VARIATION IN THE TIMING OF NIGHTLY EMERGENCE BEHAVIOR IN THE LITTLE BROWN BAT, MYOTIS LUCIFUGUS (CHIROPTERA: VESPERTILIONIDAE)

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Abstract. — Nightly emergence behavior was investigated at four maternity colonies of the little brown bat (Myotis lucifugus) in southern New Hampshire. The onset of nightly emergence is highly correlated with seasonal changes in sunset time, occurring later with respect to sunset in spring and early summer than in mid- and late summer. Cloud cover was the only environmental variable, other than sunset time, that significantly influenced variation in the onset of emergence, although precipitation influenced the duration of nightly emergence. Emergence rates varied significantly with colony size, being fastest and most variable in the two largest colonies and slowest and least variable in the smallest. The size and configuration of exits also seemed to affect emergence rates and duration of nightly emergence periods. No significant differences in emergence times were observed between pregnant and lactating females or between juvenile males and females. Average age of initial emergence of juveniles was 18 days, although the earliest nightly emergence of young bats occurred at 15 days of age. When young bats first became volant, they departed from their natal roosts later than lactating females. Nightly emergence patterns of young bats became indistinguishable from those of adults within two weeks following the onset of nightly activity. Delayed emergence of young bats, when they first begin to fly, may reduce their vulnerability to aerial predators and allow them a period to perfect flight and echolocation skills when the interference of acoustic clutter from adults is minimal.

Key words. Myotis lucifugus, behavior, Chiroptera, colony size, nightly emergence

Bats typically seek shelter in protected roosts during the day (Kunz, 1982) and emerge nightly to hunt for prey. Numerous studies have examined environmental factors presumed to affect the onset and timing of nightly emergence (reviewed in Erkert, 1982), and a general conclusion drawn from over three decades of research on this topic is that nightly emergence behavior of bats is influenced by both endogenous and exogenous factors. Most studies have focused on the role of light as a "Zeitgeber" and how this modifies endogenous rhythms, but little attention has been given to other exogenous factors which may override the influence of light. Several investigators have reported or suggested the influence of social and/or other biological variables on nightly emergence behavior (e.g. Kunz, 1974; Buchler, 1980; Swift, 1980; Racey and Swift, 1983; Avery, 1986; Bullock et al., 1987; McAney and Fairley, 1988), but few of these factors have been directly quantified.

A fruitful approach to field investigations on the activity rhythms of animals is to make concurrent measurements of biological events and of prevailing environmental conditions in search for correlations and causal relationships (Enright, 1970). In the present study, we report results of field observations on nightly emergence activity of the little brown bat (Myotis lucifugus), where we examined the effects of environmental variables, roost variables (including exit size and configuration) as well as the effects of season, colony size, age, sex, and reproductive condition on the onset, rates, and duration of nightly emergence behavior.

Materials and Methods

Nightly emergence counts were made at approximately 9-day intervals from late April through mid-September in 1974 at three M. lucifugus maternity colonies (Rice, Sargent, and Turpin) located in Hillsborough County, New Hampshire. Maternity sites and openings used as exit routes at the three sites varied markedly in size and configuration. The major exit route used by members of the Rice colony was a narrow horizontal crevice (about 3 cm x 1.4 m) located above a closed, north-facing door in a large barn. The major exit routes at the Sargent colony were several small crevices between the facing boards and the siding, along the roof line at the west end of a

large barn. Bats at the Turpin colony exited through a large (2.2 x 2.2 m), north-facing, open doorway of a small barn. Most bats emerged from these major exit routes, although some individuals used alternate routes when colony sizes were maximum. Bats which sometimes emerged from these alternate exits were not included in our estimates of total numbers present; thus, our estimates of colony size represent minimum numbers.

Observers were positioned outside and beneath the major used exits so that bats could be silhouetted against the twilight sky and counted visually as they emerged. Times of the first departing bats were recorded and the number of bats were tallied for each subsequent 5-min interval thereafter. Observations were continued until less than five bats were counted during any 5-min period following peak emergence. During the first 5-min of the emergence period some bats departed from the roost, momentarily circled near the exit, and then re-entered the roost (see Twente, 1955; DeCoursey and DeCoursey, 1964). The number of bats recorded during each 5-min interval (including the total flight count, NBATS) reflects the difference between numbers of bats flying out and those re-entering.

