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Feeding habits of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*) relative to prey abundance

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Feeding habits of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*) in eastern Oklahoma, USA, were studied from July 1987 through July 1988. Diets were determined from microscopic analysis of fecal pellets and compared with arthropods collected in Malaise traps. Although lepidopterans comprised only 21.5% of the available prey, they occurred in > 90% of the pellets examined and accounted for > 85% of the volume of prey consumed. Dipterans, coleopterans, and homopterans occurred in 18.3%, 10.6%, and 6.7% of the feces, respectively, but each accounted for < 5% of the volume of prey consumed. Trichopterans, hymenopterans, and neuropterans also were found in feces but in trace amounts. Our results support the classification of *C. t. ingens* as a moth specialist, but additional insights are needed to fully understand how its feeding tactics conform to the allotonic frequency hypothesis (i.e., avoiding detection by eared moths). Conservation of this highly endangered North American bat will require, in part, maintenance of habitats capable of supporting abundant populations of Lepidoptera.

Key words: feces, feeding habits, endangered species, Ozark big-eared bat, Oklahoma, Lepidoptera, prey abundance, allotony

INTRODUCTION

Five subspecies of big-eared bats (*Corynorhinus townsendii*) were described by Handley (1959). Three subspecies (*C. t. pallescens*, *C. t. townsendii*, and *C. t. australis*) range throughout western North America (Barbour and Davis, 1969; Kunz and Martin, 1982), while two subspecies occur as isolated populations in Arkansas and Oklahoma (*C. t. ingens*) and Kentucky, Virginia, and West Virginia (*C. t. virginianus*). The latter two subspecies are classified as federally endangered due to their restricted distribution, small populations, and

susceptibility to disturbance (Bagley, 1984; U.S. Fish and Wildlife Service, 1995). The ecology and natural history of the western subspecies of *C. townsendii* have been investigated (e.g., Dalquest, 1947; Pearson *et al.*, 1952; Twente, 1955; Humphrey and Kunz, 1976); however, it cannot be assumed that eastern subspecies exhibit the same characteristics (Clark *et al.*, 1993; Wethington *et al.*, 1996; Clark *et al.*, 2002).

Previous studies have described feeding habits of subspecies other than *C. t. ingens* (Ross, 1967, Whitaker *et al.*, 1977; Dalton *et al.*, 1986; Sample and Whitman, 1993). Those studies found that *C. townsendii* fed

primarily on lepidopterans (= moth specialists) — similar to that described for the congeneric *C. rafinesquii* (Hurst and Lacki, 1997; Lacki and Ladeur, 2001). As moth specialists, *Corynorhinus* may conform to the allotonic frequency hypothesis, which predicts that feeding tactics of some bats have evolved to use low- or high-frequency echolocation that is not detectable by eared moths (Pavey and Burwell, 1998, Bogdanowicz *et al.*, 1999; Jacobs, 2000). However, even with a single species, feeding habits can vary markedly; for example, diets of *Myotis velifer* consisted of mostly coleopterans in Kansas (Kunz, 1974) but lepidopterans in Arizona and northern Mexico (Ross, 1967).

Studies have examined diets of insectivorous bats in North America (e.g., Whitaker and Tomich, 1983; Belwood and Fullard, 1984; Brack, 1985; Brack and LaVal, 1985; Griffith and Gates, 1985; Warner, 1985; Dalton *et al.*, 1986), but feeding habits of several species have not been described. Confirmation of the feeding habits of *C. t. ingens* could not only add more insight to the allotonic frequency hypothesis but also enhance conservation of this endangered North American bat (U.S. Fish and Wildlife Service, 1995). Our objectives were to determine the feeding habits of *C. t. ingens* and compare them to an index of prey abundance.

MATERIALS AND METHODS

Study Area

Our study was conducted in Adair County, Oklahoma, which is located in the southwestern part of the Ozark Uplift in the central United States. The Ozark Plateau covers about 103,000 km² (Huffman, 1959) and has numerous limestone caves that may have served as refugia from severe post-Pleistocene winters for *C. t. ingens* and other cave-dwelling organisms (Humphrey and Kunz, 1976). Erosion of alternating layers of limestone and flint (= chert) have produced a rugged terrain of small mountains, bluffs,

and wide valleys (Blair and Hubbell, 1938). Mountains rise < 125 m from base to peak, and elevations are 260–460 m above mean sea level.

Association of blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), black hickory (*Carya buckleyi*), and winged elm (*Ulmus alata*) dominated mountain slopes. Coralberry (*Symphoricarpus orbiculatus*) and sassafras (*Sassafras varifolium*) provided a sparse shrubby undergrowth. Lowland riparian areas were dominated by silver maple (*Acer saccharinum*), red birch (*Betula nigra*), American elm (*U. americana*), cottonwood (*Populus deltoides*), sycamore (*Plantanus occidentalis*), and various oak species (Turner, 1935; Blair and Hubbell, 1938). Open areas were mainly pastures of exotic grasses managed for domestic bovids.

