

ACTIVITY PATTERNS, HABITAT USE, AND PREY
SELECTION BY THE OZARK BIG-EARED BAT
(PLECOTUS TOWNSENDII INGENS)

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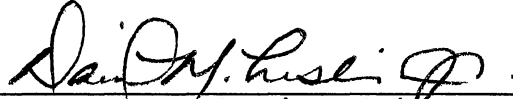
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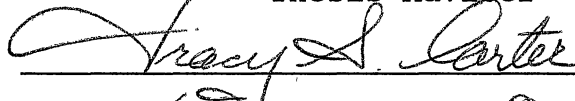
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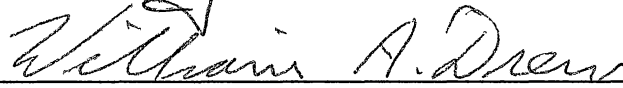
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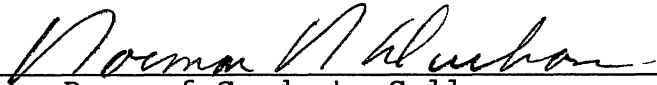


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CHAPTER I

ACTIVITY PATTERNS OF OZARK BIG-EARED BATS

(PLECOTUS TOWNSENDII INGENS)

Little is known about activity patterns of Ozark big-eared bats (Plecotus townsendii ingens), and results of studies with other subspecies of big-eared bats have been assumed to apply to the management of this endangered subspecies (Bagley, 1984; Kunz and Martin, 1982). Objectives of this study were to document seasonal changes in roost use and nightly activity patterns of Ozark big-eared bats at a maternity colony and hibernaculum. I specifically addressed: (1) numbers of bats using these caves throughout the year; (2) dates of formation and breakup for maternity colonies and hibernating clusters; (3) times of emergence and return to caves; (4) effects of weather and brightness on emergence and return to caves; and (5) activity at caves throughout the night.

METHODS

Activity patterns of Ozark big-eared bats were monitored by video-taping emergences and returns of bats through a night vision scope (Ni-Tec, Model NVS-100) that

was placed near the entrance of each cave. Images were enhanced by placing wheat lamps, with infrared gels (Kodak, Wratten 87) over the lenses, around the cave opening to illuminate bats passing through the relatively small (1.3 m X 1.0 m) entrance.

Emergence and return of bats were video-taped approximately weekly at a maternity colony from sunset to sunrise between 25 April and 22 September 1987 and 12 May through 25 July 1988. Bat activity also was monitored at a hibernaculum once every one to two weeks between 3 March and 10 June 1987 and 29 September 1987 through 5 May 1988. Sunset and sunrise times were calculated from a table for Oklahoma City, Oklahoma (Nautical Almanac Office, U.S. Naval Observatory, Washington, D. C.) and adjusted for longitude, latitude and Daylight Savings Time. Sunset was defined as 0000 h to standardize data throughout each year and between different years.

Data collected from videotapes included numbers of bats that emerged each night and time of bat activity at the cave entrance. Net numbers of bats leaving a cave were recorded at 10-min intervals. Total number of bats present each night was estimated by summing the net numbers of bats that emerged during each 10-min interval of the first two hours after sunset, or until more bats entered than emerged from the cave. The proportion of bats outside the cave was

estimated by dividing the cumulative number of bats that emerged during that time interval by the total number of bats using the cave. On most occasions, numbers of bats that emerged and returned during a night were not equal. A positive activity indicated that more bats emerged than returned to the cave during an evening; a negative activity was recorded if more bats returned than exited. Dates of formation and breakup for bats using the maternity cave and hibernaculum were determined from video recordings.

Lunar phase, cloud cover, brightness, external ambient temperature, percent relative humidity, precipitation, and wind velocity were recorded hourly throughout the night. Temperature and percent relative humidity also were recorded at 1-12 locations within 29 caves during December 1986 and/or 1987. To determine the range of conditions available to bats, a Bacharach sling psychrometer was used to estimate internal temperature and humidity approximately 20 cm below the cave ceiling throughout the length of a cave, including most chambers and passages, as well as at cave entrances.

RESULTS

Changes in Numbers of Bats

Numbers of Ozark big-eared bats increased during my study (June 1986-September 1990). Approximately 441 adult females used three maternity caves (AD-10, AD-13, and AD-

17) in June 1986 (Table 1). Because adult males and females segregate during summer, it was assumed that an equal number of males roosted in other caves. Therefore, the estimated population size was ca. 880 individuals. In 1990, the number of adult females was 852, including 309 discovered in a new cave (AD-125) in 1987. Total number of Ozark big-eared bats in Oklahoma during June 1990 was estimated at 1,700.

Two large hibernacula and two minor hibernacula are known to be used by male and female Ozark big-eared bats; however, numbers in the four caves during winter do not account for the estimated number of bats present in summer (Table 1). Thus, a large portion of the population overwinters in unknown caves, or in parts of known caves that are inaccessible to humans.

Annual Activity

Winter.--During winter months, both male and female Ozark big-eared bats occupied the coldest caves or parts of caves available. In 1986, ranges of temperatures and percent relative humidities in nine caves were 5.6-16.1°C and 55-95%, respectively. In 1987, 26 caves were examined and temperatures ranged from 7.0 to 16.7°C; relative humidities ranged from 39% to 100%. Ranges of cave temperatures and their humidities that Ozark big-eared bats were found in were 5.6-12.8°C and 60-77% in 1986 and

Table 1.--Annual summer and winter estimates of numbers of P. t. ingens occupying known maternity caves (AD-10, AD-13, AD-17, and AD-125) and hibernacula (AD-3, AD-10, and AD-125) in Oklahoma.

	AD-3 ^a	AD-10	AD-13	AD-17	AD-125 ^b	Total
Summer						
1986	-	262	103	76	-	441
1987	-	220	109	125	260	714
1988	-	226	110	75	169	580
1989	-	239	148	175	276	838
1990	-	274	137	132	309	852
Winter						
1986	242	12	-	-	-	254
1987	268	68	0	0	247	583
1988	235	-	-	-	-	235
1989	242	1	1	-	-	244

^a Access to AD-3 was denied by landowner during summer months.

^b P. t. ingens were first discovered in AD-125 in 1987. Winter counts were discontinued to prevent disturbance at the location.

8.9-9.4°C and 86-93% in 1987, respectively. In addition to cold temperature, Ozark big-eared bats seemed to prefer caves with moderate to high humidity.

Hibernating bats were found in both twilight areas of caves and total darkness further from cave entrances. Torpid bats were observed with ears either curled or erect. I have observed some individuals that appeared to be shivering within clusters of hibernating bats. On one occasion, a single Ozark big-eared bat was in flight when I entered a hibernaculum. Although I occasionally observed single individuals hanging torpid from the cave ceiling, most bats were in clusters of 2 to 135 individuals.

Ozark big-eared bats awakened throughout winter and moved among caves. On 22 December 1987, I estimated that 268 torpid bats were present in a hibernaculum, and 40 bats (14.9% of the bats present) emerged that night. I was unable to find fresh guano beneath hibernating bats, suggesting that either bats were defecating outside the cave during periods of arousal, or the bats were not eating during winter.

Bats were active at the hibernaculum 14 of 15 nights the cave entrance was video-taped during winter. Net numbers of bats observed leaving the cave ranged from -37 to 154 (Fig. 1). On three nights, more bats entered than exited the cave. The mean minimum ambient temperature on

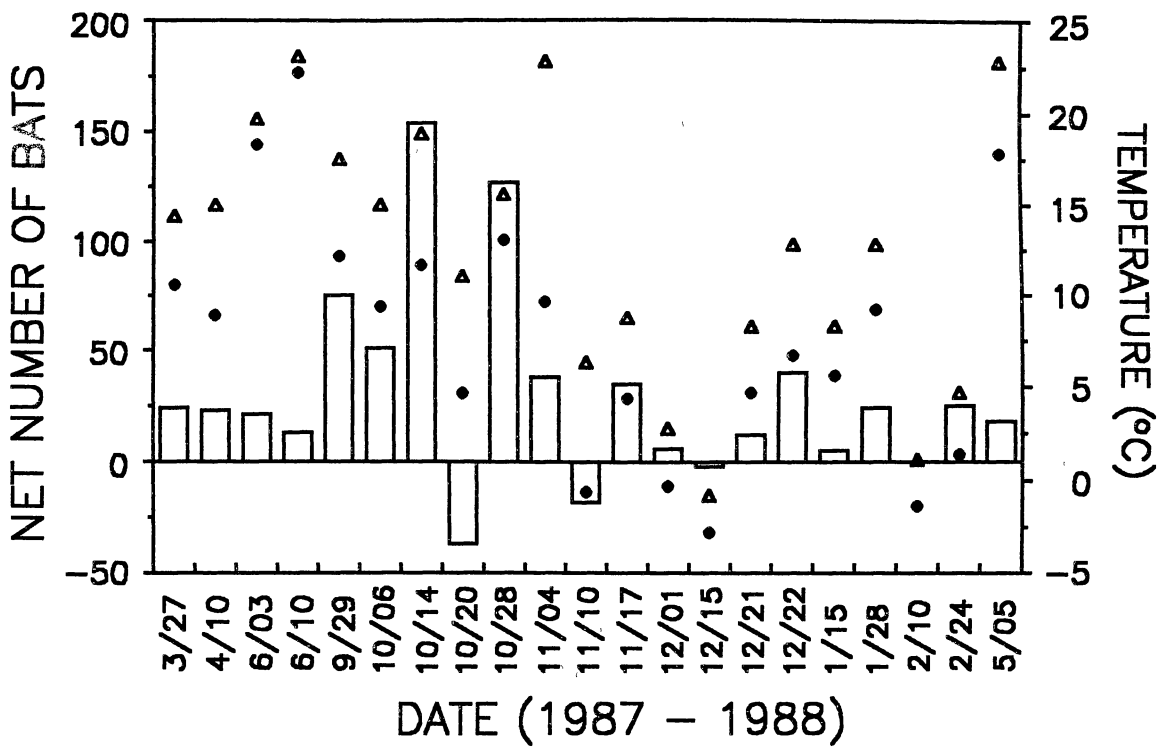


Fig. 1.--Net nightly emergence of *P. t. ingens* from a hibernaculum and range (maximum = triangles; minimum = dots) of external ambient temperatures during those nights in 1987 and 1988.

those three nights was significantly less than that of all other nights ($F = 6.66$, $d.f. = 1$, $P = 0.02$). The mean minimum temperature on nights bats left the hibernaculum, and apparently moved to other caves, was 9.7°C (range = $-0.3-22.2$, $SE = 1.4$) and on nights when bats moved into the hibernaculum, the mean minimum temperature was 0.4°C (range = $-2.8-0.4$, $SE = 2.2$).

In winter, most activity occurred during the first two hours after sunset (Fig. 2). When external ambient temperatures were below freezing, more bats entered the cave than left. When temperatures were above freezing, bats left the cave and did not return prior to morning.

Breakup of hibernating clusters was gradual and incomplete as several males were found in the hibernaculum throughout summer. Individual males also were observed in various caves, tallus cracks, and cliff overhangs throughout the region during summer, autumn, and occasionally winter. Although non-reproductive females may roost in similar locations as males during summer, I was unable to determine the sex of all individuals; however, all bats that I observed roosting alone were males.

