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Editor: RICHARD F. JOHNSTON

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OCCASIONAL PAPERS

**of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas**

NUMBER 36, PAGES 1-24

APRIL 16, 1975

**POPULATION ECOLOGY OF THE GRAY BAT
(*MYOTIS GRISESCENS*): FACTORS INFLUENCING
EARLY GROWTH AND DEVELOPMENT**

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ABSTRACT

Female *Myotis grisescens* maintain high body temperatures at maternity roosts throughout the period of lactation, even at low ambient temperatures (13.9°C). The energetic cost of large differentials between body and ambient temperatures is greatly reduced by formation of large colonies, clustering behavior, and choice of roost configurations that maximize retention of dissipated body heat.

Growth rates of postnatal, preflight *M. grisescens* were studied at caves having a variety of ambient temperatures (13.9-26.3°C) and roost types, and numbers of young ranging from 600 to 22,100. Rates of weight gain varied from 0.20 to 0.39 gm/day and correlated best with the number of young bats present on a roost.

INTRODUCTION

Literature on the growth and development of bats is extensive; a partial listing includes studies under laboratory conditions (Orr, 1954; Jones, 1967; Kleiman, 1969; Kulzer, 1970; Maeda, 1972) as well as in the field (Pearson, Koford and Pearson, 1952; Davis, Barbour and Hassell, 1968; Davis, 1969; Dwyer, 1963, 1970; Krátky, 1970; Rakhmatulina, 1972; O'Farrell and Studier, 1973; Kunz, 1973, 1974). When growth rates between species have been compared, growth has been treated as though it were constant for each species, with little consideration given to the influence of environmental variables. Although rates of growth and development are known to be correlated with temperature (Eisentraut, 1937; Pearson, Koford and Pearson, 1952; Dwyer and Hamilton-Smith, 1965; Herreid, 1967; Kleiman, 1969; Racey, 1969; Orr, 1970), Kunz (1973, 1974) provided the only major papers which report even the approximate

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temperature conditions under which a study of growth was conducted. The relative importance to growth rate of other factors such as roost configuration, porosity of roost surface, colony size, and behavioral thermoregulation is virtually unknown.

Based on extensive observations of gray bat colonies in Alabama, Florida, Tennessee and Virginia from 1960 to 1968, I hypothesized that cave temperature and colony size were the most important factors affecting gray bat preflight growth and development. The purpose of this paper is to present the findings of my further investigation into the effect of temperature, as modified by roost configuration and surface porosity, colony size, and behavioral thermoregulation, on rates of growth in the young of a colonial species of cave bat.

DESCRIPTION OF STUDY AREA

Myotis grisescens is a monotypic species that occupies a limited geographic range in limestone karst areas of the southeastern United States. With only one known exception (Gunier and Elder, 1971) colonies are restricted to caves or cave-like habitats at all seasons. For the growth observations of this study, I visited summer colonies of gray bats in 56 caves from Jackson Co., Florida, north to Scott Co., Virginia, and west to Stewart Co., Tennessee, and Lauderdale Co., Alabama. Six caves exemplifying the range of variables to be observed were then chosen as primary study localities (Table 1). All are located in the Tennessee River drainage system in Alabama and Tennessee (Fig. 1), and occur in areas with the following kinds of potential natural vegetation as described by Kuehler (1964): Appalachian oak forest (cave nos. 9, 12, 25); oak-hickory-pine forest (38, 50); oak-hickory forest (41). Extensive areas of both forest and cultivated fields surround each site.

Within the geographic area of this study, differences in latitude (range 34° 37'N to 36° 29'N) and total cave length (63 m in cave 50 to more than 2000 m in cave 41) appear to affect cave temperatures less than factors such as elevation of the inner cave relative to entrance level, number and size of entrances, and presence of inflowing streams. Two localities provide examples of the effects of one or more of these characteristics.

Cave 50 is the smallest of the study localities, with an interior located above the elevation of its entrances. This heat trapping quality and small size combined would undoubtedly allow ambient cave temperature to be more easily modified by the heat produced by the bat colony found there, which is the largest one in the study. Indeed, the cave's 26°C temperature during the maternity period was at least 8°C above that of any other cave observed in the southeast, with the exception of a non-study cave containing a non-maternity colony of about 250,000 bats. Cave 38 is also small, but has its interior at a level below that of the entrances, allowing colder outside air to flow in and become trapped there during winter and

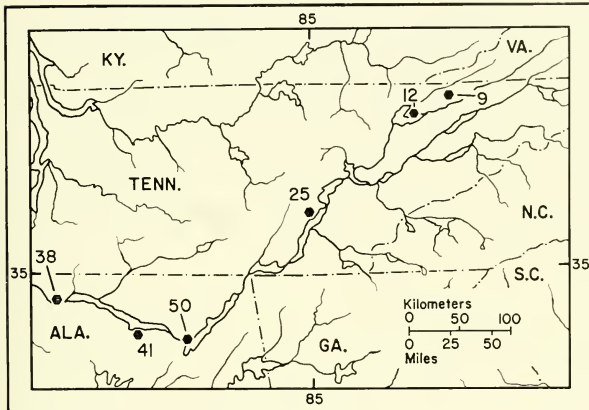


FIG. 1.—Locations of study caves in 1970.

spring. As a result, ambient temperature prior to the bats' arrival was only 12.8°C at the favored maternity roost. The cave was chosen for study in order to observe the effect of low temperature on juvenile growth rates. The specific characteristics of the room and roost chosen for maternity purposes, however, allowed the temperature to be changed markedly during the maternity period, as will be discussed later.

At all study caves maternity roosts were in high places on nearly horizontal or slightly domed ceilings. The roost in cave 38 was at the top of a large, noticeably domed area in such a ceiling. Air movement across all roosts appeared to be minimal. Surfaces of relatively porous limestone seemed to be preferred. Extended use

TABLE 1.—CHARACTERISTICS OF THE STUDY LOCALITIES: TEMPERATURE DATA FOR THE MATERNITY PERIOD OF 1970.