Prey Abundance

We sampled aerial arthropods with Malaise traps (Model 2875A, Bioquip Products, Santa Monica, California, USA) from sunset to sunrise approximately weekly on 32 nights from 7 July 1987 through 25 July 1988. Four traps were set simultaneously from late spring to early autumn in 1987 (7 July–22 September) and 1988 (12 May–25 July) near a cave used as a maternity site by *C. t. ingens*. Two of the four traps were placed in woodland habitat contiguous with the maternity cave and two traps were placed in an adjacent pasture. From autumn through early spring (29 September 1987–5 May 1988), two traps were run simultaneously in woodland habitat adjacent to a hibernaculum of *C. t. ingens*. There were no open habitats ≤ 200 m of the hibernaculum; therefore, only wooded sites were sampled during that time. We raised the Malaise traps an additional 1.3 m above the ground with conduit extensions to better approximate at least part of the foraging stratum of bats and exclude nonvolant insects. Trapping began at sunset and collecting jars were cleared at 2-h intervals throughout the night. Insects were transferred to plastic bags, air dried the following day, and stored in a desiccator before identification.

Insects were examined under a 40 × dissecting microscope and classified to order or family (Borror *et al.*, 1981). Body length (mm) was recorded for each insect, unless damage prevented it. Representative samples from each family were crushed with dissecting needles and permanently mounted on microscope slides to aid in insect identification in fecal samples. Because of the potential limitations associated with trap type (Kunz, 1988) and placement (Whitaker, 1994), we considered the arthropod data as a general index of prey abundance.

Fecal Collection and Analysis

Feces were collected approximately weekly (June–September 1987 and May 1988) at the maternity cave near where insects were sampled. A cloth sheet was placed in flyways inside the maternity cave to collect fecal pellets. We avoided specific roosting sites to minimize disturbance. Pellets with fungal growth or other indications of aging were discarded to synchronize fecal collections with insect samples. Feces smaller than that typical of *C. t. ingens* were discarded because they may have been from eastern pipistrelles (*Pipistrellus subflavus*), which were uncommon (i.e., we never observed > 2–4 individuals emerge during a single night) but occasionally roosted singly in the cave. As such, we do not believe that any more than a trace amount of the fecal material collected could have been from pipistrelles. Sheets were then cleared of all remaining feces to prevent mixing of weekly samples.

Feces were dried in aluminum foil cups at 100°C and stored in a desiccator before analysis. We placed each pellet in a petri dish and covered it with four parts Kodak Photo-Flo®, one part 70% isopropyl alcohol, and one part distilled water overnight for softening (Anthony and Kunz, 1977). Pellets were teased apart under a dissecting microscope, and prey items were identified by comparing parts of wings, legs, elytra, antennae, and other chitinous remains with reference slides. Food items were identified to order and occasionally to family. The dietary contribution of various arthropod orders were quantified as percent frequency (percentage of fecal pellets containing each insect order) and percent volume (average percentage by volume of all feces combined that each insect order made up) to facilitate comparisons with other studies (Korschgen, 1980).

Statistical Analyses

The sign test (corrected for continuity — Snedecor and Cochran, 1967) was used to compare arthropod abundance in open habitat and wooded habitat for each arthropod order. To determine if *C. t. ingens* demonstrated positive, negative, or no selection for arthropod orders, weekly relative abundances of arthropods captured in Malaise traps and found in feces ($n = 13$ weeks for which both data were available) were compared with Wilcoxon's signed-rank test (Sokal and Rohlf, 1981). While exceptions exist, size of a bat can determine, in part, size of prey items consumed (Ross, 1967; Black, 1974; Buchler, 1976). Buchler (1976) noted that the 6-g *Myotis lucifugus* tended to select prey with body lengths of 4–9 mm. Similarly, Black (1974) found that where bat

assemblages comprised species that weighed 5–10 g, insects of 6–10 mm body length were most abundant. *Corynorhinus t. ingens* is a relatively large vespertilionid bat (summer body mass of non-pregnant females was 10.5–15.25 g, $n = 14$; Wethington, 1994), and generally, arthropod remains (fecal components identifiable beyond order and culled wings on drop sheets) suggested that they preferred arthropods > 5 mm in body length. Therefore, to provide alternate, and presumably more realistic, estimates of prey abundance, we evaluated prey selection with all data on prey abundance and with only arthropods ≥ 5 mm in body length. Statistical significance was set at $P < 0.05$.