Summer.--Dates of maternity colony build-up varied between years. In 1987, few bats ($n < 25$) were present at the cave (AD-13) from late April through the first week of June; however, >100 bats were already present in early May

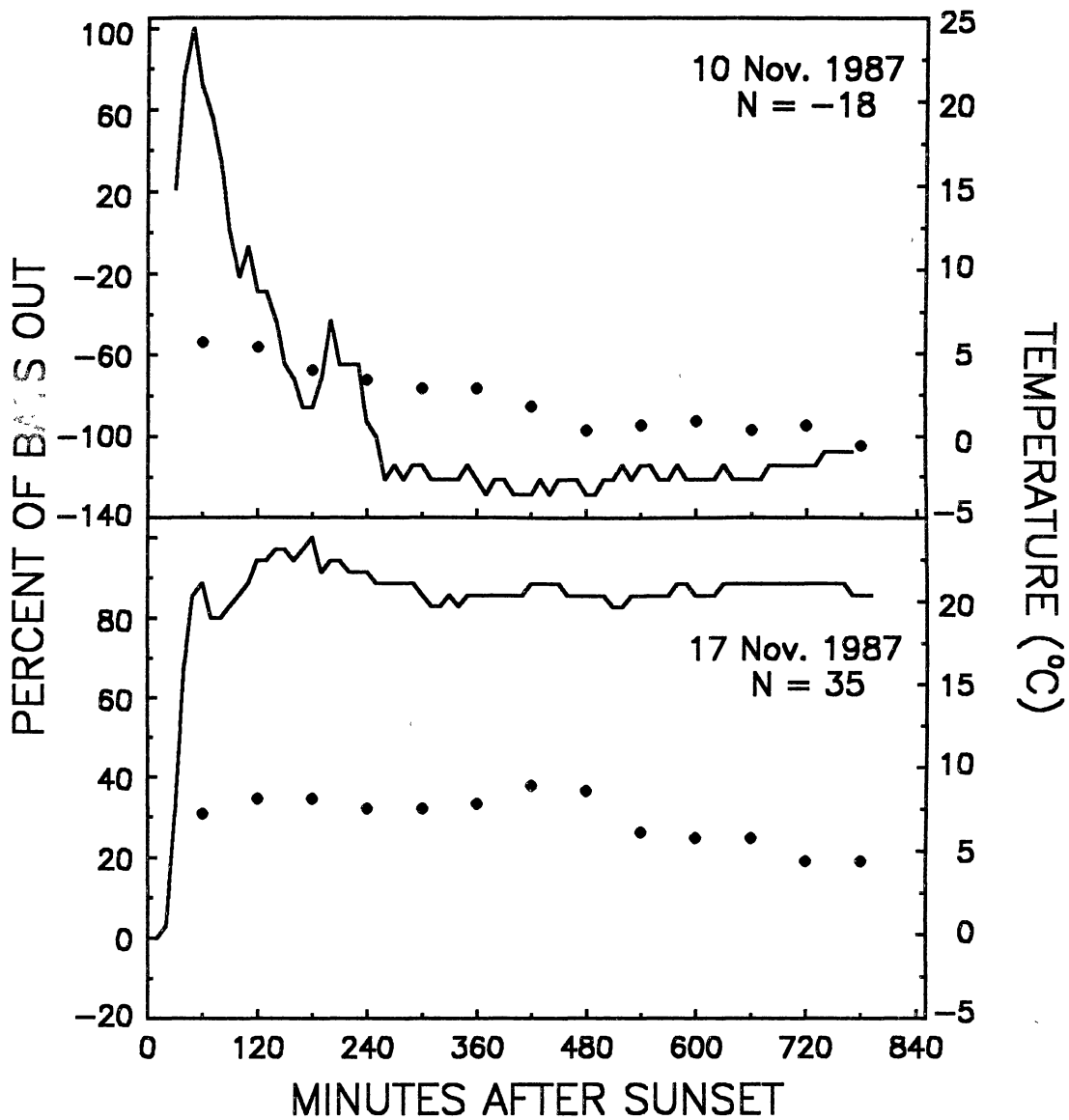


Fig. 2.--Distribution of nightly *P. t. ingens* activity at a hibernaculum on 10 November 1987 when external ambient temperatures (dots) fell below freezing and 17 November 1987 when external ambient temperatures remained above freezing.

1988 (Fig. 3). During May 1988, bats left the cave to forage after sunset and did not return until sunrise (Fig. 4). Colony formation probably was complete by early June 1988; thus, bimodal activity at that time was attributed to the behavior of near-term or postpartum females (Fig. 4). By late in the second week of June 1988, activity was trimodal in distribution (Fig. 4). Trimodal activity patterns continued for approximately 3 weeks during both 1987 and 1988. During early July, activity shifted back to a bimodal distribution, which lasted for approximately 2 weeks. After mid-July, bats again left at sunset and did not return until sunrise the following morning (Fig. 4).

Emergence

Ozark big-eared bats became active and circled inside the cave entrance prior to sunset. As ambient light decreased outside the cave, bats came closer to the entrance and flew in and out several times before leaving to forage. This activity appeared chaotic as bats dodged one another; however, the majority would circle together clockwise or counter-clockwise, and bats leaving the cave often flew nearer to the ground than those entering the cave. Emergence seemed to be a group-stimulated activity. Bats flying near the cave entrance seemed hesitant to exit; however, once one left, three or four others would follow.

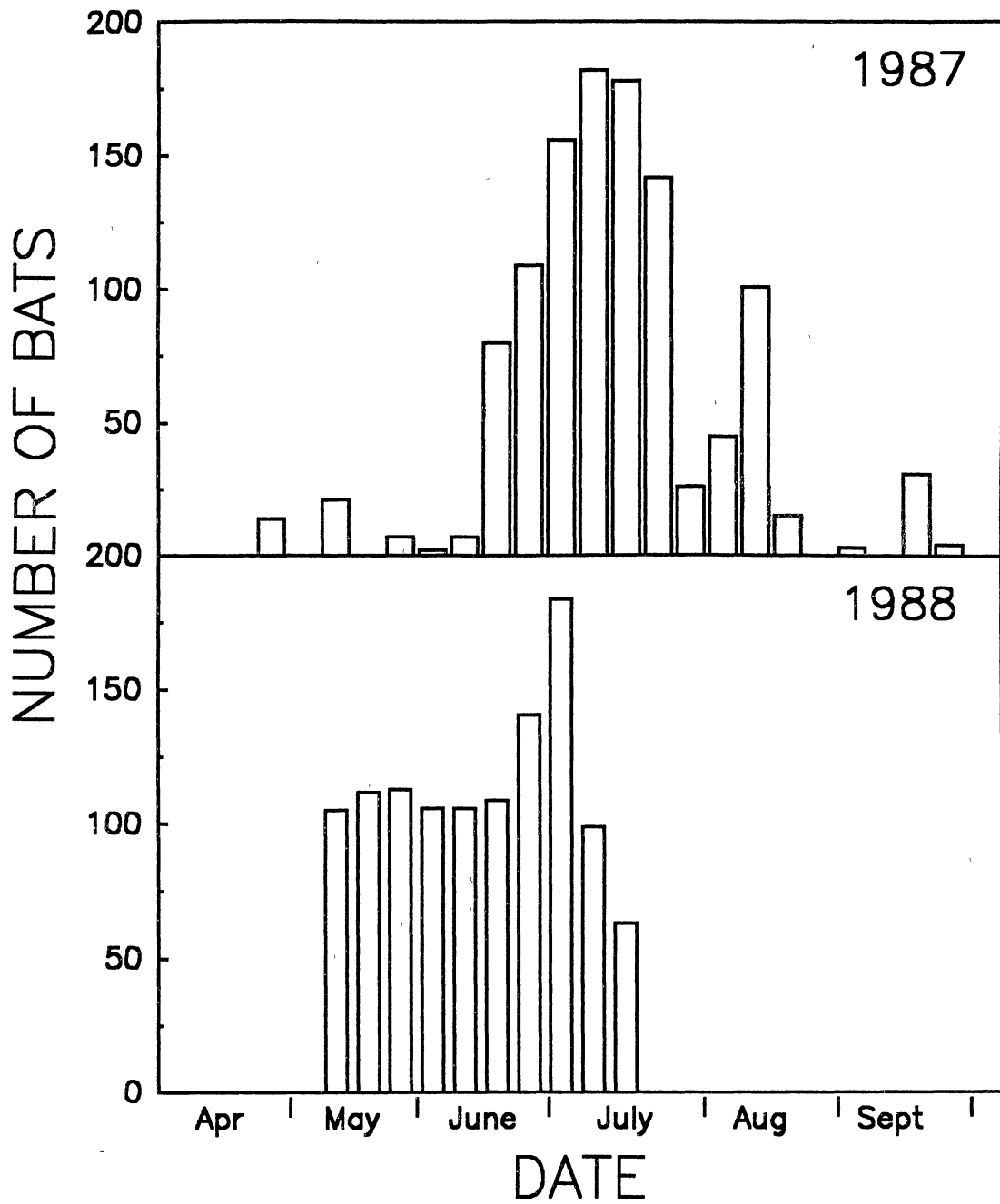


Fig. 3.--Comparison of numbers of P. t. ingens in a maternity colony during summers of 1987 and 1988. Numbers of bats present were estimated from weekly emergence counts.

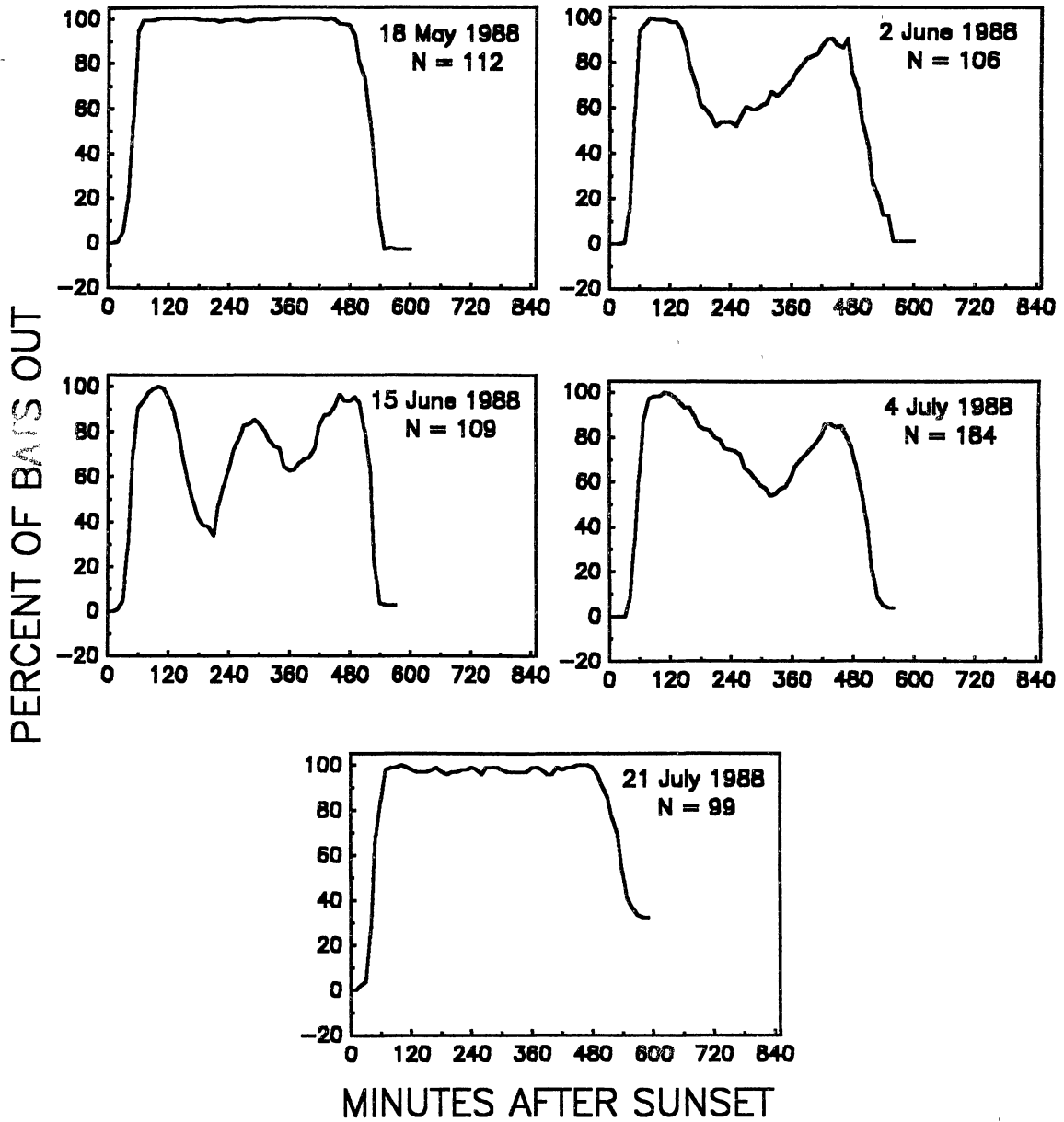


Fig. 4.--Distribution of nightly *P. t. ingens* activity at a maternity cave during colony formation (18 May), parturition (2 June), early lactation (15 June), mid-lactation (4 July), and late to post-lactation (21 July) in 1988.