Environmental variables recorded at the time of emergence included: air temperature (ATEMP: 1.5 m above the ground), cloud cover (SKY: 1 = clear, 2 = scattered clouds, 3 = partly cloudy, 4 = overcast), wind velocity (WIND: 1 = 0-5.9 knots, 2 = 6-10.9 knots, 3 = 11-15.9 knots), moon phase (MOON: 1 = new moon, 15 = full moon), and “precipitation” (PRECIP: 1 = clear, 2 = misty, 3 = light rain). SUNSET (EDT) time for each night of observation was corrected for longitude and latitude at each location. Other variables included Julian calendar (DATE) and location (LOC). We also noted the presence or absence of aerial predators at or near each roost site on nights when we made flight counts.

From raw counts we derived several additional variables for analysis, including the duration of the emergence period (BATSPAN: minutes between the first and last bat), the interval between SUNSET and the first emerging bat (FIRST), the interval between SUNSET, the time that half of the bats had emerged (MEDIAN), and the “mean” rate of emergence (MRATE), calculated as BATSPAN divided by the number of bats counted (NBATS) on a given night.

Bats captured in harp traps (Kunz and Anthony, 1977; Anthony and Kunz, 1977) were used to characterize colony composition and to test for differences in emergence times between pregnant and lactating females, and between young and adults (lactating). Bat traps were placed in open doorways or in regular flight paths as bats departed from their day roosts (see Kunz and Kurta, 1988). At a fourth site (Merrill Colony) bats were removed from traps at 5-min intervals beginning at the onset of emergence until flight activity ceased. On three nights we set traps at two different exits (east and west) to determine whether emergence times were affected by ambient light conditions, because the west-facing exit was open to the western horizon and the east-facing exit was shaded by the barn. Young and adult bats taken during each 5-min period were placed into separate holding bags until each individual could be weighed and the epiphyseal gap lengths of young bats were measured for age estimation (see Kunz and Anthony, 1982). All bats were released at the roost site within one hour of being captured.

**Results**

**Colony Size and Composition.**—Data from nightly flight counts and trapping records at maternity roosts revealed that yearling and adult female *M. lucifugus* began arriving in late April, reached peak numbers in late July, and decreased precipitously thereafter (Fig. 1). The increase in numbers observed during May and June mostly

![Fig. 1](image-url)  
Fig. 1. Seasonal changes in size and composition of a typical maternity colony of *M. lucifugus* in southern New Hampshire. Numbers of bats were determined from visual flight counts taken at approximately 9-day intervals at the Sargent colony. Since bats could not be captured at this site, age composition and changes in reproductive condition are based on bats captured at approximately 9-day intervals during nightly emergence at the Rice colony. The horizontal lines denote periods when pregnant, lactating, and post-lactating females were present in the colony. The approximate numbers and proportions of adult females (open), adult males (stippled), and juveniles (solid) emerging during nightly flight counts from late April through mid-September are shown for comparison.
reflects the influx of pregnant females and a few males, as bats arrived from hibernacula and spring transient roosts. Maximum adult colony size was reached in mid-June followed closely by a minor decrease in the number of bats. Most pups were born during the third week of June (Kunz and Anthony, 1982) with some birth dates extending into early July (T. H. Kunz, pers. obs.). The first young of the year were captured during emergence flights in early July. The increase in numbers of emerging bats recorded in mid-July mostly reflects emergence of newly volant young. As young bats were subsequently weaned, the number of adult females (post-lactating) began to decrease. By mid-September, most of the colony had dispersed to transient and swarming sites, and at this time most bats remaining at the maternity roost were young of the year. All bats had dispersed from maternity roosts by early October.

Patterns of Nightly Emergence.—The seasonal pattern of nightly emergence in *M. lucifugus* for the Sargent colony, from late April through mid-September (Fig. 2), depicts changes in colony size, onset and duration of nightly emergence activity, and nightly emergence rates. These data indicate that bats emerge earlier with respect to civil time in spring, later in mid-summer, and progressively earlier in late summer. Each nightly emergence pattern approximates a normal distribution with peak emergence occurring midway through each period. Changes in the onset of emergence times were highly correlated with seasonal changes in sunset time ($r^2 = 0.89, p = 0.001$). Quantitative analyses of nightly emergence patterns are summarized in the following sections.