RESULTS

Prey Abundance

Fourteen orders of arthropods were captured throughout the study (Table 1). Diptera, Lepidoptera, and Homoptera were the most numerous and comprised > 91% of all arthropods collected. Hymenoptera, Coleoptera, Neuroptera, Orthoptera, Hemiptera, Trichoptera, Araneae, Acari, Psocoptera, Isoptera, and Odonata each contributed < 3% to the total capture. When considering only arthropods ≥ 5 mm, Lepidoptera were most abundant (Table 1).

There were significant differences between numbers of insects captured in open and wooded habitats for seven arthropod orders. Hemipterans (sign test, $\chi^2 = 8.64$, $d.f. = 1$, $P < 0.01$), homopterans ($\chi^2 = 4.45$, $d.f. = 1$, $P < 0.01$), and neuropterans ($\chi^2 = 7.58$, $d.f. = 1$, $P < 0.05$) were more abundant in open habitats. Dipterans, hymenopterans, lepidopterans, and tricopterans were most numerous in wooded habitats ($\chi^2 = 7.11$ – 17.05 , all $d.f. = 1$, all $P < 0.01$).

Dietary Characteristics

Seven orders of arthropods were found in feces of *C. t. ingens* (Table 2). Lepidopterans, the most commonly consumed prey item, occurred in 91.4% of 104 fecal

TABLE 1. Arthropod availability (numbers and percent) including all arthropods and arthropods ≥ 5 mm in body length collected in four Malaise traps in 32 nights from July 1987 through July 1988 in eastern Oklahoma, USA

Order	All arthropods		Arthropods ≥ 5 mm	
	<i>n</i>	%	<i>n</i>	%
Diptera (flies)	2,515	52.1	81	8.0
Lepidoptera (moths)	1,040	21.5	646	63.7
Homoptera (leafhoppers, etc.)	871	18.0	78	7.7
Hymenoptera (wasps, ants, etc.)	141	2.9	89	8.8
Coleoptera (beetles)	120	2.5	50	4.9
Neuroptera (lacewings)	40	0.8	35	3.4
Orthoptera (grasshoppers)	35	0.7	10	1.0
Hemiptera (bugs)	25	0.5	12	1.2
Trichoptera (caddisflies)	18	0.4	13	1.3
Araneae (spiders)	8	0.2	0	0.0
Acari (mites)	6	0.1	0	0.0
Psocoptera (psocids)	3	<0.1	0	0.0
Isopoteria (termites)	1	<0.1	0	0.0
Odonata (damselflies)	1	<0.1	0	0.0
Unidentified	6	0.1	0	0.0

pellets examined and comprised 85.2% of the total volume of guano. Other insect orders consumed were Diptera (% of pellets = 18.3; % volume = 3.7), Coleoptera (10.6; 3.5), Homoptera (6.7; 1.7), Trichoptera (2.9; 0.3), Hymenoptera (1.9; 1.6), and Neuroptera (1.0; 0.1; Table 2). Unidentified prey remains occurred in 8.7% of the pellets, and balls of hair, apparently from grooming, were found in 13.5% of the pellets. Small amounts of dirt were found in many samples; however, a fine layer of silt from the cave ceiling often covered the collecting sheet, so it is doubtful that the

observed debris was ingested. No plant material was found in the guano.

Single fecal pellets contained remains of 1–4 arthropod orders ($\bar{x} = 1.34 \pm 0.07 SE$). When considering the percent volume of individual pellets, Lepidoptera were the only order present in 57.7% of the pellets examined and comprised between 80–99% of the remains in 26.0% of the pellets. Only 16.4% of the pellets contained < 80% Lepidoptera. One pellet contained only Homoptera (Cicadellidae), and another contained only Hymenoptera.

Of the five most common orders of arthropods available (Table 1), Lepidoptera were the only prey of *C. t. ingens* that showed positive selection, regardless of whether or not insects < 5 mm were included in the analyses (Table 3). The other four common orders were either avoided or selected in proportion to their abundances, and none of them comprised > 5% of the average weekly diet (Table 3). Coleopterans were consumed in proportion to their abundance regardless of size (Table 3). *Corynorhinus t. ingens* avoided dipterans when all sizes of insects were considered potential prey (Table 3). However, when we eliminated arthropods < 5 mm from the

TABLE 2. Prey items consumed by *C. townsendii ingens* expressed as percent frequency (percentage of fecal pellets containing each food type) and average percent volume (average percentage by volume of all feces); *n* = 104