Ozark big-eared bats began to depart between 0-45 min after sunset (\bar{X} = 25.7 min, SE = 1.6). Time of departure was not affected by brightness of the sky (Kruskal-Wallis test, chi-square approximation, χ^2 = 1.07, $d.f.$ = 1, P = 0.30). Mean emergence time was 25.0 min after sunset (range = 0-45 min, SE = 1.9, n = 28) on evenings when twilight was bright enough to cast shadows on the ground, and 28.1 min after sunset (range = 10-40 min, SE = 3.3, n = 8) when clouds obstructed light. Bats emerged earliest (at sunset) on two occasions when twilight was very bright and silhouetted them against the sky.

On three evenings it rained during the emergence period; however, activity was not delayed. Mean emergence time was 33.3 min after sunset (range = 30-40 min, SE = 3.3) on those three evenings. Harder rainfall may have delayed the time of departure, but I did not have an opportunity to observe Ozark big-eared bats under such conditions.

Between the first week of June and the second week of July, when young bats presumably were getting most of their nourishment from mothers, bats emerged from the maternity cave later than either before parturition or after young were strong fliers (Kruskal-Wallis test, chi-square approximation, χ^2 = 5.44, $d.f.$ = 1, P = 0.02; Fig. 5). Mean emergence while young were dependent was 23.9 min

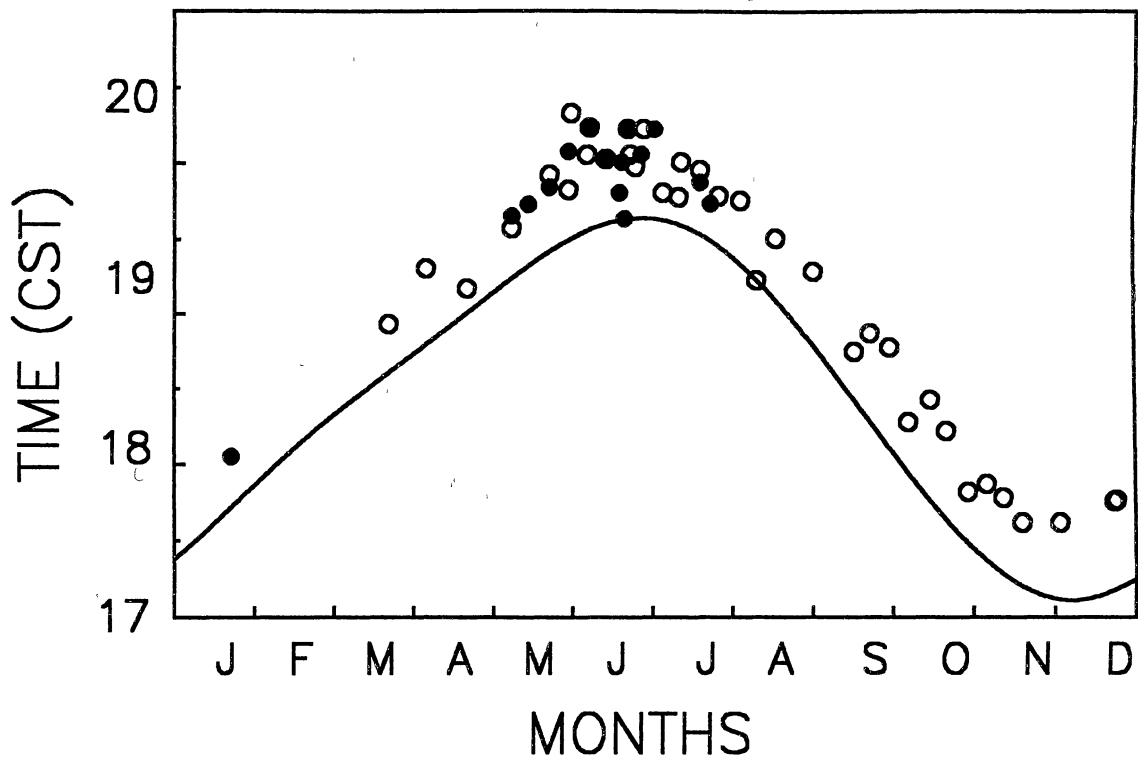


Fig. 5.--Times (0000 h Central Standard Time) of sunset (solid line) and first emergence of P. t. ingens in 1987 (open circles) and 1988 (closed circles).

after sunset (range 0-45, SE = 3.2, n = 13), but 19.7 min after sunset during the rest of the reproductive period (range = 0-30, SE = 1.8, n = 16).

DISCUSSION

Numbers of Bats

The total summer population of Ozark big-eared bats in Oklahoma was estimated at 425 bats in 1984 (Bagley, 1984). This number was obtained by doubling the number of females observed in maternity colonies during the last week of May 1983. My estimate of 1,700 for 1990 represented about a four-fold increase. Part of the increase was accounted for by a new cave, used as a hibernaculum and maternity roost, that was discovered in 1987, which increased the population estimate by 57.3%. However, if bats using this new site were not included in the population estimate, numbers still would have increased from 425 in 1984 to 543 in 1990.

In 1983, the winter population of Ozark big-eared bats in Oklahoma was estimated at 210 (Bagley, 1984). Numbers of bats using hibernacula have increased consistently throughout the duration of my study. The marked increase in winter 1987 also was greatly affected by the discovery of the new roost. Access to hibernating bats in this cave is dangerous and noisy; therefore, no additional winter counts were made.

Despite increased numbers of Ozark big-eared bats in

Oklahoma, their tendency to form large concentrations in a few caves makes them extremely vulnerable to disturbance and possible extinction. Measures must be taken to continue to monitor the population size and protect critical caves and above-ground resources.

Annual Activity

Winter.--The high amount of activity and apparent shifting in and out of the hibernaculum throughout winter were similar to the frequent movement of P. t. pallescens among caves in western Kansas and Oklahoma reported by Twente (1955). Winter emergence and foraging activity have been documented for several species of insectivorous bats on mild nights (Avery, 1985); however, the consistent bat activity in below freezing temperatures was unexpected. Ozark big-eared bats may have left the cave to void waste materials or fly to open water to drink. It is unlikely that bats were able to forage efficiently in the vicinity of the hibernaculum because insect numbers were very low during colder nights. However, insects may have accumulated over the warm water of a nearby reservoir providing a localized food source. Whitaker (1972) found insect remains in the guano of Indiana bats (Myotis sodalis) throughout winter in Kentucky.

Summer.--Temperate zone bats give birth and rear their young during summer when food supplies are abundant and

reliable (Kunz, 1974). However, the exact timing of parturition and juvenile development may vary among years due to local environmental parameters (Humphrey et al., 1977). Because females joined the maternity colony more gradually in some years than others, and dates of colony formation varied from year to year, it is difficult to pick a single date to conduct annual colony counts. Unlike Bagley and Jacobs (1985), I did not find that population counts remained stable over time for either year. Changes in numbers of emerging bats suggested that parturition probably occurred throughout a 2-3 week period.

Shifts in foraging activity (as indexed by emergence/return data) of female Ozark big-eared bats throughout summer, relative to parturition and lactation, were very similar to that observed in Virginia big-eared bats (P. t. virginianus, Bagley and Jacobs, 1985). In Oklahoma, unimodal activity occurred prior to parturition and trimodal activity was associated with newborn and non-volant babies. Watkins (1972) observed similar trimodal activity patterns for female evening bats (Nycticeius humeralis) when the young were approximately 1 week old.

I agree with the conclusion of Watkins (1972) that the shifting activity pattern reflects the return of females throughout the night to suckle young. In addition, data that I collected during radio-tracking studies corroborated

the trimodal activity pattern of females during early lactation.

Bats did not synchronously return to the cave following the initial foraging bout, nor were subsequent bouts synchronous. One conclusion might be that only part of the colony returned to roost during the night; however, all females radio tracked during early lactation in 1987 returned to the cave at least twice each night (chapter 2). Asynchronous second foraging bouts also have been reported for little brown bats (M. lucifugus, Anthony et al., 1981) and cave bats (M. velifer, Kunz, 1974). All radio-tagged females that I tracked during early lactation returned to the maternity cave asynchronously.

After young became volant, females probably did not need to return to the roost to nurse young; most bats left the roost after sunset and did not return again until sunrise. This pattern also has been noted for M. velifer in Oklahoma (Kunz, 1974). However, this does not preclude the possibility that bats were using night roosts elsewhere.

Emergence

The circling behavior of bats near a cave entrance prior to emergence has been described as light-sampling behavior (Twente, 1955). This behavior is thought to be a method of synchronizing daily and seasonal activity of bats

with changing sunset time serving as the Zeitgeber (DeCoursey and DeCoursey, 1964; Dwyer, 1964; Herreid and Davis, 1966). Because female Ozark big-eared bats in this study always roosted in dark recesses of the cave, they probably initiated flight within the cave as a result of daily biorhythms. Light-sampling likely served to fine tune activity rhythms of the colony and synchronize initial emergence.

Because females have high energy demands during lactation, emergence of Ozark big-eared bats from the maternity roost later, relative to sunset, in June and July was unexpected. However, this pattern also has been observed for other bat species (Kunz, 1974; McAney and Fairley, 1988). It is possible that females spend the extra time inside the cave grooming and nursing their young prior to foraging. Although it seems that lactating females should maximize their foraging time, the high abundance of insects during summer months probably more than offsets the lost minutes. Another explanation for delayed emergence is the longer period of twilight in summer months (McAney and Fairley, 1988), which may inhibit emergence activity.

The emergence of Ozark big-eared bats in small groups may serve a social role during departure and return to the cave. Twente (1955) conducted an experiment to determine

how P. t. pallescens located nearby cave entrances. He observed that bats released one at a time near a cave entrance during daylight would join one another in flight. When some of the bats located the cave entrance and entered, the rest would soon follow. Perhaps these bats also maintained contact with conspecifics during foraging.

Some subspecies of P. townsendii have been described as late emergers because they did not leave roosts until little or no twilight remained (Kunz and Martin, 1982). However, most P. t. ingens emerged at sunset or shortly thereafter. Departure at dusk seems to be dependent on cloud cover and other measures of brightness for many bats (Kunz, 1974; McAney and Fairley, 1988; Prakash, 1962; Stebbings, 1968); other species do not delay activity in bright moonlight (Fenton et al., 1977; Usman et al., 1980).

Time and duration of foraging of some bat species are affected by external ambient temperature and humidity (Lacki, 1984; O'Farrell and Bradley, 1970; Watkins, 1972), but these factors do not alter activity patterns for other species (Avery, 1987). Similarly, rainfall may delay or shorten the foraging time of some bats (Fenton, 1970) but not others (Fenton, 1970; Stebbings, 1968). Fenton (1970) noted that maternity colonies of females are less likely to delay foraging during storms. This may reflect the increased energy demand of lactation.

Moonlight also may affect activity of some bats (Erkert, 1982; Fenton et al., 1977; Fleming and Heithaus, 1986); however, others do not seem to respond to moonlight noticeably (Bell, 1980; Geggie and Fenton, 1985). Many bats that remain active during bright periods of night concentrate their foraging activity among shadows of trees, cliffs, or other vertical structures (Fenton et al., 1977; Reith, 1982). No effect of cloud cover or other indices of brightness was apparent for Ozark big-eared bats. Perhaps the tendency for Ozark big-eared bats to forage extensively along woodland edges or clumps of trees provides suitable protection from predators regardless of brightness.