Locality Number	Ambient Cave Temperature (°C) ¹		Gray Bat Colony Size During Maternity Period ²		
			1969—Undisturbed Adults Only	1970—During Observation	
	Range	Mean	Adults Only	Adults	Young
9	18.3-18.9	18.5	18,000	13,700	3,800
12	13.9-13.9	13.9	12,000	1,000	600
25	15.9-17.0	16.4	7,000	3,700	2,200
38	16.6-17.2	16.9	38,000	16,500	9,800
41	16.8-17.3	16.9	15,000	5,200	2,600
50	25.1-27.2	26.3	50,000	28,400	22,100

¹ Temperature readings at 3 cm below the ceiling, 10 m from the maternity cluster.

² Estimates are rounded to the nearest hundred in 1970 and to the nearest thousand in 1969.

of these sites has resulted in darkly stained and deeply etched areas where the bats cluster; a combination of bat urine and claw abrasion appears to cause the ceiling to become pitted. The depth of the etchings varied from 5 mm in cave 50 to 30 mm in cave 41. Those in caves 9, 12, 25 and 38 all averaged roughly 15 mm. The limestone in cave 41 is so porous that the weight of clustered bats has occasionally pulled pieces more than 20 cm in diameter from the ceiling. This has resulted in the formation of numerous pockets where juveniles aggregate in exceptionally dense clusters. Encrusted urea may contribute additional roughness to the roost surface in all caves.

Mean relative humidity in the six caves studied ranged from 86% to 99%, but remained relatively constant at the nursery site within each cave. Means and ranges (rounded to nearest whole percentage) for each locality were: 9, 99% (97-100); 12, 88% (85-94); 25, 86% (82-89); 38, 93% (87-98); 41, 99% (98-99); 50, 97% (96-100).

MATERIALS AND METHODS

In 1970 each of the six study caves was visited at 10-day intervals from April (except for cave 50, first visited 31 May) through 6 August (caves 38 and 41 not visited after 25 and 2 July respectively), and at 13 to 15-day intervals thereafter through the time of the bats' departure in October. Parturition commenced within the period 28 May to 4 June at all colonies and was more than 98% completed in approximately 15 days in the smallest colonies (12 and 25) and in 17 days in the remainder. Postnatal preflight growth data were gathered on the following dates: cave 50 (31 May, 10, 20 June); cave 41 (2, 12, 22 June); cave 38 (5, 15, 25 June); cave 25 (6, 16, 26 June); cave 12 (7, 17, 27 June); cave 9 (8, 18, 28 June).

As long as roosts were occupied by young bats, a motor-driven psychrometer (Bendix Psychron), accurate to within 0.2°C, was used on each visit of the study to take temperature and humidity readings 3 cm below the clustered young and 3 cm below the ceiling at a distance of 10 m from the cluster. These measurements were made immediately after evening departure of the adults. Also, one 7-day Tempscribe Remote Reading Thermograph was concealed 6 m from the normally occupied maternity roost in each cave prior to the arrival of the bats from their hibernation site (cave 50 excepted). A capillary line extended along the ceiling to a temperature probe 1.3 cm wide by 7.6 cm long, which was suspended from the center of each roost. The proximal end hung 6 cm below the ceiling where it would be barely beyond the heads of the clustered bats. The thermograph recorders were sealed in plastic bags with desiccant, and charts were changed at 10-day intervals throughout the study period. At these times they were also calibrated to the psychrometer. Accuracy of the recorders was determined to be $\pm 1^\circ\text{C}$.

Instruments were installed around two weeks before the maternity roosts were first occupied, but many bats either chose alternate roosts, positioned themselves away from the temperature probe on the same roost, or moved to another cave. Kunz (1973) experienced similar problems when studying *Myotis velifer*. In the present study only one cluster formed immediately adjacent to a probe, at locality 25. This cluster, consisting mostly of near-term pregnant females, was monitored 19-23 May. At locality 12 a thermometer was moved to a cluster of well-developed young on 7 July, and temperature was recorded until the bats changed to a different roost on the 13th. The chart readings (Fig. 2) are from these localities. All other attempts to record temperature from temperature probes failed.

At each visit to a colony, a bat trap (Tuttle, 1974a) was positioned near the cave entrance prior to emergence for the purpose of sampling the weight, reproductive condition and sex ratios of adults. Growth data were collected at the roosts only after normal evening departure of the adults and prior to their return about 1½ hours later. Maternity sites in caves 12 and 25 could be reached from a ladder, permitting observation of newborn bats and comparison of growth rates of banded cohorts. I followed Davis (1969) in assuming that neonates with attached umbilical cords were approximately one day old. On the evening of 6 June, 27 such neonates were banded at locality 25. This cohort provided a basis for comparison with 50 neonates with attached umbilical cords which were banded the following day at locality 12.

Roosts in caves 9, 38, 41 and 50 were either more than 5 m above the floor or at least partially over deep water. Consequently, growth rates in these colonies were determined by sampling mean colony growth through the capture of unbanded young of unknown age. Both absolute and mean growth data were collected at locality 25 in order to compare the amount of difference in results gathered with the two methods. With the exception of the 2 June sample from locality 41 ($N = 15$) and the 6 June sample from 25 ($N = 24$), all samples numbered from 26 to 48. Each sample consisted of young from near the cluster's edge as well as from the center, and care was taken to avoid sampling bias. In both mean growth and banded cohort sampling each individual was placed in a small plastic container and weighed to the nearest 0.1 gm on an Ohaus triple beam balance. Forearms were measured to the nearest 0.5 mm with a steel rule.

Growth rates, R , were calculated from the formula $R = (\bar{Y}_2 - \bar{Y}_1) + (\bar{Y}_3 - \bar{Y}_2)/20$ where \bar{Y}_1 , \bar{Y}_2 , and \bar{Y}_3 are the 3 samples, 10 days apart. Growth was approximately linear during the 20-day period, but the two 10-day values were averaged to alleviate possible sampling bias. I did not find weight gain in *Myotis grisescens* to be more linear

than forearm growth during the first 20 days after birth, as has been reported for *M. velifer* (Kunz, 1973). However, although forearm comparisons produced similar results, weight data appeared to show the effects of environmental variables more clearly and are used for all growth comparisons. Forearm length was used in computing the probable time of first flight in caves 12 and 25 (Fig. 5). The smallest forearm length found among 60 newly flying juveniles from these caves was 39.5 mm, with the majority being at least 40 mm. The amount of time necessary to reach 39.5 mm was then extrapolated from the mean rate of increase in forearm length in each colony.