Food item	Percent	
	frequency	volume
Lepidoptera	91.4	85.2
Diptera	18.3	3.7
Hair from grooming	13.5	1.9
Coleoptera	10.6	3.4
Homoptera	6.7	1.7
Trichoptera	2.9	0.3
Hymenoptera	1.9	1.5
Neuroptera	1.0	0.1
Unidentified prey	8.7	2.2

TABLE 3. Selection of five arthropod orders by *C. townsendii ingens* relative their abundance and percentage in the diet. To determine if bats showed positive, negative, and no selection by order and arthropod grouping (all arthropods and arthropods ≥ 5 mm in body length), weekly relative abundances of arthropod orders captured in Malaise traps and found in feces were compared with Wilcoxon's signed-rank test

Order	Arthropod grouping	n^a	Percent		Wilcoxon signed-ranked test	
			abundance	diet	P -value	selection
Coleoptera	All	12	2.3	4.2	0.56	None
	≥ 5 mm	9	7.1	3.2	0.08	None
Diptera	All	13	47.4	4.7	<0.001	Negative
	≥ 5 mm	11	5.3	2.8	0.09	None
Homoptera	All	13	18.9	2.3	<0.001	Negative
	≥ 5 mm	12	8.6	2.5	<0.05	Negative
Hymenoptera	All	13	3.1	3.8	0.09	None
	≥ 5 mm	12	10.9	4.1	<0.01	Negative
Lepidoptera	All	13	25.0	79.6	<0.001	Positive
	≥ 5 mm	13	64.7	79.6	<0.05	Positive

^a — Number of weekly comparisons from a total of 13; values < 13 indicate that one or more arthropod was not represented in captures in Malaise traps for a particular week

analysis, dipterans were consumed in proportion to their abundance but comprised only 2.8% of the average weekly diet. Homopterans were avoided overall by *C. t. ingens*, although there were several small Cicadellidae in the sample. Hymenopterans were consumed in proportion to their abundance when all sizes were combined, but they were avoided when considering only arthropods ≥ 5 mm (Table 3).

Abundances of the five most common arthropod orders were disparate relative to body length (Fig. 1). If we were correct in our assumption that *C. t. ingens* prefers arthropods ≥ 5 mm in body length, their prey base in that size grouping was considerably different than the overall prey base and suggested that Lepidoptera, Hymenoptera, and Coleoptera should be, assuming no positive or negative selection, the most abundant arthropod orders in the diet. However, only Lepidoptera were preferentially selected.

DISCUSSION

Methodological Limitations

Choice of a method to sample arthropods is difficult because each trap type has

inherent biases (Kunz, 1988) and trap placement may not adequately reflect foraging sites of bats (Whitaker, 1994). Suction traps may overrepresent smaller insects (Taylor, 1962) and light traps may overrepresent positively phototactic insects (Black, 1974). We chose Malaise traps to sample the arthropod fauna to avoid the above biases; however, we acknowledge that large Coleoptera and Hemiptera may have been underrepresented in our samples (Juillet, 1963; Kunz, 1988). For example, no Scarabaeidae were collected in the traps although we observed those beetles during nights of arthropod sampling. Some heavy-bodied Coleoptera may have flown into the net, fell to the ground, and escaped capture. In our study, Hemiptera did not occur in the diets of *C. t. ingens*, and overall, coleopterans were not selected or avoided based on our analysis of selectivity (Table 3). Therefore, increased captures of either arthropod order would not have affected our conclusions except by possibly indicating overall avoidance of coleopterans.

Although prey items may be observed in an undigested form by examining stomach contents, the endangered status of *C. t. ingens* precluded sacrificing animals