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CHAPTER II

SUMMER FORAGING ACTIVITY OF ADULT FEMALE OZARK BIG-EARED BATS (PLECOTUS TOWNSENDII INGENS)

ABSTRACT.--Foraging activity of the endangered Ozark big-eared bat (Plecotus townsendii ingens) was studied during the maternity season in June and July 1988. Eighteen adult females were tagged with 0.8-g radio transmitters and tracked for three 10-day periods (6 bats/period) that corresponded with early, mid- and late lactation. Bats traveled various directions from the maternity cave to foraging areas and demonstrated considerable site specificity. Females made three feeding bouts during early lactation and returned to the maternity cave after each. As young bats became independent, females reduced the number of visits to the cave each night. By late July radio-tagged bats exited after sunset and did not return until sunrise. Mean distances traveled from the maternity roost to centers of foraging areas also increased as lactation progressed, possibly as a result of the reduction in number of trips to the cave each night. Individuals used from one to four foraging areas throughout

the summer. Number and average size of foraging areas did not differ throughout the study period. Ozark big-eared bats foraged most often along wooded and edge habitats associated with intermittent streams and mountain slopes. Vertical structure provided by woodland edge seems to be an important habitat for this endangered subspecies.

Habitat disturbance and destruction are primary causes of bat declines in the United States, particularly for those species and subspecies that either have not or cannot exploit man-made structures (Barbour and Davis, 1969; Harvey, 1976; Humphrey and Kunz, 1976). Ozark big-eared bats (Plecotus townsendii ingens) once occurred in the Ozark Plateau region of northern Arkansas, southern Missouri, and eastern Oklahoma (Kunz and Martin, 1982). Extensive surveys of previously occupied and nearby caves in Missouri during the late 1980s produced no evidence of big-eared bats. This substantiated the assumption that this subspecies has been extirpated from Missouri (D. Figg, pers. comm.). Summer population estimates in Arkansas have decreased to <50 individuals and searches for additional roosts during 1988 were unsuccessful (M. J. Harvey, pers. comm.). The known distribution of Ozark big-eared bats is now concentrated around five caves (two maternity roosts, one hibernaculum, and two that serve both functions) in eastern Oklahoma.

Ozark big-eared bats are dependent on limestone caves throughout their life history (Bagley, 1984). Both sexes congregate in caves during winter to hibernate when prey availability and temperatures are low. In summer, females form maternity colonies where they give birth to a single offspring. Males lead a solitary existence, roosting on cliff faces, rock fissures, or in caves.

Bats that concentrate in caves are susceptible to massive reductions in numbers due to natural and anthropogenic disturbances. If caves flood, collapse, or are vandalized, many bats may be killed and those remaining have fewer roosts. Indirect losses can occur if the temperature, relative humidity, or air flow in a cave is altered and suitable microhabitat for bats is no longer available as a result of blocked entrances or changes in above-ground habitats. Such vulnerability has prompted the inclusion of many bat species and subspecies on the U.S. Fish and Wildlife Service's list of threatened and endangered wildlife and plants (Henshaw, 1972; Humphrey, 1978; Tuttle, 1979).

Management efforts to protect endangered bats include: (1) purchase of or restricted access to bat caves; (2) protection of habitats surrounding caves; and (3) regulation of land-use practices within bat foraging areas (Bagley, 1984, P. t. ingens; Brady et al., 1983, Myotis

sodalis). Measures already have been taken to protect caves harboring endangered bats (LaVal and LaVal, 1980; White and Seginak, 1987).

Surface habitats that provide space, cover, and prey for foraging bats also need protection (Lera and Fortune, 1979); however, little is known about above-ground requirements of insectivorous bats. Prior to development of radio transmitters weighing <1.0 g, researchers had to extrapolate spatial and temporal activity of small bats from mist-netting, light-tagging, or echolocation studies and information on individual activity was compromised (Wilkinson and Bradbury, 1988). This study is among the first to use telemetry to investigate foraging activities of bats in the United States.

Temporal changes in foraging relative to parturition and lactation were assessed for adult female Ozark big-eared bats by documenting: (1) numbers of foraging bouts per night; (2) amount of time spent away from the maternity roost; (3) distance from the maternity cave to foraging areas; (4) number of foraging areas per bat; (5) size of foraging areas; and (6) habitat use. Comments on telemetry equipment and techniques also are provided.

STUDY AREA

This study was conducted in Adair Co., Oklahoma, which is located in the southwestern portion of the Ozark Uplift.

The Ozark Plateau covers ca. 103,600 sq km in southern Missouri, northwestern Arkansas, and northeastern Oklahoma (Huffman, 1959) and has numerous limestone caves that may have served as refugia from severe post-Pleistocene winters for Ozark big-eared bats (Humphrey and Kunz, 1976).

Erosion of Boone chert (alternating layers of limestone and flint) produced the rugged terrain of small mountains, bluffs, and wide valleys (Blair and Hubbell, 1938).

Mountains rise <125 m from base to peak and elevations throughout the region range between 260 and 460 m.

Associations of blackjack oak (Quercus marilandica), post oak (Q. stellata), black hickory (Carya buckleyi), and winged elm (Ulmus alata) dominate mountain slopes.

Coralberry (Symphoricarpos orbiculatus) and sassafras (Sassafras varifolium) provide sparse shrubby undergrowth.

Lowland, riparian areas are dominated by silver maple (Acer saccharinum), red birch (Betula nigra), American elm (Ulmus americana), cottonwood (Populus deltoides), sycamore (Plantanus occidentalis), and various oaks (Blair and Hubbell, 1938; Turner, 1935).

I selected one cave used by female Ozark big-eared bats as the focal point of this study because a network of roads surrounding the mountain facilitated radio tracking. A maternity colony was first observed in the cave during summer 1984; the cave has been used as a maternity roost

every year since (through summer 1990). Colony size was estimated at 110 adult females when this study was initiated in 1988. There were at least five other caves on the mountain. Solitary bats (presumably males) have been observed in some caves during summer, and one served as a transient roost for Ozark big-eared bats in fall and spring.

METHODS

Bats were tracked throughout the nights of 8-17 June, 28 June-7 July, and 17-26 July 1988, which coincided with early, mid-, and late lactation, respectively. Lactation categories were based on mammary condition of females and fledging dates of young. During early lactation, all females were post-partum, milk was easily palpated from mammaries, and young were not able to fly. In mid-lactation young were volant; however, mammaries were still pendent and milk was easily exuded. Young were strong fliers by late lactation, mammaries were less swollen, and milk was difficult to extract.

Emerging bats were captured in a mist-net placed across the maternity cave entrance. Sex, age, body mass, and reproductive condition were noted for each, and an 0.8-g transmitter (model BD-1A, Holohil Systems Ltd, Ontario, Canada) was attached to the first six adult females captured. I removed the net following capture of

the sixth female to prevent further disturbance to the colony. After transmitters were securely fastened between the scapulae with liquid skin cement, bats were allowed to fly at will from a horizontal surface. Total handling time was <30 min for each.

To determine individual foraging areas, telemetry efforts were concentrated on a different bat each night. If the bat flew out of range, receiving stations were moved to new sites. If the bat was not found, locations of other bats were checked and efforts were concentrated on individuals for which the least data had been collected.

Directional fixes were taken from one stationary location and two mobile units equipped with receivers (Model TRX-1000s, Wildlife Materials, Carbondale, Illinois). The stationary receiver was placed on a cliff just above the maternity cave entrance to record times of bat departures and returns. When tracking individuals, I relocated the receiving station on the mountain to enhance signal reception. Sites for mobile receivers were limited to areas accessible to vehicles. Given an extensive road system and cooperation of landowners, mobile units usually were able to maintain contact with bats and optimize angles of fixes.

Bearings were taken at 2-min intervals with hand-held, three-element Yagi antennae using the loudest signal method

(Springer, 1979). Triangulations were synchronized by continuous radio communication, and locations of bats were plotted on 7.5-min quadrangle maps. Irregularities (i.e., non-intersecting bearings, outlying locations that occurred during localized sequential bearings, and two signals in different directions) were discarded from the data set.

The general linear model of analysis of variance (SAS Institute, 1985) was used to test for heterogeneity in: (1) time of first emergence; (2) number of feeding bouts; (3) total foraging time; (4) distance from maternity cave to foraging area; (5) number of foraging areas; and (6) size of foraging areas among the three telemetry periods. Tukey's studentized range test (SAS Institute, 1985) was used to determine differences among means of the three study periods.

Numbers of foraging areas per bat over each 10-day study period were recorded. If foraging areas of an individual overlapped between successive nights, the total area was considered one foraging area. Non-overlapping nightly foraging areas (or groups of nightly foraging areas) were not pooled. I estimated size of foraging areas using the minimum convex polygon method (Mohr, 1947) and measured distance from the maternity cave to geometric centers of activity (Hayne, 1949).

Habitat availability was determined by placing a grid

(0.32-cm squares) over topographic maps verified by ground truths. Each square was designated as either wooded, open (pastures, crops, and native grasses), or edge habitat. Bat locations were assigned the same habitat type as the square in which they occurred. Assuming some triangulation error, actual bat locations may have been ≤ 150 m from the triangulated estimate (see White and Garrott, 1986). I used chi-square analysis to test if bats used habitats in proportion to their occurrence within the study area. Avoidance or selection of a habitat was tested by calculating Bonferroni confidence intervals around the observed use of each type (Neu et al., 1974).

RESULTS

Transmitter Efficiency

Transmitters were attached to bats and operative for at least 1-10 nights ($\bar{X} = 6.7$, $SE = 0.71$, $n = 18$), and four remained attached after 10 nights. All transmitters maintained a pulse rate of ca. 80 signals/min throughout the duration of the study. Signal frequencies also were constant and did not shift ≥ 1 kHz. Maximum reception distance was ca. 2 km (linear distance) from the highest receiving point.

Bat Responses to Telemetry

I netted Ozark big-eared bats at the same maternity cave for all three telemetry trials; in spite of this

activity, radio-tagged bats did not abandon the maternity roost during the first two telemetry periods. However, during late lactation five of six bats tagged changed day roosts to another cave 1.0 km southeast of the maternity roost on the same mountain. The sixth bat may have shifted roosts as well but lost her transmitter so that her movements could not be monitored.

Bats with radio transmitters were able to take flight from a horizontal surface with no visible difficulty. Because temporal activity patterns of radio-tagged bats paralleled those of the colony as a whole and individual activity patterns recurred nightly, I assumed that tagged bats were behaving normally and that their activity patterns were representative of the colony.

Foraging Activity

Ozark big-eared bats began flying inside the cave ca. 30 min before sunset. Fluctuating signal strengths suggested that bats approached the entrance several times before departing. Radio-tagged bats left the cave 46.3 min after sunset on average (SE = 4.19, range 4-157). Mean times of emergence (min after sunset) did not change relative to parturition and lactation (F = 1.09, d.f. = 2,34, P = 0.35; Table 2).

Numbers of foraging bouts decreased as lactation progressed (F = 26.6, d.f. = 2,21, P < 0.0001; Table 2).

Table 2.--Temporal activity and foraging area parameters of adult female P. t. ingens during early, mid-, and late lactation.

Parameter	Lactation								
	Early			Mid-			Late		
	\bar{X}	<u>SE</u>	Range	\bar{X}	<u>SE</u>	Range	\bar{X}	<u>SE</u>	Range
35 Time of emergence (min after sunset)	42.2	2.8	26-62	40.9	7.1	4-61	54.6	10.5	19-157
Number of feeding bouts/night	3.0	0.0	3	2.6	0.4	1-3	1.1	0.1	1-2
Time away from maternity cave (min)	352.3	5.6	337-364	464.3	22.0	434-507	483.7	7.3	470-495
Distance to foraging areas (km)	1.0	0.4	0.3-2.0	2.2	0.4	1.3-4.0	3.7	0.8	1.1-7.0
Number of foraging areas	1.7	0.3	1-2	1.5	0.3	1-2	2.3	0.8	1-4
Size of foraging areas (ha)	118.4	59.4	10-332	235.5	102.8	43-727	69.1	16.7	21-156

Mean numbers of feeding bouts were not significantly different ($P > 0.05$) between early and mid-lactation. In early lactation, females exhibited three foraging periods each night and returned to the maternity roost between bouts. During mid-lactation, numbers of foraging bouts ranged from 1-3 ($\bar{X} = 2.6$). Bats returned to the cave fewer times ($P < 0.05$) during late lactation, usually departing at sunset and returning just before sunrise the next morning.