The number of juveniles present on each roost was calculated by multiplying the area covered by juveniles times the estimated number per unit area. The mean density found in hand-netted clusters of adults and juveniles after the maternity period was 1828/m², with a range of 999-2575/m² depending on roughness of roost surface and temperature (16 samples taken). The smaller young were estimated to cluster in densities of from 1000 to 3300/m², but since it was not possible to check the accuracy of these estimates by making actual counts of the numbers of young due to the extreme disturbance which would have resulted, these figures could be as much as 25% low. Estimates based on this method were repeatable to within approximately $\pm 10\%$.

Estimating the number of adults in the colonies was difficult due to a number of factors. Maternity colonies of the gray bat cannot be approached for direct area estimates while the adults are present without danger of causing heavy mortality of the young, which are frequently dropped by escaping parents. Water and highly irregular floors beneath the roosts prevented estimates based on the area covered by recent guano, and emergence counts were not practical where there were multiple exits or dense foliage near exits. Although one or the other of the latter two methods could have been used at any one site, no one of these methods was possible at all sites. For consistency among colonies, then, only a fourth method was utilized.

Since the gray bat female bears only one young per season, the number of juveniles on the roost can be assumed to equal the number of lactating females during the period when no young are flying. The number of adults present was therefore calculated from the formula $NC = JR \times AT/LT$ where JR equals the number of juveniles estimated to be on the roost, LT equals the number of lactating females trapped at the cave entrance, AT equals the total number of adults and yearlings trapped, and NC equals the total colony size excluding juveniles. Total adult sample sizes from the traps ranged from 90 to 210, with a mean of 131. I believe that any bias that may

have resulted from this method was similar for all colonies and therefore of little consequence for the purpose of this study.

As noted above, maternity colonies of gray bats are very easily disturbed. Early in the maternity period of 1968, other investigators had severely disturbed the colony of approximately 12,000 adults in cave 12, and most of the females had removed their young to another cave. The remainder of the colony (ca. 1000) moved from the usual site to an alternate, less favorable roost to rear their young. Both colony size and roost choice had returned to normal in 1969. During the 1970 study I intentionally disturbed the preferred roost again in order to observe growth of young on the alternate roost, which appeared to be more fully exposed to the low ambient cave temperature. However, after the onset of parturition great care was taken to avoid disturbing any of the colonies; even so, some bats still moved. Many switched to alternate caves during the period of study in 1970, resulting in markedly reduced colony sizes at study sites as shown in Table 1. By 1971, however, the study colonies had returned to near-normal size.

HYPOTHESIS AND PREDICTIONS

The hypothesis tested was that postnatal preflight growth rate in the gray bat is proportional to temperature when colony size is constant, or is proportional to colony size when temperature is constant, assuming comparable roost conditions. The importance of increasing colony size is to increase total heat production and to reduce heat loss to clustered individuals; roost conditions also influence the amount of heat loss, as will be discussed later. Prior to the beginning of the 1970 growth studies I planned several specific comparisons and predicted their results. As already mentioned, I intentionally caused a temporary reduction in colony size in cave 12 and forced the bats to move to a position more directly exposed to low ambient temperature. I then predicted that growth rates in this colony would be much slower than those observed in cave 25, where both colony size and roost temperature were greater. I also predicted that growth in cave 50 would be the most rapid of the six colonies due to its combination of high temperature and exceptionally large colony size.

I was uncertain of the outcome at cave 9 due to the fact that adults of this colony were known to travel an exceptionally long distance to forage nightly (Tuttle, 1974b). The effect of this added energy expenditure was unknown. Preflight growth in 9 was predicted to be faster than in 25 and slower than in 50, since the colony was intermediate between the two in both size and temperature conditions. The colony in cave 41 was larger and at a higher temperature than the one at 25, but smaller and at a lower temperature than colony 9. Therefore, I predicted that its growth rate would fall between those of 25 and 9.

Prior to 1970 I had visited cave 38 only once, when few bats were present, and had estimated colony size based on the area covered by recent guano. Having observed that the ambient temperature of this cave while unoccupied approximated that of cave 12, I decided to compare these two for the effect of colony size at similar temperatures. Since its colony was larger than any except that of locality 50, my prediction was that growth rate in cave 38 would far exceed that at 12, and be greater than that of 25. Overall then, colonies were predicted to have the following order of growth rates, low to high: 12, 25, 38, 41, 9, 50.

RESULTS

Temperature and thermoregulation.—Psychrometer temperature readings 3 cm below the young tended to be influenced by the immediate excitation level of each cluster and were too variable to be meaningful. Even ambient cave temperatures at a distance from a cluster were strongly influenced by the bats. However, it was obviously the temperature as modified by the colony's presence to which the juveniles were exposed, rather than the unoccupied cave temperature. Although they were not the most meaningful, ambient readings 10 m from the maternity clusters during the maternity period appeared to provide the most reliable information, and were used for all subsequent inter-colony temperature comparisons. These ambient temperatures remained virtually constant in all six caves during the period of preflight growth (Table 1), with fluctuations averaging only 0.8°C (range $0.0\text{--}2.1^{\circ}\text{C}$) over the entire time. Bats in only two colonies (38 and 50) detectably raised the ambient cave temperature at a distance of 10 m from the roost, and most of this change occurred before parturition.

Although ambient temperature in cave 50 probably rose sharply soon after the arrival of the bats, I was unable to visit the cave early enough to record this event. In cave 38, however, temperature changes were documented. Before the bats arrived in mid-April, the temperature in the room containing the unoccupied maternity roost was 12.8°C . At a non-roost area 20 m away the temperature was 11.7°C . The non-roost site was at approximately the same level and distance from the cave entrance, but was shielded from warmer air in the roosting area by a low place in the ceiling. Low position relative to the entrance shielded both areas from outside fluctuations of the warmer summer air. Roughly 7 days after the arrival of bats, the temperature in the same room (14 m in diameter and 2-5 m high) 10 m from the roost had risen to 15.6°C and that at the non-roost site to 12.4°C . By 25 June ambient temperature in the roost room had risen to 17.2°C as opposed to only 14.2°C in the non-roost area. Temperature 3 cm below the edge of the clustered young was 19.4°C while 21.7°C was recorded 3 cm below the center of the cluster (psychrometer values).