**Onset of Emergence.**—A general seasonal trend in onset of nightly emergence in *M. lucifugus* is illustrated in figure 2. Analysis of emergence patterns for each colony revealed that the interval between SUNSET and FIRST was greatest at the Turpin colony ($\bar{x} = 3.6\min \pm 4.4\ SD, \ range = -2 \ to \ 15, \ n = 13 \ nights, \ maximum \ estimated \ colony \ size, \ N = 120$), smallest at the Rice colony ($\bar{x} = -0.4\ min \pm 7.2\ SD, \ range = -11 \ to \ 12, \ n = 18; \ N = 1190$) and intermediate at the Sargent colony ($\bar{x} = 2.1\ min \pm 4.8\ SD, \ range = -5 \ to \ 10, \ n = 15; \ N = 640$). Bats were observed emerging before SUNSET on two occasions at the Turpin colony, on five occasions at the Sargent colony, and on nine occasions at the Rice colony. Because of the large seasonal variation in FIRST at each location, one-way analysis of variance (ANOVA) failed to detect a significant difference among colony means ($F = 1.97, p = 0.15$).

![Fig. 2. Seasonal and nightly changes in emergence activity, colony size and emergence rates at a *M. lucifugus* maternity colony (Sargent). Emergence rates were based on visual counts taken at 5-minute intervals from the onset of emerge until activity ceased (see text for further explanation). Total numbers of bats refer to those counted on a given night.](image-url)
We used multiple regression analysis to examine effects of environmental variables on FIRST. When data from all colonies were pooled, DATE ($b = -0.08; p = 0.0006; r^2 = 0.96$) and SKY ($b = 2.08; p = 0.03; r^2 = 0.97$) were the only variables that explained a significant amount of variation in FIRST. The interval between SUNSET and FIRST decreased in length from spring to mid-summer. From our data, it is unclear whether this pattern reflects the response of bats to seasonal changes in light intensity at sunset or to seasonal changes in the duration of twilight (see Voute et al., 1974). Our results do indicate, however, that cloud cover influences FIRST, with bats leaving sooner on cloudy nights than on clear nights. Moreover, on nights with heavy rain ($n = 2$) bats either delayed emergence or the emergence flight was interrupted until the rain ceased. Accurate flight counts could not be made on nights of heavy rain; consequently, the data for these nights were not included in the following analyses.

**Median Emergence Time** — To reduce the effects of occasional early flyers (common on cloudy nights) and late flyers (young bats), we examined the relationship between SUNSET and MEDIAN (the time when half of all bats had emerged). The interval between SUNSET and MEDIAN did not differ significantly among colonies (Rice: $\bar{x} = 24.2$ min $\pm 10.5$ SD, $n = 18$; Sargent: $\bar{x} = 20.8$ min $\pm 5.7$, $n = 15$, and Turpin: $\bar{x} = 23.6$ min $\pm 6.9$, $n = 13$), based on one-way ANOVA, $F = 0.79$, $p = 0.46$. Bats at the largest colony (Rice) had the shortest interval between SUNSET and MEDIAN. DATE was the only variable explaining a significant amount of variation in MEDIAN in a multiple regression analysis ($b = -0.14; p = 0.0001; r^2 = 0.91$).

**Duration of Nightly Emergence** — The duration of nightly emergence (BATSPAN) varied among locations (LOC), each of which differed in exit configuration and colony size. The longest BATSPAN ($\bar{x} = 46.8$ min $\pm 10.6$ SD, $n = 18$) was observed at the largest colony (Rice), whereas the shortest average BATSPAN ($\bar{x} = 35.8$ min $\pm 6.9$ SD, $n = 16$, $\bar{x} = 34.2$ min $\pm 10.7$ SD, $n = 13$) were recorded at the two smallest colonies, respectively (Sargent and Turpin). Results of one-way ANOVA indicate a significant difference among these means ($F = 8.6; p = 0.001$). Using results from a Duncan multiple range test ($\alpha = 0.05$), BATSPAN was significantly longer at the largest colony. There was no significant difference between BATSPAN at the two smallest colonies. The longest separate nightly BATSPAN (70 min) was observed at the largest colony (Rice), and this was observed in mid-May before the colony had reached its peak adult numbers. The shortest nightly BATSPAN (29 min) was observed at this same colony in mid-September after the colony had declined precipitously in numbers. The longer BATSPAN observed at the Rice colony, relative to the other two colonies, may reflect the fact that most bats exited through a small horizontal crevice and some bats may have had to wait for others before they could emerge. Extended BATSPANS observed at the Rice colony in mid-summer may reflect a delayed emergence of young bats for the same reason. The shortest nightly BATSPANS at all colonies were observed in early spring and late summer when colony sizes were the smallest.