Duration of the first foraging bout in early lactation ranged from 24 to 130 min ($\bar{X} = 90$, $SE = 12.7$). Mean time spent away from the roost during the first foraging bout differed among individuals ($F = 4.08$, $d.f. = 3,7$, $P = 0.06$). Time of first exit and return became predictable from night to night for many individuals. Subsequent foraging bouts were less regular and varied in duration for all bats.

Total time spent outside the cave differed significantly among the three study periods ($F = 35.23$, $d.f. = 2,7$, $P = 0.002$; Table 2). Mean foraging time during early lactation was significantly less ($P < 0.05$) than that of mid- or late lactation. No significant difference occurred between the latter two periods.

During early and mid-lactation, bats seemed to be actively foraging most of the time that they were outside

the maternity cave. Radio signals were not lost or stationary for >3 min as would be expected if they used night roosts. During late lactation, signals were lost briefly, but often reappeared in the location where last heard. Instead of returning to the maternity cave, females may have used trees, crevices, or caves near foraging areas as night roosts, as reported for other subspecies of P. townsendii (Dalquest, 1947; Pearson et al., 1952).

Foraging Areas

Mean distances from the maternity cave to geometric centers of individual foraging areas increased as lactation progressed ($F = 4.77$, $d.f. = 2,15$, $P = 0.02$; Table 2). During early lactation mean distance to geometric centers of foraging areas was 1.0 km (Fig. 6) and increased to 2.2 km in mid-lactation (Fig. 7). Bats flew the greatest mean distance (3.7 km) during late lactation (Fig. 8). One female foraged as far as 7.3 km N of the maternity cave during late lactation. She was observed in the same location throughout two nights of intensive tracking, as well as during periodic checks on other nights. Two additional females foraged near an Ozark big-eared bat hibernaculum located 6.3 km SSE of the maternity cave (Fig. 8).

Numbers of foraging areas per bat ranged from 1 to 4 ($\bar{X} = 1.82$, $SE = 0.30$, $n = 11$; Table 2, Figs. 6-8) and did

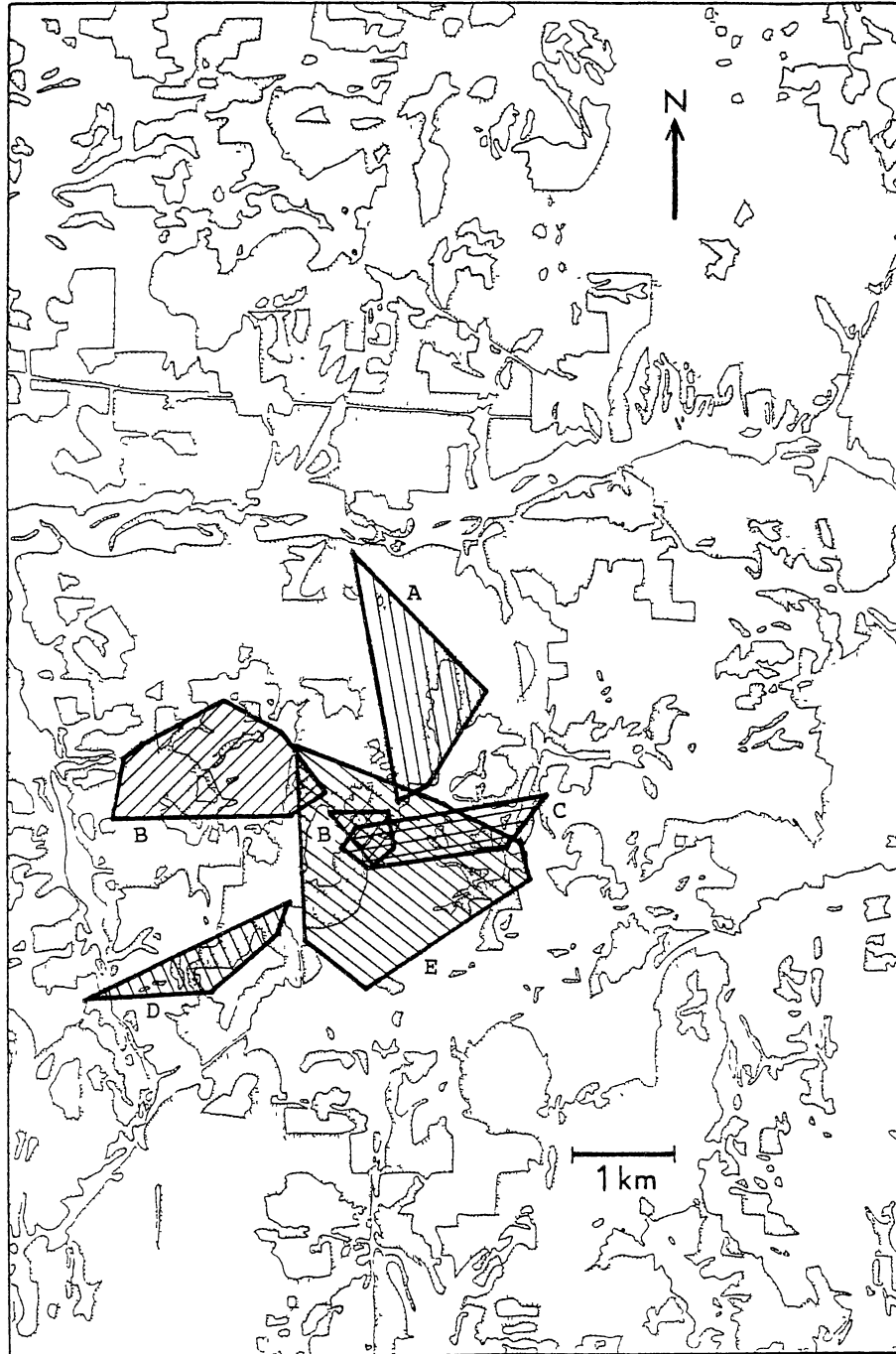


Fig. 6.--Foraging areas of five adult female *P. t. ingens* (A, B, C, D, and E) during early lactation (8-17 June 1988). Stippled and non-stippled areas denote forested and non-forested habitats, respectively.

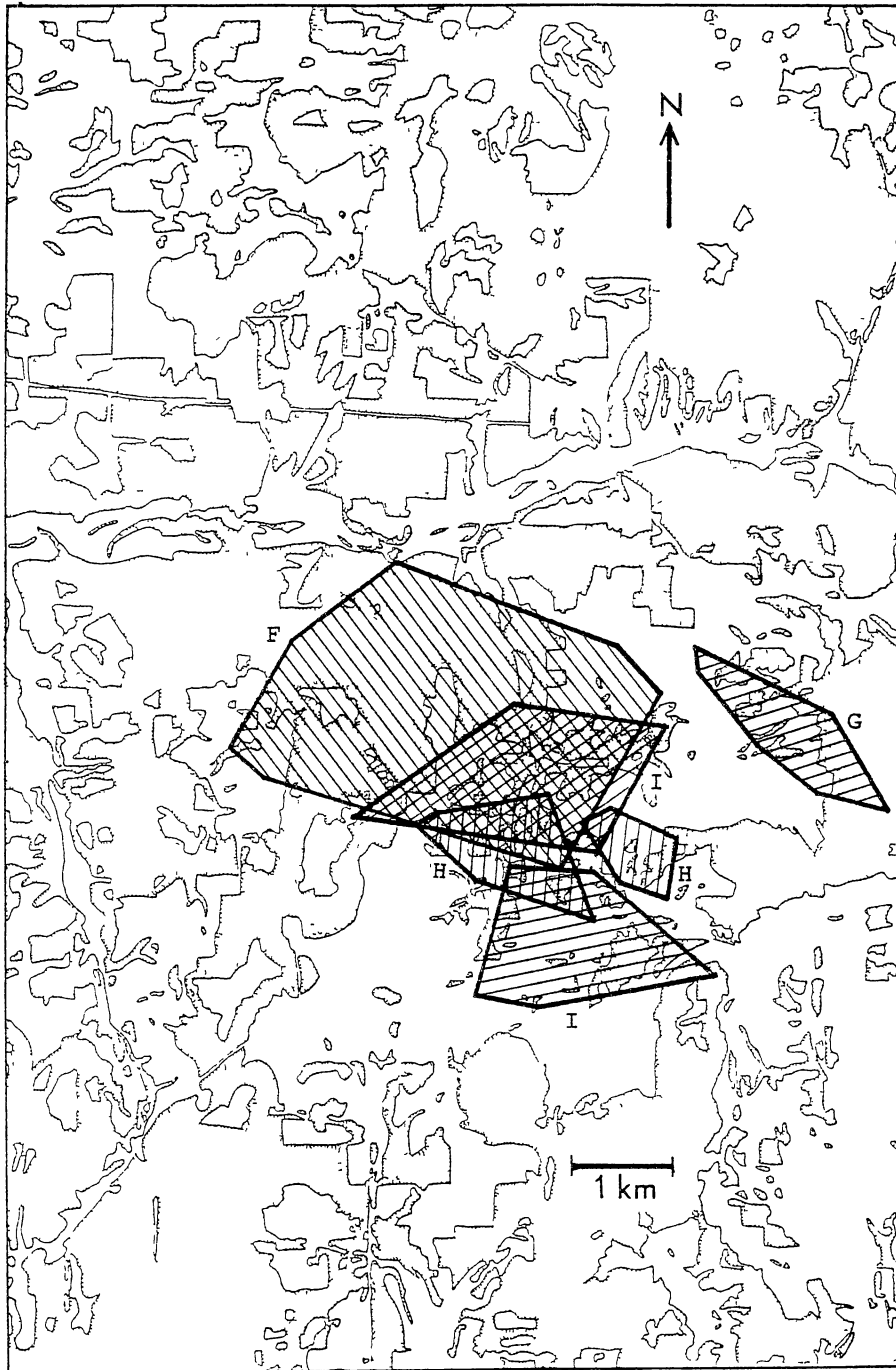


Fig. 7.--Foraging areas of four adult female *P. t. ingens* (F, G, H, and I) during mid-lactation (28 June-7 July 1988). Stippled and non-stippled areas denote forested and non-forested habitats, respectively.