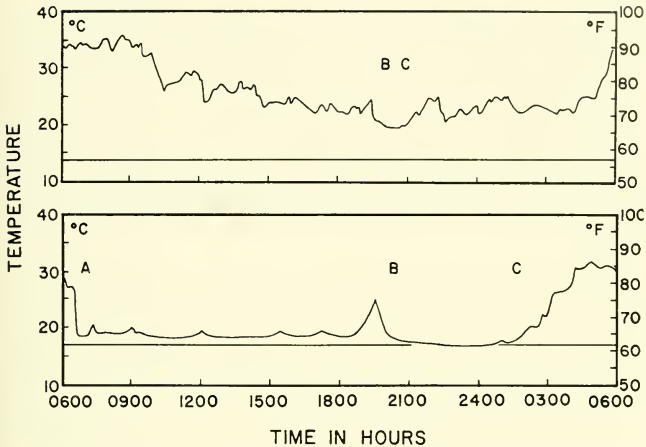


FIG. 2.—Microenvironmental temperatures recorded immediately below two roosts within a 24-hour period. Upper chart: the temperature fluctuations below a cluster of nursing females and their young, cave 12, 11-12 July. Lower chart: readings below a cluster of pregnant females prior to parturition, cave 25, 20-21 May. The straight line indicates ambient cave temperature in each case. In the lower chart point A marks the time when the bats fell into torpor. In both charts the approximate time of evening emergence (B) and time of first return of adults to the roost (C) are indicated.

The continuous daily fluctuation of temperature immediately below clusters of bats was recorded by temperature probes in two instances (Fig. 2), as mentioned previously. The bottom chart shows 24 hours of temperature change in cave 25 as recorded below a cluster of pregnant females 7 days prior to first parturition. It indicates a drop of roughly 10°C in less than 30 minutes following return of the last bats to the roost at dawn (A), whereupon they became torpid. Thereafter, the temperature just below the cluster remained about 2°C above ambient, except for regular periods of slight increase, until about one hour prior to emergence. Following a 7°C rise in temperature to 25°C the bats departed (B), and the roost returned to ambient. A few bats returned by 0100, but the main return to the roost did not begin until around 0200 (C). Temperature then rose almost constantly to 33°C just before 0500, and remained above 27°C until the last bats had returned between 0615 and 0630.

The upper chart in Figure 2 shows a 24-hour record of temperature below a cluster of nursing females and their young in cave 12. Some of these young first flew 6 days later. In spite of the lower

ambient temperature in this cave, the bats maintained a roost temperature of 34-36°C for more than 3 hours after the final return of adults at dawn. Thereafter, temperature gradually decreased throughout the day, but never fell below 22°C until after the evening emergence of adults (B). Just prior to the return of some of the adults (C) the roost temperature fell to its lowest point (19.2°C) in the 24-hour cycle). Even this point, however, is 5°C above ambient, and the daily mean was more than 10°C greater than ambient. It can also be seen that adults began returning from foraging up to 5 hours earlier at the location where young were present.

Although I never closely approached maternity colonies during the day, I could easily listen to colonies 25, 38 and 50 from the cave entrances; they were always active and noisy, regardless of the time of day. It is assumed that colonies 9, 12 and 41 also remained active, and this contention is strongly supported by the tempscribe recording of roost temperature in cave 12. In contrast, males and non-reproductive females were frequently found in a torpid condition when roosting in caves with ambient temperatures below 16°C, and tended to be less active even at higher temperatures.

Since my activities at maternity sites caused some disturbed mothers to remove their offspring from their normal roosts to "bachelor" roosts in nearby caves, it was possible to observe activity levels of females and young in a nonmaternity colony. On 16 June I found a cluster of 544 bats which contained 24 mothers (6 captured and banded previously at cave 25) with young, 9 pregnant females, and 487 other adult and yearling bats without young in an alternate cave used by the colony from cave 25. Ambient temperature was 13.6°C. In this case, all of the 544 bats present were torpid and required several minutes to arouse.

Growth.—From a sample of 94 newborn bats from 6 caves, the mean weight (\pm S.D.) at birth was calculated to be 2.9 ± 0.24 gm (range 2.4-3.4; no significant difference between males and females). Mean weights (in gm) of unbanded young in the three successive samples taken at 10-day intervals in the five caves were as follows: cave 50 (2.99, 4.91, 7.34); 41 (3.20, 5.68, 7.45); 38 (3.35, 6.04; 7.12); 25 (3.91, 5.29, 6.79); 9 (3.42, 5.08, 6.82). Mean weights of the banded cohort samples of newborn bats were 3.01, 5.17 and 6.99 at colony 12, and 3.00, 5.80, and 8.00 at colony 25.

As noted previously, the growth rate at colony 25 was calculated from both colony and banded cohort means; an average weight gain of 0.25 gm/day was found for the banded cohort of known age as opposed to 0.14 gm/day for the colony mean, taken from randomly sampled unbanded young. This indicated that growth rates calculated from the colony mean underestimated the average rate of individual growth by 57.6%, primarily due to continued parturition

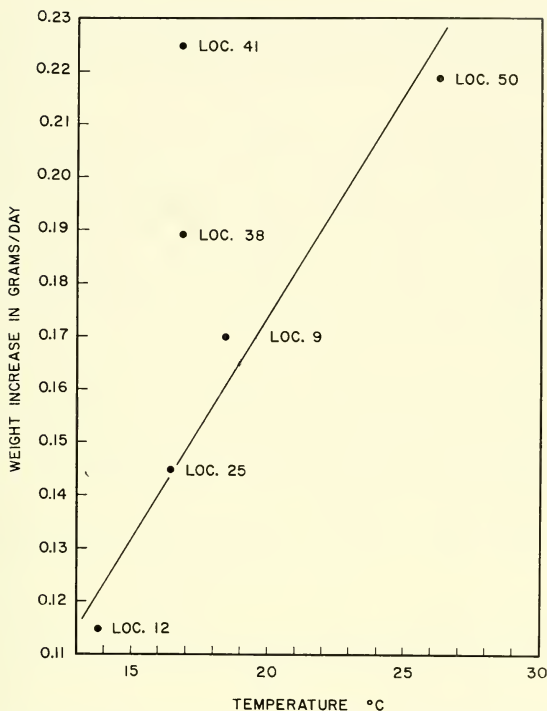


FIG. 3.—The relationship between ambient cave temperature and rate of weight increase of preflight young in the six study localities. Growth rate values are taken from colony means. Line fitted by eye to points 12, 25, 9, and 50.

and the resultant inclusion of newborn in the samples. Thus, in order to compare the rate of growth in cave 12, where the banded cohort method was used exclusively, with rates observed in other caves, where calculations were based on samples of colony means, I multiplied the actual individual rate in cave 12 (0.20 gm/day) by 0.576. This gave the value of 0.12 used in Figures 3 and 4.