Multiple regression analysis was used to assess the effects of environmental variables on BATSPAN. Data from the three colonies were pooled and two dummy variables, coded for LOC, were entered as independent variables. Other independent variables included DATE, SUNSET, NBATS, SKY, MOON, ATEMP, PRECIP, WIND. Inter colony differences and seasonal trends in BATSPAN discussed above were evident in significant partial regression coefficients for LOC ($b = 8.64; p = 0.002$) and DATE ($b = -0.07; p = 0.05; r^2 = 0.53$). The only other variable that significantly entered the regression was PRECIP ($b = 7.1$, $p = 0.01; r^2 = 0.43$). Mean BATSPAN was 37.6 min $\pm 9.4$ SD ($n = 40$) on clear nights, 51.2 min $\pm 1.45$ SD ($n = 5$) on misty nights, and 50.0 min $\pm 14.1$ ($n = 2$) on nights with light rain. One-way ANOVA indicated a significant difference among these means ($F = 5.16, p = 0.01$) and a Duncan’s multiple range test ($\alpha = 0.05$) showed a significant difference in BATSPAN between clear nights and the two other “precipitation” categories (misty and light rain). There was no significant difference in BATSPAN on nights with light rain and mist.

**Emergence Rates** — Emergence rates (MRATE) varied significantly among colonies, with the largest colony (Rice) exhibiting the highest and most variable rates, and the smallest (Turpin) showing the slowest and least variable rates. MRATE was $13 \pm 7.04$ bats per min ($n = 18$, range = 3 to 25) at the Rice colony, $9 \pm 4.58$ bats per min ($n = 16$, range = 3 to 19) at the Sargent colony, and only $2 \pm 1.22$ bats per min ($n = 13$, range 1 to 5) at the Turpin colony. One way ANOVA indicates a significant difference among these means ($F = 17.87, p = 0.0001$). A Duncan’s multiple range test ($\alpha = 0.05$) indicated that all possible combinations of means were significantly different. Multiple regression analysis of pooled data indicates that none of the environmental variables affected
MRATE. The only variables entering the regression equation were NBATS (b = 0.02, p = 0.001; r² = 0.86) and LOC (b = 1.45, p = 0.004; r² = 0.88).

Effects of Reproductive Condition, Sex, and Age. We pooled data from the Rice, Sargent, and Turpin colonies to test for effects of reproductive condition on emergence times. We used a X² test to evaluate the null hypothesis that there was no difference in the numbers of bats in each of the two reproductive conditions captured during the first and second half of nightly emergence periods. This analysis shows no significant difference in emergence times between late pregnant and early lactating females captured on the same nights (Table 1); thus, in subsequent analyses of emergence times we pooled data for adult females. Adult males and non-pregnant adult females were not captured in sufficient numbers to permit a comparable analysis.

We also tested for differences in emergence times between adult females and newly volant young captured at the Merrill colony by comparing mean capture times on six nights over a 14-day period beginning from the onset of nightly emergence by young bats (Table 2). On three different nights we captured bats as they departed from both the east-facing and west-facing exits. In the period following the onset of flight (6-13 July), mean emergence times of young bats were significantly later than those of adults. The nightly emergence of young bats during this period averaged 10-15 min later than adults. Approximately two weeks after young began to fly, their temporal emergence patterns were indistinguishable from those of adults (Fig. 3).

To determine if a relationship exists between age of young and time of emergence, we ran correlations between age, as determined by total epiphyseal gap (Kunz and Anthony, 1982), and time of emergence on those dates when a sufficient number of young were captured for reliable statistical analysis. Using one-way ANOVA we found no significant differences among young males and females in their times of nightly emergence on each

Table 1. A comparison of numbers of M. lucifugus captured in harp traps placed at the exits of maternity roosts during the first (early) and second half (late) of nightly emergence periods (n = 6 nights) when both pregnant and lactating females were present in the colony. (Data are pooled from Rice, Sargent, and Turpin colonies.) A Chi-square test indicated no significant difference in emergence times between pregnant and lactating females (X² = 1.02, P < 0.05).

