983), and the percent-volume of Lepidoptera in the diet did not differ significantly among years; Brack

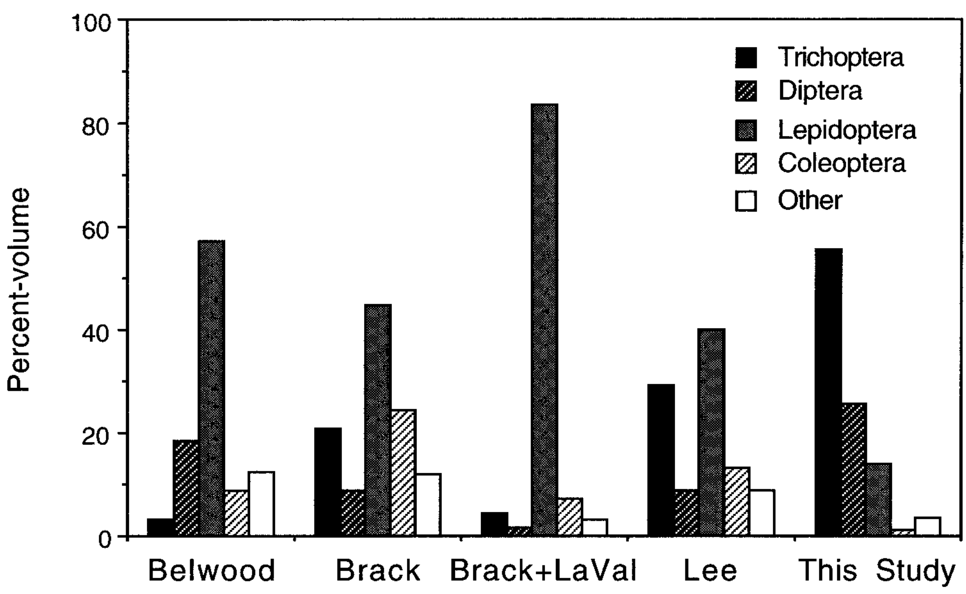

FIG. 1.—Percent-volume of various insect taxa in the diet of the Indiana bat, as reported by Belwood (1979), Brack, (1983), Brack and LaVal (1985), Lee (1993) and the present study

(1983) also indicated no significant differences in the diet of males (the only group tested) that were captured early or late in the night. Finally, Lee (1993) collected pellets from 23 female Indiana bats that were mist-netted in central and northern Indiana and found 40% Lepidoptera, 29% Trichoptera, 13% Coleoptera, and 9% Diptera. Hence, previous studies at more southern sites consistently showed that the diet of Indiana bats was dominated by Lepidoptera (Fig. 1). This dominance of Lepidoptera occurred throughout the night and across years and was evident in pellets collected from individuals of varying age and sex, as well as pellets obtained from maternity roosts.

Although our study was similar to previous reports in showing that the diet of the Indiana bat consisted primarily of soft-bodied insects (Table 1), our results indicated that the diet of females and young at a northern colony was not dependent upon moths. In Michigan, Indiana bats took prey from 10 insect orders, as well as spiders, but these bats concentrated on Trichoptera and Diptera. These two orders comprised ca. 81% of the foods eaten, and their dominance was evident both among and within years (Tables 1–2); Lepidoptera, in contrast, contributed only ca. 14%, or less than half the amount found in any previous study (Fig. 1).

Overall diet in Michigan was not only different from that in southern locations; trends within a year also differed. Brack (1983), for example, reported that consumption of Lepidoptera increased from May through August, while Trichoptera decreased. Such a pattern was not evident in our study; there was no statistical difference in the abundance of caddisflies during pregnancy, transition or lactation, whereas moths actually decreased during lactation (Table 2). In addition, if the same trend occurred in Michigan, our sample from 1994, which was gathered late in the season (22 July to 28 August), should have had a very low proportion of caddisflies, yet those pellets actually yielded the greatest percentage of Trichoptera (71%, Table 1).

Similarly, Belwood (1979) reported a significant increase (from 31% to 70%) in moth consumption and a significant decrease (from 41% to 16%) in fly consumption during lactation compared to pregnancy. She hypothesized that the shift to moths during lactation was an attempt by females to obtain prey that were energetically or nutritionally more rewarding. Such speculation was logical considering the huge increase in energy required by bats during lactation (Kurta *et al.,* 1989), but if her hypothesis were correct, one would have expected Indiana bats in Michigan to follow the same pattern. However, moth consumption in Michigan actually declined, while flies substantially increased, during lactation (Table 2). We suspect that these conflicting reports of seasonal changes in diet simply reflect availability of insects in the habitats in which the bats chose to forage, and such changes may not necessarily have an adaptationist explanation.

Small myotine bats, such as the Indiana bat, are generally believed to be opportunistic foragers (Belwood and Fenton, 1976; Fenton and Morris, 1976; Vaughan, 1980). The speed of a flying bat and the short detection range inherent in the use of echolocation make discrimination among different types of prey difficult (Barclay and Brigham, 1994). Selectivity in terms of prey, to a large degree, likely results from selection of a particular habitat to forage in, rather than selection of a particular type of insect *per se,* and once the habitat is chosen, the bats may simply feed on whatever appropriate-size insect is most abundant (Brack, 1983; Aldridge and Rautenbach, 1987; Brigham, 1990; Barclay and Brigham, 1994; Whitaker, 1995). Consequently, consumption of insects associated with terrestrial environments (Lepidoptera and Coleoptera) by Indiana bats in southern states indicates that these bats often foraged in upland habitats (Belwood, 1979; Brack, 1983; Lee, 1993), whereas the consumption of insects generally associated with aquatic environments (Trichoptera and

PE-48

Diptera) by Indiana bats in Michigan indicates that these bats foraged primarily in wetland habitats.

Differences between Indiana bats in Michigan and more southern areas are not restricted to dietary and foraging patterns; previous work also indicates substantial differences in roosting behavior. For example, those that summer in Michigan consistently form smaller colonies, use different species of trees, choose trees in sunnier locations, and roost more frequently in wetlands than do southern populations (Gardner *et al.,* 1991; Callahan, 1993; Kurta *et al.,* 1993, 1996). These differences in roosting and foraging behavior may reflect regional differences in availability of habitats or insects (Brack, 1983; Price, 1984; Dunn, 1996), increased or decreased competition from other species (as membership of the local chiropteran community changes across the continent, Findley, 1993), or perhaps true regional preferences by different populations of bats.

Whatever its cause, such variation is potentially important to the management and recovery of this and other endangered species and indicates that any sound management plan must consider the behavior of an animal in all parts of its range. This is particularly true for the Indiana bat, because not only does this species show apparent regional differences in foraging and roosting behavior, but population declines of the Indiana bat also show regional variation. The Indiana bat in some areas of its range, such as Missouri, is on the verge of extinction, while other populations are holding steady (Clawson, 1987; Indiana Bat Recovery Team, 1996); hence future solutions to the decline of the Indiana bat likely will reflect regional differences in the behavior and ecology of the species. In any event, suggestions for aiding any endangered species of bat by facilitating the diversity and abundance of a particular type of insect prey (*e.g.,* Rydell *et al.,* 1996) should be viewed with caution, until diet is sampled throughout the range of the species.

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PE-48

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