Pending further comparison of the two methods for calculating growth rates, all rates presented in Figures 3 and 4 should be divided by 0.576 before being compared to rates from other studies based on individuals of known age. This results in the following rates of weight gain (colony means and corrected values, in gm/day) for the six caves studied: (9) 0.17, 0.30; (12) 0.12, 0.20; (25) 0.14, 0.25; (38) 0.19, 0.33; (41) 0.22, 0.39; (50) 0.22, 0.38.

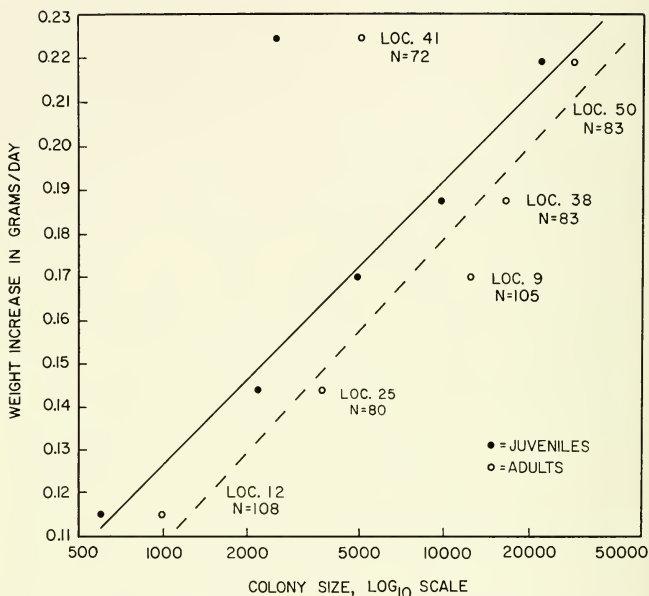


FIG. 4.—A comparison of adult colony size (broken line, open figures) and numbers of preflight young (solid line, closed figures) with the rate of juvenile weight increase in the six colonies. Growth rate values are taken from colony means. Lines fitted by eye.

Growth comparisons among the six caves, using means from samples of bats having a maximum age difference of 17 days, indicated a wide range of rates. Although there seemed to be a linear relationship between rate of weight gain and ambient temperature in caves 9, 12, 25 and 50, caves 38 and 41 were exceptions (Fig. 3). When rates of weight gain were then compared with the number of young on each roost (Fig. 4), an approximately linear relationship was evident, with the exception of cave 41. Lacking enough evidence to do otherwise, I have fitted a straight line to the points in Figure 4 which represent adult colony size. However, it is possible (Fig. 4) that large colonies are capable of raising ambient cave temperatures proportionally more than small ones, yielding a curvilinear relationship between adult colony size and juvenile growth.

Banded cohorts of known age were compared between colonies in caves 12 and 25 and were found to differ significantly (no overlap of 95% confidence limits after first weighing), with weight gain

in cave 25 more rapid than that in cave 12 (Fig. 5). Juveniles from cave 25 were calculated to be able to fly first when 24 days old as compared with 33 days to first flight for cave 12, a difference of 9 days.

DISCUSSION

Temperature and thermoregulation.—Previous authors, reviewed most recently by Henshaw (1970) and Lyman (1970), have concluded that, although tropical microchiropterans may remain homeothermic during periods of inactivity, temperate species undergo torpor during diurnal rest. Henshaw stated that "Most of the temperate zone bats occurring in North America and Europe have been studied; each has been found to hibernate in the classical pattern during the winter, and also to become torpid whenever they were inactive. In each case body temperature declined almost to the ambient temperature."

The rationale for assuming that temperate bats fail to maintain high body temperature at rest is the energy cost. The high cost of homeothermy is unquestioned (Herreid, 1963a, b; Stones, 1965; Arata, 1972; McNab, 1973). Stones (1965) found that *Myotis lucifugus* required three times as much food at 70-78°F (21-26°C) as

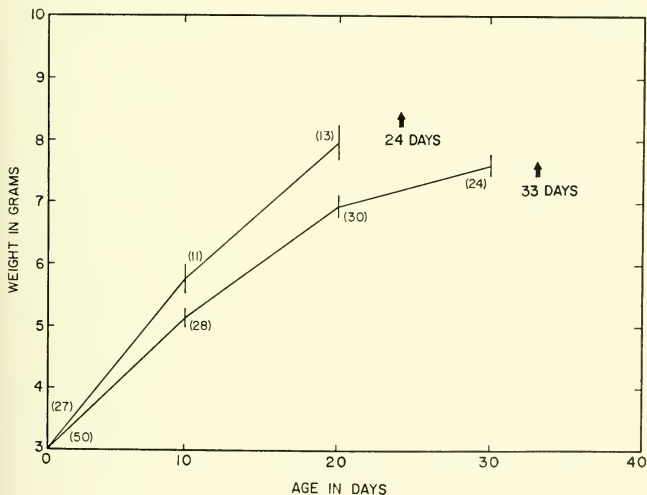


FIG. 5.—A comparison of weight gain of banded cohorts from colonies 12 (lower line) and 25 (upper line). Vertical bars indicate 95% confidence limits. Arrows mark the estimated time of first flight. Sample sizes are enclosed in parentheses.

they did at 92°F (33°C). Studier, Lysengen and O'Farrell (1973) calculated the cost of lactation in *M. lucifugus* and *M. thysanodes* and concluded that these species could not afford to remain homeothermic concurrent with this process. Stones and Wiebers (1967) have, however, demonstrated that *M. lucifugus* can remain homeothermic during lactation if provided with adequate nutrition. Although Lyman (1970) concluded that temperate microchiropterans seemed to fall into torpor at rest, he noted that nearly all of the studies reviewed were done under laboratory conditions. Both Henshaw and Lyman stressed that there are many sources of serious error in laboratory studies, especially when extrapolating from them to the natural behavior of colonial species.