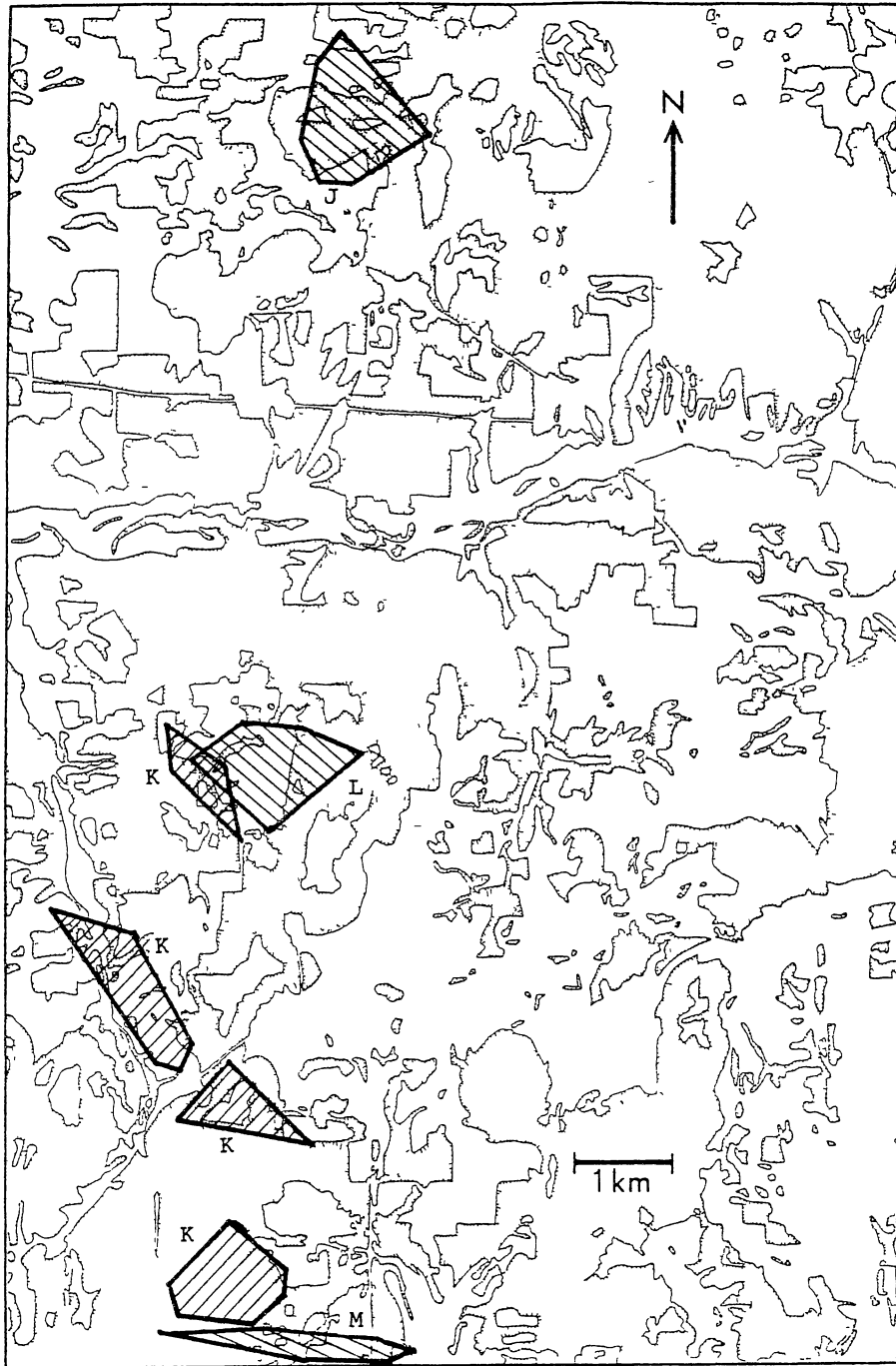


Fig. 8.--Foraging areas of four adult female *P. t. ingens* (J, K, L, and M) during late lactation (17-26 July 1988). Stippled and non-stippled areas denote forested and non-forested habitats, respectively.

not differ throughout the study ($F = 0.58$, $d.f. = 2, 8$, $P = 0.58$). Four females (E, F, G, and J) that were tracked more than one night used the same areas each night (Figs. 6, 7, and 8, respectively) and four others (B, H, I, and K) had multiple foraging areas (Figs. 6, 7, and 8, respectively). Bats B and H alternated between two areas each night (Figs. 6 and 7, respectively); bat I foraged in one area four nights then shifted to a second area for at least two nights (Fig. 7), and bat K used four foraging areas, each progressively further south of the maternity roost (Fig. 8). Size of foraging areas varied considerably within each study period (Table 2) but did not differ significantly relative to maturation of young ($F = 1.73$, $d.f. = 2, 15$, $P = 0.21$).

Habitat Use

The study area was comprised of 29.7% open, 32.3% edge, and 38.0% woodland habitats. Adult female big-eared bats did not forage in these habitats as expected during early, mid-, or late lactation ($\chi^2 = 19.8, 23.7, \text{ and } 45.6$, respectively, $d.f. = 2$, $P < 0.001$). Edge habitat was used more than expected ($P < 0.01$), and bats were in forested areas less than expected ($P < 0.05$) throughout the study (Fig. 9). Open habitat was used in proportion to its availability during early and late lactation but was avoided ($P < 0.05$) in mid-lactation. On moonlit nights, I

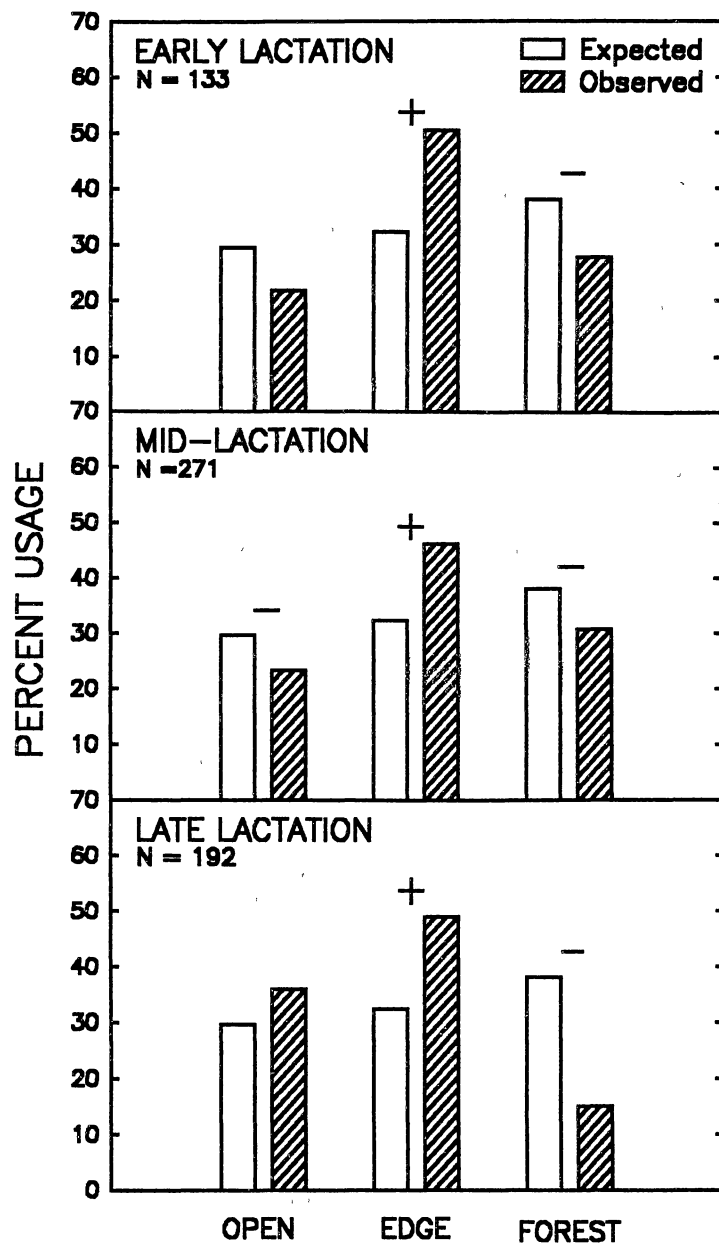


Fig. 9.--Comparison of percent usage (observed) and percent availability (expected) of open, edge, and forested habitat types by adult female *P. t. ingens* during early (8-17 June), mid- (28 June-7 July), and late (17-26 July) lactation in 1988. Bonferroni confidence intervals around the proportion of usage were used to test for selection (+) or avoidance (-) of each habitat type.

observed big-eared bats foraging in close proximity to vertical structures, such as trees and cliffs.

There was no difference in habitat use by bats between early and mid-lactation ($\chi^2 = 0.66$, d.f. = 2, p > 0.5; Fig. 10). However, habitat use during late lactation differed significantly from that of early and mid-lactation ($\chi^2 = 11.49$ and 17.73 , d.f. = 2, p < 0.005 and 0.001, respectively). During late lactation, bats occurred in open habitat more frequently and used woodlands less than during early or mid-lactation (Fig. 10).

DISCUSSION

Telemetry Considerations

Attaching a transmitter to a volant animal almost certainly affects flight energetics and maneuverability. A general rule is that a transmitter should not exceed 5% of the animal's mass (Cochran, 1980); however, ability of bats to carry loads varies considerably among species (Aldridge, 1987; Davis and Cockrum, 1964). When deciding whether to apply radio transmitters to bats, it is important to: (1) consider the wing loading of that species; (2) assess possible problems with a test animal (i.e., difficulty taking flight, behavior suggesting discomfort when roosting, temporal or spatial foraging activity that varies from the colony as a whole, or reluctance to fly); and (3)

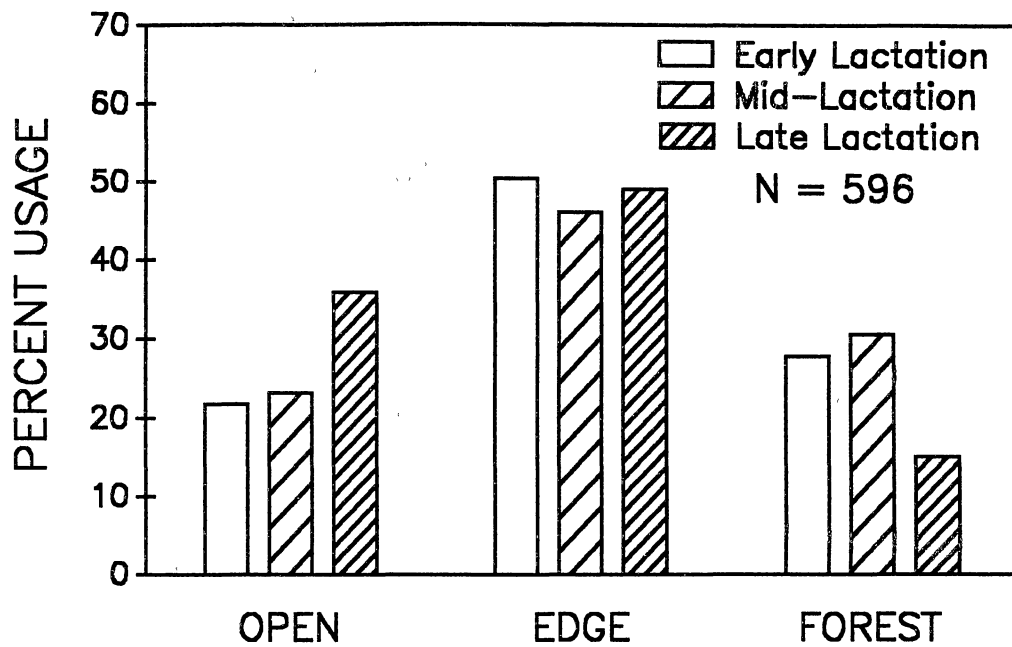


Fig. 10.--Comparison of percent usage of open, edge, and forested habitats by *P. t. ingens* during early (8-17 June), mid- (28 June-7 July), and late (17-26 July) lactation in 1988.

consider the benefit to the species by collecting telemetry data.

Transmitters used in this study were 6.7% of the body mass of Ozark big-eared bats. Although this was slightly above the recommended limit, radiotelemetry was warranted for the following reasons: (1) the lightest product available was used; (2) *P. townsendii* have low wing loading (Davis and Cockrum, 1964; Farney and Fleharty, 1969) that allows them to carry heavier loads than other bat species; and (3) the endangered status of Ozark big-eared bats made it necessary to locate foraging areas in an effort to protect those habitats toward recovery of the subspecies.

Although radiotelemetry provides information on movements of individuals that otherwise could not be obtained easily, accuracy of bearings is of concern (Lee et al., 1985; Springer, 1979). Bats are especially challenging to track due to their high mobility and nocturnal habits, coupled with limitations in transmitter size suitable for use on small chiropterans (Aldridge and Brigham, 1988; Stebbings, 1982; Walton and Trowbridge, 1983).

Many subspecies of big-eared bats are easily disturbed by human activity. Nursery colonies of *P. t. pallescens*, found in gypsum caves of western Oklahoma and Kansas, shifted roosts after they were banded or disturbed by

spelunkers (Humphrey and Kunz, 1976). Similarly, nursery colonies in California moved to alternative caves after banding (Pearson et al., 1952). Plecotus townsendii virginianus may have abandoned a cave following routine censusing in Kentucky (D. Yancy, pers. comm.); however, a colony in Virginia exhibited no such response following emergence counts or light-tagging (V. Dalton, pers. comm.). When bats shift roosts following disturbance, there is concern that they may have moved from a location that provided optimum temperature, humidity, and protection to a less suitable place. The move could result in predation, loss of embryos or young, slowed development, or critically reduced fat stores (Humphrey and Kunz, 1976; Mohr, 1972).