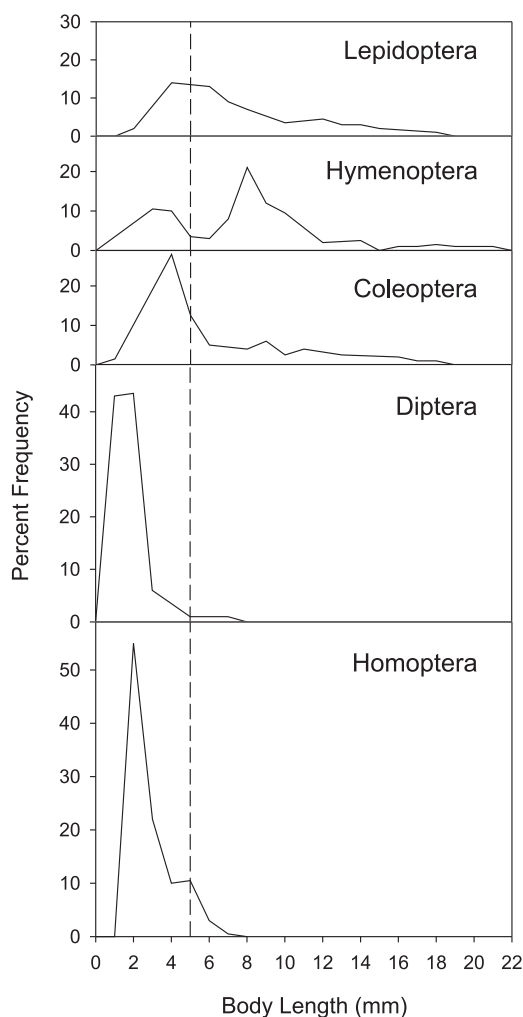


FIG. 1. Percent frequency of body lengths of the five most common arthropod orders captured in Malaise traps near caves occupied by *C. townsendii ingens*; vertical dashed line delimits proportions of arthropods above and below the 5-mm body length used to evaluate prey selection

for dietary analysis. Instead, fecal contents were analyzed because feces could be collected in flyways with minimal disturbance to the bats. Kunz and Whitaker (1983) concluded that fecal analysis can be used as a reliable index of the diets of insectivorous bats. We could seldom identify arthropod remains to family with confidence because *C. t. ingens* culled diagnostic hard-body parts (wings, elytra, and legs) before inges-

tion, and body parts that were ingested were highly fragmented. However, we could identify remains to order, except for a few cases where prey items had to be listed as unidentified (Table 2).

Dietary Characteristics

Some insectivorous bats are opportunistic feeders and consume prey in proportion to relative abundance or exploit dense swarms of insects (e.g., Belwood and Fenton, 1976; Fenton and Morris, 1976; Eckrich and Neuweiler, 1988). Other species are specialists, and many may be categorized as either beetle or moth strategists (Black, 1974), although such distinctions are not absolute (Fenton *et al.*, 1977). Old World *Barbastella* (Rydell *et al.*, 1996; Sierro and Arlettaz, 1997) and *Plecotus* (Feldman *et al.*, 2000) tend to be moth specialists, and the latter is quite similar to *Corynorhinus* in taxonomy (Tumilson and Douglas, 1992; but see Bogdanowicz *et al.*, 1998, and Hoofer and Van Den Bussche, 2001) and feeding habits (Ross, 1967; Whitaker *et al.*, 1977; Dalton *et al.*, 1986; Sample and Whitman, 1993; Hurst and Lacki, 1997; Lacki and Ladeur, 2001).

Corynorhinus t. ingens preferentially selected lepidopterans over other available arthropods, which confirmed that this subspecies is a moth strategist. Similar preferences have been observed for other subspecies of *C. townsendii*. Lepidoptera were found in 92.1% of the stomachs of *C. t. pallascens* collected from New Mexico and Arizona (Ross, 1967) and 99.7% of those collected from Oregon (Whitaker *et al.*, 1977). In Virginia, Lepidoptera comprised 97.1% of the volume of feces of *C. t. virginianus* (Dalton *et al.*, 1986). In West Virginia, 90.8–96.7% of the volume of the diet of *C. t. virginianus* was lepidopterans (Sample and Whitmore, 1993). As in our study, Hurst and Lacki (1997) found seven

orders, dominated by Lepidoptera, in feces of *C. rafinesquii*, albeit they noted Hemiptera and we noted Neuroptera.

Although dipterans were the most abundant arthropods, they were consumed significantly less than expected. Most noticeable was the absence of small flies in feces, particularly the families Cecidomyiidae, Chironomidae, and Psychodidae, which comprised 45.6%, 33.3%, and 5.5%, respectively, of Diptera collected in Malaise traps. If these small flies were consumed by bats, it is likely that whole wings would have been present in feces. Similar to our results, Buchler (1976) reported a paucity of cecidomyiid flies in stomachs of *Myotis lucifugus*, despite their abundance in suction-trap samples. Unpalatability or inability to detect small flies using echolocation may explain their absence in the diet. However, unpalatability evidently is not a factor for *M. lucifugus* that readily ate Cecidomyiidae fed to them in captivity (Buchler, 1976). Inability to detect small flies probably is not a problem for *Corynorhinus* because they are able to detect and avoid wires < 0.2 mm in diameter (Grinnell, 1963).

Optimal foraging theory suggests that not all sizes of arthropods should be exploited by bats (e.g., Jones, 1990). Bats should ignore small arthropods that yield less energy than their capture justifies. They also should avoid large arthropods that require considerable energy and time to handle (LaVal and LaVal, 1980). Arthropod length has a highly positive correlation with biomass, and even slight increases of body lengths should yield considerably more energy (Rogers *et al.*, 1976, 1977; Sage, 1982). Jones (1990) demonstrated that *Rhinolophus ferrumequinum* does not feed opportunistically but rather conforms to optimal foraging theory by selecting for prey size and profitability, albeit variation occurred temporally. Based on our analysis of prey selection, *C. t. ingens* appears to adopt

a similar foraging strategy. However, feeding habits of bats may vary with sex, age, and reproductive condition (e.g., Belwood and Fenton, 1976) and temporally within a single night (Eckrich and Neuweiler, 1988); clearly, additional information is needed to fully understand the foraging ecology of many bat species, including *C. townsendii*.