One major error would be introduced if thermoregulatory activities were induced by stimuli not present in the laboratory. This has been suggested by Herreid (1967). As he observed, "In the laboratory test the bats, in a postabsorptive state and lacking stimulation by environmental changes, tended to remain at the lower end of their metabolic range while bats in the cave were comparatively active." The instance during my study of nursing females taking their young from the maternity colony at cave 25 to a non-maternity roost in another cave is consistent with Herreid's observation. Whereas bats in all maternity colonies were found to remain active when non-volant young were present, maintaining high roost temperatures, the displaced females fell into torpor along with the surrounding, "non-regulating bats." This behavior has important implications for those conducting or interpreting laboratory thermoregulatory studies.

Unfortunately, little effort has been made to study thermoregulation under natural conditions. In the two cave-dwelling species that have been investigated in the field, *Tadarida brasiliensis* (Herreid and Schmidt-Nielsen, 1966) and *Miniopterus schreibersi* (Dwyer, 1964), a high degree of homeothermy has been demonstrated in maternity colonies. Both, however, appear to be of tropical origin (Dwyer and Hamilton-Smith, 1965), which has been used to explain their homeothermic ability. The former species migrates to warmer southern latitudes for winter (Cockrum, 1969), whereas the latter appears to hibernate locally (Dwyer, 1966).

Myotis grisescens, however, appears to be of temperate origin. This is suggested by its regular fall movements of more than 430 km from subtropical southern climates in Florida to hibernation caves in the colder North (Tuttle, 1974c). In addition to reversing the usual direction of subtropical or tropical migratory species' movement (toward warmer climates), *M. grisescens* selects the coldest hibernating caves of all the *Myotis* found in the range of my study. A laboratory study by Stones and Wiebers (1967) indicates that another species of probable temperate origin, *M. lucifugus*, can

maintain high body temperature at an ambient temperature of 22°C, and Harmata (1969) reports that a large maternity colony of *Myotis myotis* remained active in a cave where the ambient temperature was only 8-9°C. Kunz (1973) gives evidence of thermoregulation in a large (5000) colony of *M. velifer* in a barn and suggests similar ability for a cave colony of equal size. The area of origin of this species is uncertain.

The thermoregulatory ability of the gray bat is verified by the tempscribe recordings (Fig. 2, upper chart) taken from the maternity colony in cave 12. This exceptionally small colony of only 600 young and 1000 adults had been forced to occupy a relatively exposed site where potential for heat retention was minimal. In spite of this unusual stress, at an ambient temperature of only 13.9°C, they clearly were able to maintain roost temperatures well above ambient. For the first 3 hours after return of the adults at dawn a differential of roughly 21°C was maintained over ambient temperature, and a difference of 5°C persisted even during the period after all adults left to feed. Since the temperature probe monitored only the air temperature immediately below the cluster, it is assumed that these are minimal readings, underestimating the actual homeothermic ability of these bats.

In contrast, there was an almost immediate drop in temperature (Fig. 2, lower chart) below a cluster of near-term pregnant females that apparently fell into torpor soon after coming to rest in cave 25 where ambient temperature was nearly 17°C. The only apparent difference in roost conditions of colonies 12 and 25 was the higher ambient temperature of the latter. Thus, in spite of the much larger colony size in cave 25 in comparison to colony 12, temperature rapidly approached ambient when the bats in the cluster ceased to regulate their temperature at a high level. Clearly the high temperatures recorded in cave 12 are the result of active regulation and not simply the result of passive failure of clustered bats to dissipate heat.

To my knowledge, tempscribe recordings from colony 12 provide the first conclusive evidence of homeothermic ability in a temperate bat species under natural cave conditions. Of particular interest is the fact that these conditions (small colony, 13.9°C ambient temperature) were quite stressful. The assumption that temperate microchiropterans lack the ability to remain homeothermic at rest obviously must be reevaluated. It is my contention, based on the results of this study, that not only does active thermoregulation occur in temperate cave-dwelling bats despite the energetic cost, but also that normal growth of young bats in cold environments would not be possible in the absence of homeothermy in the lactating adults.

If this is so, it is evident that adaptations conserving energy

through reduction of heat loss must be strongly selected for in species that form maternity colonies in environments as cold as temperate region caves. Species that rear their young in cave environments characteristically form large maternity colonies, which often raise cave temperatures significantly. This has been observed repeatedly in *Tadarida brasiliensis* (Cagle, 1950; Henshaw, 1960; Davis, Herreid and Short, 1962; Herreid, 1963b) and also in *Miniopterus schreibersi* (Dwyer, 1963; Dwyer and Hamilton-Smith, 1965) and *Myotis austroriparius* (Rice, 1957). Dwyer and Hamilton-Smith (1965) noted the importance of colony size in relation to increasing air temperature.

Clustering is an adaptation that greatly decreases heat loss and aids in maintenance of high body temperatures (Herreid, 1963b; Fenton, 1970; Kunz, 1973). This in turn leads to greater efficiency of digestion and assimilation of food (Twente, 1955) and promotes rapid rates of growth (Davis, Herreid and Short, 1962; Dwyer, 1963; Dwyer and Hamilton-Smith, 1965; Watkins, 1972). Herreid (1967) found that solitary individuals of *Tadarida brasiliensis* used much more energy in maintenance than did groups of either young or adults. Moreover, he noted that "a group of four used 3.5 times as much oxygen per gram as a group of 16." Twente (1955) pointed out the strong tendency of bats in general toward increased clustering behavior during lactation, and the marked clustering behavior of young bats is well known. Dwyer (1966) concluded that "ambient temperature plays a dominant role in the biology of *M. schreibersi*," and stated that "temperature selection behavior, clustering and modification of roost temperatures (especially at maternity colonies), when combined with body temperature regulation (Dwyer, 1964) seem to be appropriate adaptations to [low cave temperatures]."

My study indicates that, under some circumstances, choice of roosting sites with maximal heat retention properties may be as important as colony size and clustering. The importance of such factors is probably inversely proportional to colony size. Maximization of heat retention is achieved by choice of roosting places located in small chambers (Dwyer, 1963), in high places in domed ceilings (Davis, Herreid and Short, 1962) or in domes or small pockets within these locations (Dwyer, 1963; Dwyer and Hamilton-Smith, 1965; Dwyer and Harris, 1972). In addition, Twente (1955) observed that the degree of roughness of the roost surface and surrounding cave walls is important in breaking up possible air currents. My observations indicate that depth of etching and porosity of the rock surface from which the bats hang may also be of considerable importance. Accordingly, Twente noted that metabolic heat is readily lost to cave walls, which have much higher heat

conductivity than either air or water (conductivity increasing with wall density).