Ozark big-eared bats did not abandon the maternity cave in June, even though I netted and attached transmitters to females twice. I did not enter the cave to see if bats shifted roost locations. My activity may have prompted movement of bats from the maternity cave to the transient roost in late July; however, such shifts were not unusual. Ozark big-eared bats have been found in the transient cave annually (since 1986) during late summer. The transient roost also is used by bats during spring, but only a few solitary individuals have been found there during summer or winter. I suspect that this cave serves

swarming behavior as described for other bat species (Cope and Humphrey, 1977; Schowalter, 1980).

Foraging Strategies

Energetic demands are high for pregnant bats and culminate during lactation (Kunz, 1987). Although shifts in foraging time and duration could accommodate changing energy needs of females (Racy and Swift, 1985; Swift, 1980), length of foraging periods may be constrained because their presence at the maternity roost provides thermal regulation, nutrition, and protection for offspring (Barclay, 1989). The observed reduction in numbers of nightly visits to the maternity cave and increased foraging time during late lactation may have allowed female Ozark big-eared bats to recover from depleted fat stores after offspring were large enough to forage and thermoregulate on their own.

Distances to foraging areas likely were constrained by the number of visits females made to the maternity cave during early and mid-lactation. As juveniles became less dependent on their mothers, females did not have to return to the roost as often and were able to forage further away. If females then were able to find more high-density patches of insects, the energy that they saved searching and pursuing prey may have offset the energetic cost of flying greater distances to get there. After offspring began

foraging, competition for food probably increased near the maternity roost (Kunz, 1974). Assuming that young bats did not travel far until they became more skilled fliers, the adults may have foraged further away to reduce competition.

Individual foraging areas seldom overlapped temporally; however, given the small sample size, I was unable to determine if Ozark big-eared bats defended foraging territories. Intraspecific competition has been observed for some bat species under conditions of low food availability or when resources were clumped (Racy and Swift, 1985). Weekly insect samples taken at the study site indicated that prey densities in June and July were high (chapter 3); thus, the likelihood of competitive interactions was reduced.

Habitat Use

Edge habitat may have been the preferred foraging area of Ozark big-eared bats because it provided cover for both bats and moths. Uncluttered situations allow for easy feeding because bats do not have to dodge branches while pursuing prey and are able to discriminate insects at greater distances; however, open habitats provide no structural protection from predators (Erkert, 1982). Alternatively, trees provide cover and an abundance of moths for bats, but the habitat is cluttered. By foraging along woodland edges, Ozark big-eared bats benefited from a

less cluttered environment, but cover was nearby and prey densities were high.

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CHAPTER III

FOOD HABITS OF OZARK BIG-EARED BATS

(PLECOTUS TOWNSENDII INGENS)

ABSTRACT.--Food habits of Ozark big-eared bats (Plecotus townsendii ingens) in eastern Oklahoma were studied from July 1987 through July 1988. Diets were determined from microscopic analysis of fecal pellets and compared with insects 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 pellets, respectively, but each accounted for <5% of the volume. Trichopterans, hymenopterans, and neuropterans also were found in trace amounts.

Five subspecies of big-eared bats (Plecotus townsendii) were described by Handley (1959). Three subspecies (P. t. townsendii, P. t. pallescens, and P. t. australis) range throughout western North America (Barbour and Davis, 1969; Kunz and Martin, 1982). Two subspecies occur as isolated

populations in Arkansas and Oklahoma (P. t. ingens) and Kentucky, Virginia, and West Virginia (P. t. virginianus). These latter two subspecies were classified as endangered due to their restricted distribution, small population size, and susceptibility to disturbance (Bagley, 1984). The ecology and natural history of the western subspecies of big-eared bats have been investigated (e.g., Dalquest, 1947; Humphrey and Kunz, 1976; Pearson et al., 1952; Twente, 1955); however, it cannot be assumed that eastern subspecies exhibit similar characteristics.

Previous studies have described the food habits of subspecies other than P. t. ingens (Dalton et al., 1986; Ross, 1967; Whitaker et al., 1977). These studies found that P. townsendii fed primarily on lepidopterans; however, diets of other bat species have varied regionally. For example, Myotis velifer diets consisted of mostly coleopterans in Kansas (Kunz, 1974), but lepidopterans in Arizona and northern Mexico (Ross, 1967).

In the past decade, numerous studies have examined diets of insectivorous bats in North America (e.g., Belwood and Fullard, 1984; Brack, 1985; Brack and LaVal, 1985; Dalton et al., 1986; Griffith and Gates, 1985; Warner, 1985; Whitaker and Tomich, 1983); however, several species remain for which food habits are unknown. Of particular concern are species and subspecies with special status,

such as P. t. ingens. My objectives were: (1) to determine the food habits of P. t. ingens in eastern Oklahoma and (2) to compare food items with prey availability.

STUDY AREA AND METHODS

My study was conducted in the Boston Mountains of eastern Oklahoma. The region occupies the southwestern end of the Ozark uplift (Huffman, 1959) and has numerous limestone caves. Mixed oak (Quercus spp.) and hickory (Carya spp.) complexes dominate mountain slopes and riparian areas. Most valleys and mountain tops have been cleared for crops and livestock grazing.

Prey Sampling and Identification

I sampled the aerial insect fauna from sunset to sunrise approximately weekly on 32 nights from 7 July 1987 through 25 July 1988 with Malaise traps (Model 2875A, Bioquip Products, Santa Monica, CA). During spring and summer (7 July-22 September 1987 and 12 May-25 July 1988), four traps were run simultaneously near a cave used as a maternity site by P. t. ingens. Two traps were placed in woodland habitat contiguous with the maternity cave, and two 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 P. t. ingens. No open habitats were ≤ 200 m of the hibernaculum; therefore, only wooded sites

were sampled during that time.

I raised the Malaise traps an additional 1.3 m above the ground with conduit extensions to approximate the foraging stratum of bats and to exclude non-volant 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 dessicator prior to identification.

Insects were examined under a 40 X dissecting microscope and classified to order or family (Borror et al., 1981). Moths <4 mm body length were classified as microlepidoptera. 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.

Guano Collection

Guano was collected approximately weekly from the maternity cave near where insects were sampled. A cloth sheet was placed in flyways inside the maternity cave to collect fecal pellets. I 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 P. t. ingens were discarded because they

may have been from eastern pipistrelles (Pipistrellus subflavus), which occasionally roosted in the cave. Sheets were then cleared of all remaining guano to prevent mixing of weekly samples.

Feces were dried in aluminum foil cups at 100°C and stored in a dessicator prior to analysis. I 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 portions 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 insect orders are presented as percent frequency (percentage of fecal pellets containing each insect order) and percent volume (percentage of all feces combined that each insect order makes up) to facilitate comparisons with other studies (Korschgen, 1980).

Statistical Analyses

The sign test (corrected for continuity) was used to look for significant differences between numbers of insects collected in open habitat and wooded habitat for each order. Strauss' (1979) index of electivity was used to

examine prey selectivity by P. t. ingens on those dates for which guano collection and insect sampling coincided. Orders with electivity values ≥ 0.1 were considered significant departures from random. A Wilcoxon's signed-rank test (Sokal and Rohlf, 1981) was performed on the weekly comparisons to identify significant departures from random selection for each of the major insect orders throughout the study period.

RESULTS

Prey Availability

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

There were significant differences between numbers of insects captured in open and wooded habitats for seven insect orders. Hemipterans ($P < 0.01$), homopterans ($P < 0.01$), and neuropterans ($P < 0.05$) were more abundant in open habitats. Dipterans, hymenopterans, lepidopterans, and tricopterans were most numerous in wooded habitats ($P < 0.01$)

Table 3.--Arthropod availability (numbers and percent) including all arthropods and arthropods ≥ 5 mm body length collected in Malaise traps from July 1987 through July 1988.

Order	All Arthropods		Arthropods ≥ 5 mm	
	n	%	n	%
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, etc.)	141	2.9	89	8.8
Coleoptera (beetles)	120	2.5	50	4.9
Neuroptera (lacewings)	40	0.8	35	3.5
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
Unidentified	6	0.1	0	0.0
Acari (mites)	6	0.1	0	0.0
Psocoptera (psocids)	3	*	0	0.0
Isoptera (termites)	1	*	0	0.0
Odonata (damselflies)	1	*	0	0.0

* <0.1 percent

Diet

Seven orders of insects were found in feces of P. t. agens. Lepidoptera, the most commonly consumed prey item, occurred in 91.4% of 104 fecal pellets examined, and comprised 85.2% of the total volume of guano (Table 4). 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 4). Unidentified prey remains occurred in 8.7% of the pellets, and balls of hair, apparently the result of 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, thus it is doubtful that the observed debris had been ingested. No plant material was found in the guano.

Single fecal pellets contained remains of 1-4 (\bar{X} = 1.34) insect orders. When considering the percent volume composition of individual pellets, Lepidoptera was the only order present in 57.7% of the pellets examined, comprised between 80-99% of the remains of 26.0% of the pellets, and 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 insects available,

Table 4.--Prey items consumed by P. t. ingens expressed as percent frequency (the percent of fecal pellets containing each food type) and average percent volume (the average percent by volume of all guano).

Food item	Percent frequency	Percent volume
Lepidoptera (moths)	91.4	85.2
Diptera (flies)	18.3	3.7
Hair	13.5	1.9
Coleoptera (beetles)	10.6	3.5
Unidentified prey	8.7	2.2
Homoptera (leafhoppers, etc.)	6.7	1.7
Trichoptera (caddisflies)	2.9	0.3
Hymenoptera (ants, wasps, etc.)	1.9	1.6
Neuroptera (lacewings, etc.)	1.0	0.1

lepidopterans were the preferred prey of P. t. ingens whether or not insects <5 mm were included in the analyses (Wilcoxon's signed-rank test, $\underline{P} < 0.05$, Table 5). Although lepidopterans comprised only 21.5% of all insects collected, they occurred in 91.4% of the fecal pellets examined and comprised 85.2% of the volume (Table 4). Positive selectivity (Strauss' electivity index) was observed each week from May through July for all size categories. When only insects ≥ 5 mm were considered, there was a shift toward randomness beginning in August.

Dipterans were more than twice as abundant as lepidopterans and comprised 52.1% of all insects sampled; however, they were found in only 18.3% of the fecal pellets examined. Plecotus townsendii ingens avoided dipterans when all sizes of insects were considered potential prey ($\underline{P} < 0.05$; Table 5). Of all dipterans captured, 96.2% had a body lengths <5 mm (Fig. 11). Such small insects may not represent potential prey to bats and as such should not be included in analyses. When I removed insects <5 mm from the analysis, the number of dipterans consumed was not significantly different from the number available in the habitat ($\underline{P} > 0.05$, Table 5).

Homoptera was the third most abundant insect in the habitat (18.0% of trap samples), but they were avoided by the bats ($\underline{P} < 0.05$; Table 5). There were several small

Table 5.--Electivity values (Strauss, 1979) and Wilcoxon's signed-rank values for prey items consumed by P. t. ingens including all insects and insects ≥ 5 mm collected in Malaise traps considered potential prey. (The symbols +, R, and - represent positive, random, and negative selection, respectively).