<table>
<thead>
<tr>
<th>Emergence Period</th>
<th>Pregnant</th>
<th>Lactating</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>17</td>
<td>60</td>
<td>77</td>
</tr>
<tr>
<td>Late</td>
<td>14</td>
<td>30</td>
<td>44</td>
</tr>
<tr>
<td>Total</td>
<td>31</td>
<td>90</td>
<td>121</td>
</tr>
</tbody>
</table>

Assignment of bats to early and late emergence periods was based on the total number of bats captured on a given night.

Table 2. Comparison of mean emergence times of young and adult M. lucifugus captured in traps placed at exits of a maternity roost in southern New Hampshire (MW = Merrill West, ME = Merrill East). East and west exits used by bats at the Merrill colony differed in the exposure to the western horizon at sunset.

<table>
<thead>
<tr>
<th>Location</th>
<th>Date</th>
<th>Mean ± SD (n)</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Young</td>
<td>Adult</td>
<td></td>
</tr>
<tr>
<td>MW</td>
<td>6</td>
<td>2054 ± 16.6 (15)</td>
<td>2028 ± 10.7 (45)</td>
<td>41.21</td>
</tr>
<tr>
<td>ME</td>
<td>7</td>
<td>2041 ± 19.3 (36)</td>
<td>2025 ± 4.8 (42)</td>
<td>32.19</td>
</tr>
<tr>
<td>MW</td>
<td>10</td>
<td>2032 ± 15.3 (13)</td>
<td>2025 ± 4.8 (30)</td>
<td>7.94</td>
</tr>
<tr>
<td>ME</td>
<td>13</td>
<td>2038 ± 16.4 (45)</td>
<td>2029 ± 13.7 (38)</td>
<td>26.80</td>
</tr>
<tr>
<td>MW</td>
<td>13</td>
<td>2026 ± 13.7 (40)</td>
<td>2021 ± 4.2 (17)</td>
<td>1.33</td>
</tr>
<tr>
<td>ME</td>
<td>17</td>
<td>2023 ± 3.9 (45)</td>
<td>2025 ± 4.6 (23)</td>
<td>2.16</td>
</tr>
<tr>
<td>MW</td>
<td>17</td>
<td>2026 ± 13.7 (41)</td>
<td>2021 ± 4.2 (29)</td>
<td>4.64</td>
</tr>
<tr>
<td>ME</td>
<td>20</td>
<td>2024 ± 4.6 (39)</td>
<td>2022 ± 4.6 (19)</td>
<td>1.27</td>
</tr>
<tr>
<td>MW</td>
<td>20</td>
<td>2023 ± 3.3 (35)</td>
<td>2023 ± 4.0 (23)</td>
<td>0.72</td>
</tr>
</tbody>
</table>
emergence counts are most reliable if bats emerge from a single exit where they can be fully silhouetted against the sky (Humphrey and Cope, 1976). Unfortunately, flight counts alone do not provide information on colony composition or make it possible to compare the behavior of young and adult bats. When data from flight counts are combined with trapping results, however, it is possible to gain additional information about sex, age, and reproductive condition. The most reliable estimates of colony composition can be obtained by trapping bats during their nightly emergence, as long as the traps do not significantly alter the emergence behavior of the bats (see Kunz and Anthony, 1977, Kunz and Kurta, 1988). This method of assessing colony composition is far superior to estimates based on roost captures, since roosting bats may be segregated by sex, age, and reproductive condition. Notwithstanding, colony composition and colony-size estimates based on captures with harp traps are not without their biases (see Kunz and Anthony, 1977).

**Colony Size and Composition**—Most adult female *M. lucifugus* in New Hampshire are pregnant when they arrive at maternity roosts, and most give birth during the last two weeks of June and first week of July. In our study, maximum adult colony sizes were reached in mid-June. Subsequently, we observed a small decrease in numbers around the time of parturition (Figs. 1 and 2). Similar observations have been reported for *M. velifer* (Kunz, 1973) and *M. lucifugus* (Humphrey and Cope, 1976). This decrease in numbers may reflect the dispersal of adult males and non-pregnant females from maternity roosts near the time that pups are born, or perhaps can be attributed to delayed nightly emergence by some females (and thus not included in flight counts) if they were attending pups (Kunz, 1974, O’Farrell and Studier, 1975, O’Shea and Vaughan, 1977).