It is evident that through clustering behavior and selection of certain roost site configurations, bats can markedly alter the micro-environment to which young are exposed. For this reason ambient cave temperature at a distance of 10 m from the roost cannot adequately reflect the actual temperature faced by the young, and one would expect to find growth rates exceptionally high wherever colonies are able to find roosts in heat-trapping domes or in other places affording maximal opportunity for microenvironmental alteration. I believe that this can explain an apparent contradiction in the literature to the hypothesized effect of temperature on growth.

In his 1973 study, Kunz speculated that growth rates in *M. velifer* would be affected by ambient temperature but found no significant growth difference between maternity colonies in a barn (averaging 30°C, ranging from 24-36°C) and in a cave (20°C). This is not surprising since a number of the potentially important variables were not considered. The colonies were of equal size, but only the colony in the cave was able to form a single large cluster; the barn colony was spread out, roosting between a number of separate joists supporting a loft floor. Although the average differential between body and ambient temperature was more than 5°C less in the barn than in the cave, an apparent advantage, the relative effects of differences in cluster size and in the heat-retaining properties of the two roosts were not investigated. It is interesting to note, however, that the preflight growth rate in the cave colony of *M. velifer* (0.36 gm/day) was only 0.025 gm/day more rapid than would have been predicted (Fig. 3) for *M. grisescens* at the same ambient temperature. Also, it is only 0.031 gm/day above the expected value based on colony size (Fig. 4). Kunz's growth rate was multiplied by 0.576 for these comparisons, as explained earlier.

Growth.—The fact that the various caves were visited as much as 9 days apart for each sampling was considered a potential source of bias favoring those caves visited later. Since the mean weights at the first sampling over a period of 9 days gave a colony rank order (low to high) of 50, 41, 38, 9, 25 and the order of visitation (first to last) was 50, 41, 38, 25, 9, it is apparent that some bias could have been involved. In particular, if young of all colonies reached a uniform final weight this would have biased the growth rate calculations considerably. However, mean weights at the final preflight samplings 20 days later for each cave were quite varied, and although the order of visitation (again over a period of 9 days) was the same as at the first sampling, the mean weights (low to high) gave a rank order of 25, 9, 38, 50, 41, almost completely reversed.

Furthermore, when the difference between the estimated birth weight of 2.9 gm and the final mean weight (of unbanded young)

was divided by the number of days from May 31 (median date on which parturition began) to the final sample, an order of growth rates (low to high) of 9, 25, 38, 41, 50 was obtained. This differed by two reversals from the order (low to high) of 25, 9, 38, 50, 41, calculated from the formula used in this paper. Rates of colonies 50 and 41, although reversed, were similar with both methods, and the growth rate of 41 remained exceptionally high in relation to its colony size and ambient temperature in these calculations.

The other reversal was suspect; colony 25 was sampled before 9 but had a considerably higher first mean weight, indicating that parturition at cave 25 might have commenced earlier in the 7-day period than it did at 9. Indeed, newborn young were found on the roost in colony 25 3 days earlier than at colony 9. If these adjustments are made in the calculations, the order for these two colonies then matches that presented in Figures 3 and 4. In any case, the method described in this paragraph provides evidence that weight at the first sample and date of visit did not introduce major bias into the comparison of growth rates. Obviously, both methods of calculating the mean colony growth rates are only approximations; since estimates of parturition dates were so difficult and made such a difference in the results with the method described above, the original formula (utilizing sample means and the number of days between the samples) was used to calculate all figures presented on means of unbanded young.

When preflight growth rates from colony means in this study are adjusted to individual growth rates as previously described, they fall well within the range obtained by other investigators. I found a range of weight gain (rounded to the nearest hundredth) of from 0.20 to 0.39 gm/day for *M. grisescens*, while rates for other species studied under natural conditions have varied as follows (in gm/day): *Eptesicus fuscus*, 0.3-0.4 (Davis, Barbour and Hassell, 1968); *Antrozous pallidus*, 0.3-0.4 (Davis, 1969); *Pipistrellus pipistrellus*, 0.11 (Rakhmatulina, 1972); *Myotis velifer*, 0.36 (Kunz, 1973); *Myotis thysanodes*, 0.33 (O'Farrell and Studier, 1973). In a laboratory study Kleiman (1969) found mean growth rates (in gm/day) of approximately 0.6 for *Nyctalus noctula*, 0.4 for *P. pipistrellus* and 0.9 for *Eptesicus serotinus*. These are the highest rates yet reported and may reflect unnatural laboratory advantages (compare Kleiman's 0.4 rate for *P. pipistrellus* with the field study value of 0.11 above; see also Jones, 1967). The range of 0.1 to 0.4 reported for *P. pipistrellus* and the range of 0.20 to 0.39 found in this study for *M. grisescens* clearly demonstrate the fallacy of assuming that any particular growth rate is typical of a species.

Even for a single colony the mean rate of growth may not be constant from year to year. Although parturition dates appeared to remain relatively constant during these years, young in colony 12

grew slowly in 1968 (20% flying, 9 July), rapidly in 1969 (50% flying, 1 July and all flying before 10 July), and slowly again in 1970 (35% flying, 7 July). Although ambient cave temperature varied only 1°C in the three years, juvenile colony size was 500 in 1968, 4000 in 1969, and 600 in 1970 (fluctuation caused by disturbance, as discussed previously). In 1968 and 1970 additional stress resulted when this colony was forced to roost on a horizontal ceiling rather than its normal rough-surfaced dome roost. It would appear, then, that the primary variables during these different years were colony size and roost conditions, which greatly affected temperatures at the roost.

In 1969 juvenile colony sizes were approximately equal but the adult colony at 25 was 42% smaller than at 12. Visual inspection of the clustered preflight young in the two caves on consecutive evenings indicated that the mean growth rate of colony 25 was slightly lower than that of 12. However, in 1970 both juvenile and adult colony size at 25 was 73% larger than that at 12. Ambient temperatures were constant in both caves from 1969 to 1970, with cave 25 2.5°C higher than cave 12. When the absolute growth rates of banded cohorts were observed in 1970, growth in colony 25 was significantly more rapid than that in 12 as predicted, and young in the former flew in 24 days, 9 days earlier than the young of colony 12 (Fig. 5). In this case, colony size and roost choice were again the major factors changing from one year to the next.