When we considered all sizes of potential prey, *C. t. ingens* preferentially consumed lepidopterans throughout the study. However, when insects < 5 mm were removed from the analyses, selection of lepidopterans decreased somewhat (Table 3), and dietary diversity increased (Clark, 1991), perhaps in response to decreased numbers of available arthropods. For example, Anthony and Kunz (1977) found that when insect abundance was high, adult female *Myotis lucifugus* selectively foraged on beetles and mayflies, which were uncommon in samples from light traps. When insect abundance was relatively low, females consumed 3–10-mm insects in proportion to their abundance. Similarly, temporal changes in use of lepidopterans has been suggested for *C. rafinesquii*, based on the abundance of culled moth wings in occupied caves (Lacki and Ladeur, 2001).

While it is apparent that *C. t. ingens* and other *C. townsendii* subspecies specialize on moths, the intricacies of how they confirm to the allotonic frequency hypothesis (Parvey and Burwell, 1998; Bogdanowicz *et al.*, 1999; Jacobs, 2000), relative to their specific feeding tactics, remain unresolved. *Corynorhinus townsendii* can emit low frequency calls (ca. 20 kHz) before capture of prey (Grinnell, 1963; Kunz and Martin, 1982), and as such, according to the predictions of Bogdanowicz *et al.* (1999: figure 2b), they can be group with other bat taxa that appear to have evolved to avoid detection by eared moths. However, according to M. J. O'Farrell (pers. comm.), *C. townsendii* usually emits detectable calls

(O'Farrell and Gannon, 1999; O'Farrell *et al.*, 1999) at 40–25 kHz and 80–50 kHz, which may not be optimum for avoiding detection by eared moths (e.g., Bogdanowicz *et al.*, 1999). Wind-loading characteristics (Wethington, 1994) and seasonal habitat preferences for forest and edge (Clark *et al.*, 1993; Wethington *et al.*, 1996) suggest that *C. t. ingens* can forage effectively in 'cluttered' habitats, and they may spent considerable time 'gleaning' moths off foliage (Barbour and Davis, 1969; M. J. O'Farrell, pers. comm.), perhaps when moths are least vigilant and most vulnerable. *Corynorhinus t. ingens* also uses open habitats presumably for foraging (Clark *et al.*, 1993; Wethington *et al.*, 1996) and thus seems to use multiple tactics to obtain their preferred prey, as has been noted for *Lasiurus cinereus semotus* (Jacobs, 1999). Clearly, more research is needed to fully understand the feeding tactics of *Corynorhinus* and to enhance recovery and conservation of its endangered North American subspecies.

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LITERATURE CITED

- ANTHONY, E. L. P., and T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 775–786.
- BAGLEY, F. M. 1984. A recovery plan for the Ozark big-eared bat and the Virginia big-eared bat. United States Fish and Wildlife Service, Twin Cities, Minnesota, 55 pp.
- BARBOUR, R. W., and W. H. DAVIS. 1969. Bats of America. University Press of Kentucky, Lexington, 286 pp.
- BELWOOD, J. J., and M. B. FENTON. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, 54: 1674–1678.
- BELWOOD, J. J., and J. H. FULLARD. 1984. Echolocation and foraging behaviour in the Hawaiian hoary bat, *Lasiurus cinereus semotus*. *Canadian Journal of Zoology*, 62: 2113–2120.
- BLACK, H. L. 1974. A north temperature bat community: structure and prey populations. *Journal of Mammalogy*, 55: 138–157.
- BLAIR, W. F., and T. H. HUBBELL. 1938. The biotic districts of Oklahoma. *American Midland Naturalist*, 20: 425–454.
- BOGDANOWICZ, W., S. KASPER, and R. D. OWEN. 1998. Phylogeny of plecotine bats: reevaluation of morphological and chromosomal data. *Journal of Mammalogy*, 79: 78–90.
- BOGDANOWICZ, W., M. B. FENTON, and K. DALESZCZYK. 1999. The relationships between echolocation calls, morphology, and diet in insectivorous bats. *Journal of Zoology (London)*, 247: 381–393.
- BORROR, D. J., D. M. DE LONG, and C. A. TRIPLEHORN. 1981. An introduction to the study of insects. Fifth ed. Saunders College Publishing, Philadelphia, 827 pp.
- BRACK, V., JR. 1985. The foraging ecology of some bats in Indiana. *Indiana Academy of Science*, 94: 231–237.
- BRACK, V., JR., and R. K. LAVAL. 1985. Food habits of the Indiana bat in Missouri. *Journal of Mammalogy*, 66: 308–315.
- BUCHLER, E. R. 1976. Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). *American Naturalist*, 110: 619–628.
- CLARK, B. S. 1991. Activity patterns, habitat use, and prey selection by the Ozark big-eared bat (*Plecotus townsendii ingens*). Ph.D. Thesis, Oklahoma State University, Stillwater, 80 pp.
- CLARK, B. S., D. M. LESLIE, JR., and T. S. CARTER. 1993. Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*). *Journal of Mammalogy*, 74: 422–427.
- CLARK, B. S., B. K. CLARK, and D. M. LESLIE, JR. 2002. Seasonal variation in activity patterns of endangered Ozark big-eared bats (*Corynorhinus townsendii ingens*). *Journal of Mammalogy*, 83: 590–598.