As young bats become volant, we would expect a dramatic, if not near doubling of bats observed in flight counts. Although we observed a small increase in the number of bats emerging at this time (Figs. 1 and 2), a doubling of colony size was not observed by the time all young bats had become volant. This may be attributed to the fact that the birth period extends over a period of about three weeks, and young bats typically begin to emerge nightly from their roost at the age of 18-23 days. Thus, by the time the last pup in a colony is born, those born early in the birth period would have been able to fly. In fact, we suspect that some of the earliest-born pups may have been weaned and already dispersed to transient roosts or swarming sites before the latest pups were born.

**Discussion**

Flight counts of emerging bats can provide valuable information on colony size and emergence rates and seasonal pattern of emergence (Figs. 1 and 2). Nightly
O'Farrell and Studier (1975) also found no evidence of a colony peak corresponding to emergence flights of young bats in New Mexico and attributed their observation to a prolonged birth period. They suggested that young bats probably emerged from roosts too late in the evening to be included in their visual flight counts. We concur that emerging pups are likely to be overlooked in flight counts, especially before they assume an adult-like emergence pattern.

Factors Affecting Onset of Emergence.—Our findings are consistent with observations that the onset of nightly emergence is closely synchronized with seasonal changes in sunset time (reviewed in Erkert, 1982). The general pattern that emerges from our study is that the onset of nightly emergence in *M. lucifugus* begins later with respect to sunset time in spring and early summer than during late summer and early autumn. These results contrast with those of O'Farrell and Studier (1975) who reported a constant relationship between emergence and sunset time for populations of this species in New Mexico. Earlier departure relative to sunset could be expected in spring and autumn, especially if flying insects are more abundant before sunset (see Nyholm, 1965).

Our findings that nightly emergence in *M. lucifugus* begins earlier on cloudy nights than on clear nights is consistent with observations made on other species (reviewed in Erkert, 1982; also see McAney and Fairley, 1988, McWilliam, 1989). Although heavy precipitation may delay the onset or prolong the duration of nightly emergence (increased BATSPAN), mist and light rain appears to have little or no effect on the onset of nightly emergence in *M. lucifugus*. Heavy rain appears to delay the onset of emergence in most species that have been studied (e.g. Erkert, 1982; Avery, 1986, Bullock et al., 1987, McAney and Fairley, 1988, McWilliam, 1989).

We found no evidence that wind delayed or accelerated nightly emergence in *M. lucifugus*.

Although ambient temperature at the time of emergence was not a significant variable affecting emergence time in our study, roost and/or cluster temperatures during the day preceding emergence may be a factor which effects the physiological state of the animals and hence emergence activity. Since most temperate-zone bats are thermally labile, especially in spring and fall, onset of nightly emergence could be delayed if individuals enter torpor during the day, and are not fully aroused at the time of emergence. Although the effects of depressed
body temperature of bats during the roosting period on pre-emergence arousal have not been explored, reduced body temperatures in non-volant mammals is known to reduce their sensitivity to light (Nielson, 1984). O'Shea and Vaughan (1977) suggested that the slow rates of departure in Anourous pallidus during spring and autumn may reflect variation in rates of arousal from daily torpor. Wolz (1988) reported that delayed onset of emergence in Myotis bechsteini was correlated with low ambient temperatures. Whether or not torpid bats arouse and depart in a timely fashion may also be influenced by the amount of food eaten and, hence, the amount of metabolizable energy available during the roosting period (Kurta, 1991).

Although M. lucifugus began to emerge sooner from east (shaded from western horizon) versus west-facing exits at the Merrill colony, the mean emergence times at these two locations were not significantly different (see Table 2). These observations are consistent with those of Twente (1955) and Kunz (1974) who noted that some M. velifer emerged earlier from exits that were shaded (those facing east or in deeply-shaded canyon) than from those having a western exposure. McAney and Fairley (1988) reported that Rhinolophus hipposideros made exploratory flights at exits that were shaded by trees further emphasizes the importance of local factors affecting the onset of nightly emergence.