Insect Order and Date	Electivity Index		Wilcoxon's signed-rank test	
	≥ 5 mm	Combined	≥ 5 mm	Combined
Coleoptera			R(24.0)	R(38.0)
30 June 1987	-(0.10)	R(0.05)		
7 July 1987	-(0.11)	R(0.00)		
14 July 1987	R(0.03)	R(0.06)		
21 July 1987	R(0.03)	R(0.00)		
28 July 1987	R(0.01)	R(0.01)		
5 August 1987	-(0.10)	R(0.09)		
11 August 1987	R(0.00)	R(0.01)		
18 August 1987	R(0.08)	R(0.01)		
25 August 1987	R(0.01)	R(0.01)		
1 September 1987	+(0.19)	+(0.19)		
23 September 1987	R(0.00)	R(0.00)		
18 May 1988	R(0.02)	R(0.04)		
26 May 1988	-(0.14)	R(0.06)		
Diptera			R(29.0)	-(0.0)**
30 June 1987	R(0.08)	-(0.29)		
7 July 1987	R(0.06)	-(0.51)		
14 July 1987	R(0.04)	-(0.48)		

Table 5.--Continued

Insect Order and Date	Electivity Index		Wilcoxon's signed- rank test	
	≥ 5 mm	combined	≥ 5 mm	combined
21 July 1987	-(0.10)	-(0.53)		
28 July 1987	R(0.03)	-(0.51)		
5 August 1987	+(0.11)	-(0.34)		
11 August 1987	R(0.00)	-(0.61)		
18 August 1987	R(0.02)	-(0.51)		
25 August 1987	+(0.30)	R(0.04)		
1 September 1987	R(0.02)	-(0.44)		
23 September 1987	R(0.07)	-(0.39)		
18 May 1988	R(0.07)	-(0.50)		
26 May 1988	R(0.03)	-(0.41)		
Homoptera			-(11.0)*	-(0.0)**
30 June 1987	R(0.04)	-(0.35)		
7 July 1987	R(0.06)	-(0.25)		
14 July 1987	R(0.04)	-(0.10)		
21 July 1987	R(0.06)	-(0.21)		
28 July 1987	R(0.09)	-(0.19)		
5 August 1987	R(0.08)	-(0.11)		
11 August 1987	R(0.03)	R(0.09)		
18 August 1987	+(0.15)	R(0.01)		
25 August 1987	-(0.35)	-(0.35)		

Table 5.--Continued

Insect Order and Date	Electivity Index		Wilcoxon's signed- rank test	
	≥5 mm	combined	≥5 mm	combined
1 September 1987	R(0.00)	R(0.04)		
23 September 1987	R(0.07)	-(0.28)		
18 May 1988	R(0.05)	R(0.09)		
26 May 1988	R(0.03)	R(0.07)		
Hymenoptera			-(6.0)**	R(25.0)
30 June 1987	-(0.10)	R(0.04)		
7 July 1987	-(0.15)	R(0.03)		
14 July 1987	-(0.10)	R(0.03)		
21 July 1987	R(0.06)	R(0.02)		
28 July 1987	R(0.09)	R(0.02)		
5 August 1987	R(0.05)	R(0.02)		
11 August 1987	-(0.11)	R(0.02)		
18 August 1987	-(0.14)	R(0.03)		
25 August 1987	R(0.04)	+(0.12)		
1 September 1987	-(0.10)	R(0.04)		
23 September 1987	R(0.06)	+(0.26)		
18 May 1988	R(0.05)	R(0.01)		
26 May 1988	R(0.00)	R(0.01)		

Table 5.--Continued

Insect Order and Date	Electivity Index		Wilcoxon's signed- rank test	
	≥5 mm	combined	≥5 mm	combined
Lepidoptera			+(14.0)*	+(0.0)**
30 June 1987	+(0.41)	+(0.77)		
7 July 1987	+(0.39)	+(0.77)		
14 July 1987	+(0.10)	+(0.58)		
21 July 1987	+(0.36)	+(0.80)		
28 July 1987	+(0.19)	+(0.68)		
5 August 1987	-(0.18)	+(0.27)		
11 August 1987	+(0.14)	+(0.73)		
18 August 1987	+(0.18)	+(0.60)		
25 August 1987	R(0.03)	+(0.27)		
1 September 1987	R(0.01)	+(0.36)		
23 September 1987	-(0.20)	R(0.09)		
18 May 1988	+(0.64)	+(0.58)		
26 May 1988	+(0.28)	+(0.60)		

* $\underline{p} < 0.05$

** $\underline{p} < 0.01$

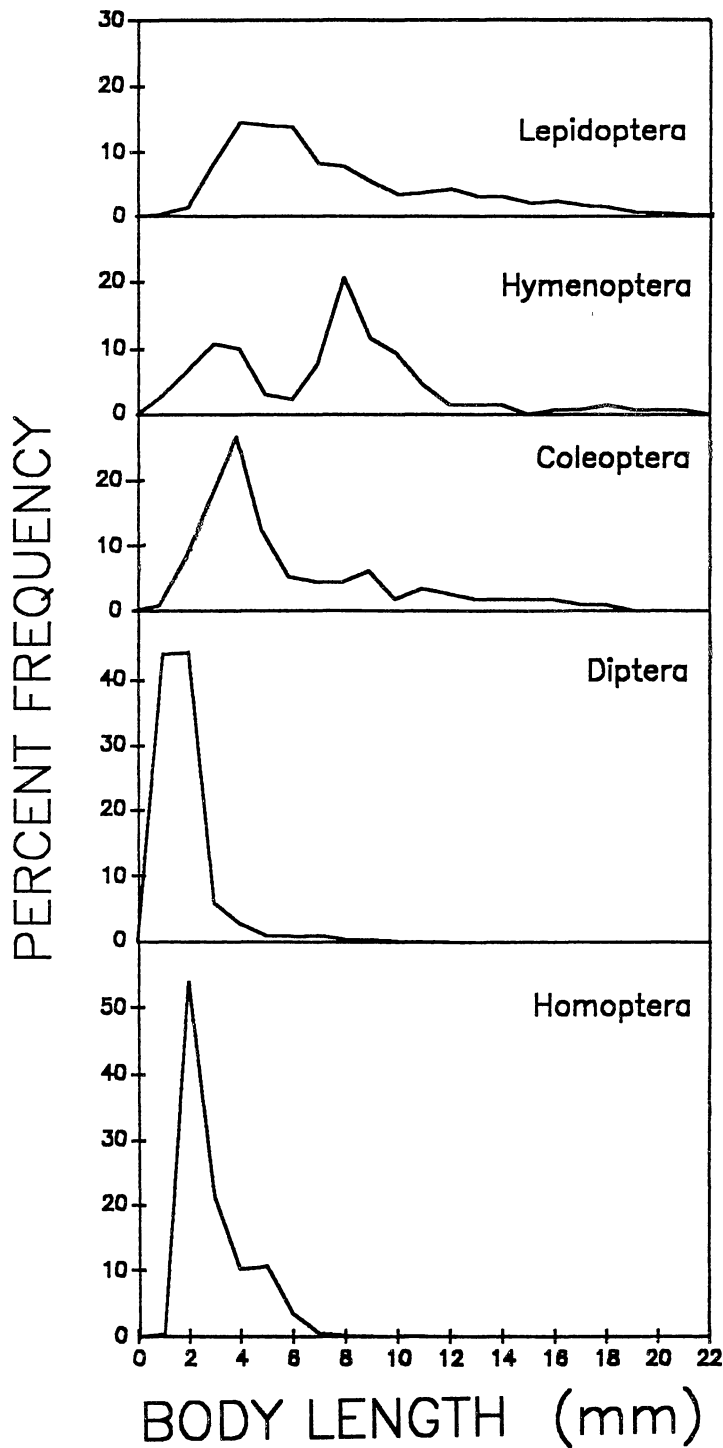


Fig. 11.--Distributions (percent frequency) of body lengths of Lepidoptera, Hymenoptera, Coleoptera, Diptera, and Homoptera captured in Malaise traps near caves occupied by *P. t. ingens*.

Cicadellidae in the sample; however, when insects <5 mm were removed from the analysis, homopterans were still avoided.

Coleopterans were consumed in proportion to their availability regardless of insect size ($P > 0.05$; Table 5). Hymenopterans were consumed in approximately the same proportion as their occurrence throughout the study period when all sizes were combined ($P > 0.05$). However, when insects ≥ 5 mm were considered, hymenopterans were avoided ($P < 0.01$).

DISCUSSION

Methodology

Choice of a method to sample insects is difficult because each trap type has inherent biases (Kunz, 1988). Suction traps tend to overrepresent smaller insects (Taylor, 1962) and light traps overrepresent positively phototaxic insects (Black, 1974). I chose Malaise traps to sample the insect fauna in an attempt to avoid the above biases; however, large Coleoptera and Hemiptera may be underrepresented by these traps (Juillet, 1963). For example, no Scarabaeidae were collected in the traps although I observed numerous June beetles during nights of insect sampling. Heavy-bodied Coleoptera probably flew into the net, fell to the ground, and escaped capture.

Although prey items may be observed in an undigested

form by examining stomach contents, the endangered status of P. t. ingens precluded sacrificing animals for dietary analysis. Instead, fecal contents were analyzed because guano could be collected in flyways and beneath the roost with minimal disturbance to the bats. I could seldom identify insect remains to family with confidence because P. t. ingens culled diagnostic hard-body parts (wings, elytra, and legs) prior to ingestion, and body parts that were ingested were highly fragmented. However, I could identify remains to order, except for a few cases where prey items were listed as unidentified (Table 4).

It may be unrealistic to attempt to classify fecal remains of insects beyond order. Kunz and Whitaker (1983) evaluated the reliability of fecal analysis for determining the diet of insectivorous bats. They concluded that reasonable estimates of prey consumption could be made; however, some insect orders fed to the bats were not always detected in the feces, and occasionally remains were misclassified. If I had attempted to classify insect fragments in the feces to the familial level, the number of errors probably would have increased.

Diet

Some insectivorous bats are opportunistic feeders and consume prey in proportion to relative availability or exploit dense swarms of insects (e.g., Belwood and Fenton,

1976; Eckrich and Neuweiler, 1988; Fenton and Morris, 1976). 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).

P. t. ingens preferentially selected lepidopterans over other available insects, which suggests that this subspecies is a moth strategist. Similar preferences have been observed for other subspecies of P. townsendii. Lepidoptera were found in 92.1% of the P. t. pallescens stomachs 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 P. t. virginianus guano (Dalton et al., 1986).

Although dipterans were the most abundant insects available, they were consumed significantly less than expected. Most noticeable was the absence of small flies in the guano, particularly the families Cecidomyiidae, Chironomidae, and Psychodidae which comprised 45.6%, 33.3%, and 5.5%, respectively, of the Diptera collected in Malaise traps. If these small flies were consumed by bats, it is likely that whole wings would have been present in guano. Similarly, Buchler (1976) reported a paucity of cecidomyiid flies in stomachs of Myotis lucifugus, despite their abundance in suction trap samples.

Flies ≥ 5 mm long were consumed in proportion to their availability. This suggests that perhaps not all insects collected in traps are regarded as suitable prey by bats. 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 which readily ate Cecidomyiidae fed to them in captivity (Buchler, 1976). Inability to detect small flies probably is not a problem as bats are able to detect and avoid wires < 0.2 mm in diameter.

Optimal foraging theory suggests that not all sizes of insects should be exploited. Bats should ignore small insects that yield less energy than their capture justifies. They also should avoid large insects that require considerable energy and time to handle (LaVal and LaVal, 1980). Insect 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).

Size of a bat also may determine, in part, the size of prey items consumed (Black, 1974; Buchler, 1976; Ross, 1967). Plecotus townsendii ingens is a relatively large vespertilionid bat (the summer mass of adult non-pregnant females was 11.5-14.5 g), which suggests that they should consume insects with body lengths ≥ 5 mm (Buchler, 1976).

Temporal Changes in Selectivity

Plecotus townsendii ingens preferentially consumed moths throughout the study, when I considered all sizes of potential prey. However, when insects <5 mm were removed from the analyses, preference for Lepidopterans was reduced in August and September (Table 5). This increase in dietary diversity may have been a response to decreased numbers of available insects. For example, Anthony and Kunz (1977) found that when insect abundance was high, adult female M. lucifugus selectively foraged on beetles and mayflies, which were uncommon in light trap samples. When insect availability was relatively low, females consumed 3-10 mm insects in proportion to their availability.

Food habits may vary according to sex, age, and reproductive condition of bats (e.g. Belwood and Fenton, 1976) and may vary temporally within the same night (Eckrich and Neuweiler, 1988). When food is scarce, bats should exhibit generalistic foraging strategies, and exhibit greater selectivity when prey items are abundant (Emlen, 1966; MacArthur and Pianka, 1966). Additional data need to be collected during winter to better document seasonal shifts in selectivity for P. t. ingens and throughout the year for bats of known sex and age.

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