With the important effects of roost configuration, porosity of roost surface, colony size and behavioral thermoregulation on micro-environmental roost temperature in mind, it is now possible to interpret the test of my original hypothesis. The observed increasing order of growth rates in my six study caves (12, 25, 9, 38, 50, 41) differed somewhat from the predicted order (12, 25, 38, 41, 9, 50), with the young in caves 38 and 41 exceeding expectations. When rates are compared with ambient temperature (Fig. 3), those in both caves exceed expected values; however, when compared with colony size (Fig. 4), only growth in cave 41 remains exceptional. It appears from these comparisons that colony size is more predictive of growth rate than is ambient cave temperature, which is itself influenced by colony size. It also seems evident that juvenile colony size is a better indicator of potential growth rate than are adult numbers.

The great impact of colony size on growth is accentuated by one of the exceptions to my predictions. Although I placed colony 38 ahead of 25 solely because of the former's larger size, the growth rate of 38 in actuality surpassed that of colony 9 as well. Both of these colonies (9 and 25) were at higher ambient temperatures but were smaller in size than 38. As noted before, the relatively large colony (9800 young) in cave 38 occupied a domed area where the

young were able to maintain high temperature within a restricted area, also contributing to the high growth rate.

The other colony (41) that was an exception to my predictions was relatively small (2600 young) as well as roosting in a cave of moderately low ambient temperature (16.9°C). Factors other than colony size and cave temperature must account for its rate of growth, which was unexpectedly high in both methods of calculating colony means. The maternity roost in cave 41 differed from all others in this study in that it was located on an exceptionally porous surface where the young clustered in pockets 20 cm in diameter at the highest point of a domed ceiling. Within these rough-surfaced pockets young bats were able to cluster at least 25% more densely than was possible at other sites. The very rapid growth of this small colony can be explained, then, by the ideal heat-trapping nature of the roost in association with increased clustering density. Colonies in caves 9, 12, 25 and 50 were much more comparable to one another in that roost surfaces were similar, lacking special heat-trapping pockets. It is apparent that in these caves, growth was correlated with both ambient temperature and colony size.

Concluding remarks.—Although it is not usually necessary or possible for any one colony to find a roost that is characterized by all of the heat conserving factors mentioned above, it is clear that the intensity of selection for these factors will increase greatly with reduction of either colony size or ambient temperature. It can be predicted, then, that the greatest diversity of bat roosting behavior will be found in caves of relatively high ambient temperature, or in those occupied by colonies large enough to modify temperature in spite of some unfavorable conditions.

At least one additional trend should be observed if I am correct in assuming that homeothermy is essential to the growth and development of the preflight young of cave-dwelling bats. The proportion of species rearing young in caves should be greatest in warm regions of the earth and decrease with increasing latitude. Decrease in cave occupancy during the maternity period would reflect the rising metabolic demands imposed by maintenance of increasingly large differentials between body and ambient temperatures (Dwyer, 1971).

In North America only five species of the genus *Myotis* are thought to prefer caves for the rearing of young. Three, *M. thysanodes*, *M. velifer* and *M. yumanensis*, occupy caves of the southwest and two, *M. austroriparius* and *M. grisescens*, occur in the southeast (Barbour and Davis, 1969). Of these, only *M. grisescens* is normally restricted to caves (Hall and Wilson, 1966). *M. velifer* appears to prefer caves but sometimes abandons them for buildings, especially in the north (Barbour and Davis, 1969; Kunz, 1973). *M. thysanodes* and *M. yumanensis* form large cave colonies in the south

(Barbour and Davis, 1969) but are reported with decreasing frequency from caves as latitude increases, probably abandoning caves entirely beyond about 40°N latitude. In Canada, Cowan and Guiguet (1965) report these species only from attics in buildings. The northern maternity habits of *M. austroriparius* are apparently unknown (Barbour and Davis, 1969), but I predict abandonment of caves in the north because of the bats' small numbers and body size.

M. grisescens appears to be the best adapted of the North American *Myotis* cited above to invasion of relatively cold caves. Nevertheless, even this species has not been able to extend its range beyond about 39°N latitude in spite of an abundance of available caves. Only *M. thysanodes* and *M. yumanensis*, which have been able to abandon caves in summer, have been successful in extending their range much farther northward. Several European bats, however, have succeeded in exploiting the colder caves of higher latitudes (45-50°N). *Miniopterus schreibersi*, *Myotis myotis*, *Rhinolophus euryale* and *R. ferrumequinum* are reported to form maternity colonies in caves where the range of ambient temperatures is only 9-13°C (Gaisler, 1970). These bats are considerably larger than their North American counterparts and this, at least in part, may account for their success in exploiting colder northern caves (Dwyer, 1971). *M. myotis*, for example, weighs up to 45 gm (Walker, 1964) whereas the largest members of this genus in North America, *M. velifer* and *M. grisescens*, rarely exceed 15 gm (Kunz, 1971; Tuttle, unpublished data).

ACKNOWLEDGMENTS

This paper represents a part of a Ph.D. dissertation under the guidance of Robert S. Hoffmann, Department of Systematics and Ecology, The University of Kansas. James R. and Francis D. Alexander, James E. Hall, Joseph C. Howell, Barbara Myers, Marilyn J. Osterlund, Paul B. Robertson, Horace L. and M. June Tuttle, and John Van Swearingen III assisted me in the field. Other hospitalities were extended by James H. and Frances Johnston, Jr. Mark B. Katz and Diane E. Stevenson provided assistance in data analysis and made editorial suggestions. Thomas H. Kunz and Richard J. Wassersug also criticized the manuscript, and Norman A. Slade furnished advice on statistical matters.

Bat bands were supplied by the Bat Banding Office, Fish and Wildlife Service, U. S. National Museum, Washington, D.C., and field work was supported by grants from the Committee on Systematics and Evolutionary Biology (NSF grant GB 4446X1 to J. Knox Jones, Jr.), the Watkins Museum of Natural History Grants, and the Biomedical Sciences Support Grants, all administered through The University of Kansas, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History. Com-

puter time was made available through the University of Kansas Computation Center.

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Key Word Index.—Homeothermy; growth; *Myotis grisescens*; bats; development of young; population ecology.

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