- DALQUEST, W. W. 1947. Notes on the natural history of the bat *Corynorhinus rafinesquii* in California. *Journal of Mammalogy*, 28: 17–30.
- DALTON, V. M., V. BRACK, JR., and P. M. MCTEER. 1986. Food habits of the big-eared bat, *Plecotus townsendii virginianus*, in Virginia. *Virginia Journal of Science*, 37: 248–254.
- ECKRICH, M., and G. NEUWEILER. 1988. Food habits of the sympatric insectivorous bats *Rhinolophus rouxi* and *Hipposideros lankadiva* from Sri Lanka. *Journal of Zoology (London)*, 215: 729–737.
- FELDMAN, R., J. O. WHITAKER, JR., and Y. YOM-TOV. 2000. Dietary composition and habitat use in a desert insectivorous bat community in Israel. *Acta Chiropterologica*, 2: 15–22.
- FENTON, M. B., and G. K. MORRIS. 1976. Opportunistic feeding by desert bats (*Myotis* spp.). *Canadian Journal of Zoology*, 54: 526–530.
- FENTON, M. B., N. G. H. BOYLE, T. M. HARRISON, and D. J. OXLEY. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica*, 9: 73–85.
- GRIFFITH, L. A., and J. E. GATES. 1985. Food habits of cave-dwelling bats in the central Appalachians. *Journal of Mammalogy*, 66: 451–460.
- GRINNELL, A. D. 1963. The neurophysiology of audition in bats: intensity and frequency parameters. *Journal of Physiology*, 167: 38–66.
- HANDLEY, C. O., JR. 1959. A revision of American bats of the genera *Euderma* and *Plecotus*. *Proceedings of the United States National Museum*, 110: 95–246.
- HOFFER, S. R., and R. A. VAN DEN BUSSCHE. 2001. Phylogenetic relationships of plecotine bats and allies based on mitochondrial ribosomal sequences. *Journal of Mammalogy*, 82: 131–137.
- HUFFMAN, G. G. 1959. Mississippian stratigraphy and tectonics of the Oklahoma Ozark area. *Tulsa Geological Society Digest*, 27: 104–176.
- HUMPHREY, S. R., and T. H. KUNZ. 1976. Ecology of a Pleistocene relict, the western big-eared bat (*Plecotus townsendii*), in the southern Great Plains. *Journal of Mammalogy*, 57: 470–494.
- HURST, T. E., and M. J. LACKI. 1997. Food habits of Rafinesque's big-eared bat in southeastern Kentucky. *Journal of Mammalogy*, 78: 525–528.
- JACOBS, D. S. 1999. The diet of the insectivorous Hawaiian hoary bat (*Lasiurus cinereus semotus*) in an open and a cluttered habitat. *Canadian Journal of Zoology*, 77: 1603–1608.
- JACOBS, D. S. 2000. Community level support for the allotonic frequency hypothesis. *Acta Chiropterologica*, 2: 197–207.
- JONES, G. 1990. Prey selection by the greater horse-shoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *Journal of Animal Ecology*, 59: 587–602.
- JUILLET, J. A. 1963. A comparison of four types of traps used for capturing insects. *Canadian Journal of Zoology*, 41: 219–223.
- KORSCHGEN, L. J. 1980. Procedures for food-habits analysis. Pp. 114–127, in *Wildlife management techniques manual*. Fourth ed. (S. D. SCHEMNITZ, ed.). The Wildlife Society, Washington, D.C., 686 pp.
- KUNZ, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology*, 55: 693–711.
- KUNZ, T. H. 1988. Methods of assessing the availability of prey to insectivorous bats. Pp. 191–210, in *Ecological and behavioral methods for the study of bats* (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.
- KUNZ, T. H., and R. A. MARTIN. 1982. *Plecotus townsendii*. *Mammalian Species*, 175: 1–6.
- KUNZ, T. H., and J. O. WHITAKER, JR. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. *Canadian Journal of Zoology*, 61: 1317–1321.
- LACKI, M. J., and K. M. LADEUR. 2001. Seasonal use of lepidoteran prey by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *American Midland Naturalist*, 145: 213–217.
- LAVALL, R. K., and M. L. LAVALL. 1980. Prey selection by the slit-faced bat *Nycteris thebaica* (Chiroptera: Nycteridae) in Natal, South Africa. *Biotropica*, 12: 241–246.
- O'FARRELL, M. J., and W. L. GANNON. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy*, 80: 24–30.
- O'FARRELL, M. J., B. W. MILLER, and W. L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, 80: 11–23.
- PAVEY, C. R., and C. J. BURWELL. 1998. Bat predation on eared moths: a test of the allotonic frequency hypothesis. *Oikos*, 81: 143–151.
- PEARSON, O. P., M. R. KOFORD, and A. K. PEARSON. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquii*) in California. *Journal of Mammalogy*, 33: 273–320.
- ROGERS, L. E., W. T. HINDS, and R. L. BUSCHBOM. 1976. A general weight vs. length relationship for insects. *Annals of the Entomological Society of America*, 69: 387–389.
- ROGERS, L. E., R. L. BUSCHBOM, and C. R. WATSON. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, 70: 51–53.

- ROSS, A. 1967. Ecological aspects of the food habits of insectivorous bats. *Proceedings of the Western Foundation of Vertebrate Zoology*, 1: 205–264.
- RYDELL, J., G. NATUSCHKE, A. THEILER, and P. E. ZINGG. 1996. Food habits of the barbastelle bat, *Barbastella barbastellus*. *Ecography*, 19: 62–66.
- SAGE, R. D. 1982. Wet and dry-weight estimates of insects and spiders based on length. *American Midland Naturalist*, 108: 407–411.
- SAMPLE, B. E., and R. C. WHITMORE. 1993. Food habits of the endangered Virginia big-eared bat in West Virginia. *Journal of Mammalogy*, 74: 428–435.
- SIERRO, A., and R. ARLETTAZ. 1997. Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecologica*, 18: 91–106.
- SNEDECOR, G. W., and W. G. COCHRAN. 1967. *Statistical methods*. Sixth ed. Iowa State University Press, Ames, 593 pp.
- SOKAL, R. R., and F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*. 2nd edition. W. H. Freeman and Company, San Francisco, California, 859 pp.
- TAYLOR, L. R. 1962. The absolute efficiency of insect suction traps. *Annals of Applied Biology*, 50: 405–421.
- TUMLISON, R., and M. E. DOUGLAS. 1992. Parsimony analysis and the phylogeny of the plecotine bats (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, 73: 276–285.
- TURNER, L. M. 1935. Notes on forest types in northwestern Arkansas. *American Midland Naturalist*, 16: 417–421.
- TWENTE, J. W., JR. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology*, 36: 706–732.
- U.S. FISH AND WILDLIFE SERVICE. 1995. Ozark big-eared bat (*Plecotus townsendii ingens* [Handley]) revised recovery plan. United States Fish and Wildlife Service, Ecological Services, Tulsa, Oklahoma, 51 pp.
- WARNER, R. M. 1985. Interspecific and temporal dietary variation in an Arizona bat community. *Journal of Mammalogy*, 66: 45–51.
- WETHINGTON, T. A. 1994. Foraging activity, habitat use, and cave selection by the endangered Ozark big-eared bat (*Plecotus townsendii ingens*). M.Sci. Thesis, Oklahoma State University, Stillwater, 53 pp.
- WETHINGTON, T. A., D. M. LESLIE, JR., M. S. GREGORY, and M. K. WETHINGTON. 1996. Pre-hibernation habitat use and foraging activity by endangered Ozark big-eared bats (*Plecotus townsendii ingens*). *American Midland Naturalist*, 135: 218–230.
- WHITAKER, J. O., JR. 1994. Food availability and opportunistic versus selective feeding in insectivorous bats. *Bat Research News*, 35: 75–77.
- WHITAKER, J. O., JR., and P. Q. TOMICH. 1983. Food habits of the hoary bat, *Lasiurus cinereus*, from Hawaii. *Journal of Mammalogy*, 64: 151–152.
- WHITAKER, J. O., JR., C. MASER, and L. E. KELLER. 1977. Food habits of bats of western Oregon. *Northwest Science*, 51: 46–55.

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