Factors Affecting the Duration of Nightly Emergence —Our study has identified several variables that influence duration of nightly emergence in M. lucifugus. These include DATE, NBATS, and size and configuration of exit routes. Both DATE and NBATS were variables that significantly entered a multiple regression. Duration of nightly emergence was greatest in large colonies and least at small colonies. The significance of DATE and NBATS can best be explained as responses to seasonal changes in day length and duration of twilight, since these two variables are highly correlated. The longer duration of emergence in M. lucifugus in mid-summer also reflects a later departure of volant young during their first 10 days of nightly emergence (Fig. 4). It appears that the later emergence times of young bats prolongs the period of emergence especially when young bats first begin to fly. This observation is consistent with those of McAney and Fairley, (1988) who reported longer emergence periods and later mean emergence times in Rhinolophus hipposideros during late summer, when the colony was largest. Wolz (1988) also reported that colony size was an important variable that influenced emergence behavior of Myotis bechsteini, although Dwyer (1964) found no correlation between colony size and the duration of emergence in Miniopterus schreibersi.

Variation in size and configuration of exits used by bats may account for some of the observed variation in the duration of nightly emergence in M. lucifugus, although observations to this effect are confounded by colony size and the lack of quantifiable data. Colonies at sites where exits were relatively small (Rice and Sargent) had longer emergence periods than the one with a large exit (Turpin). This interpretation is consistent with reports by Swift (1980), Avery (1986), and Bullock et al. (1987) who noted that emergence behavior of Pipistrellus pipistrellus was influenced by both colony size and roost configuration.

Emergence Rates.—Nightly emergence rates of M. lucifugus varied with colony size, being highest and most variable in large colonies and lowest and least variable in small colonies. Observations from several studies indicate that emergence rates vary seasonally, which reflect changes in colony size and reproductive condition. Swift (1980) found a strong correlation between colony size and emergence rates in P. pipistrellus, and this observation was confirmed by Bullock et al. (1987). In both of the above studies, "outbursts" of emergence activity were most common in large colonies and those with constricted exit routes. Similar patterns of nightly emergence have been reported for Myotis velifer (Kunz, 1974), M. bechsteini (Wolz, 1988), and Tadarida pumila (McWilliam, 1989). Such rhythmic departures of groups or "departure by coup" may serve as a predator deterrent (Leen and Novick, 1977, Brigham and Fenton, 1986), although we found no evidence of emergence outbursts in M. lucifugus. Similarly, McAney and Fairley (1988) found no evidence of outbursts during emergence in Rhinolophus hipposideros (but see Speakman et al., 1992).

Swift (1980) noted that emergence rates of P. pipistrellus increased in late summer and suggested that this increase may have been attributed to hunger drives of young bats, based on evidence from Stebbings (1968) that lightweight bats emerged sooner than heavy ones. Avery (1986), however, found no evidence to support Stebbings' hypothesis that lighter bats (presumably those with higher energy demands) emerged earlier than heavier bats. The later emergence of younger bats, when they first begin to fly, may explain why Avery (1986) found no evidence to support the "hunger hypothesis", since young of the year typically weigh less than adults.
Effects of Age, Sex, and Reproductive Condition.—The lack of information on the effects of age, sex, or reproductive condition on emergence behavior is not surprising since most published studies on nightly emergence have relied almost exclusively on visual (e.g., Humphrey and Cope, 1976; Kunz, 1974; Swift, 1980; Avery, 1986; Bullock et al., 1987; McAney and Fairley, 1988; Speakman et al., 1992) or electronic recordings of flight counts (Englander and Laufen, 1968; Voute et al., 1974; Wolz, 1988; Speakman et al., 1992). Our findings that age of young bats is an important variable influencing the time of nightly emergence is most obvious during the fledgling period when young bats were first beginning to fly (Figs. 3 and 4). When young M. lucifugus first emerged from their natal roosts, they did so after most adults had departed. The juvenile patterns of emergence characteristic of young bats becomes indistinguishable from those of adults over a two week period. Kunz (1974) suggested that the later nightly emergence by young M. velifer allows them to perfect flight and echolocation skills in the absence of acoustic clutter from adults. Our observation of a progressive change from a juvenile to an adult-like emergence pattern is consistent with Buchler’s (1980) observations that young M. lucifugus take about two weeks to develop adult-like echolocation and foraging skills.

The later departure of young M. lucifugus when they first begin to fly also supports the hypothesis that young bats learn to forage independently of their mothers (Buchler, 1980). Our findings are consistent with those of Audet (1990) who reported a later emergence for young M. myotis when they first began to fly, and her findings that radiotagged young foraged in areas separate from their mothers. These observations contrast with reports on other species where mothers appear to play a role in the development of foraging behavior in young bats (e.g., Antrozous pallidus—O’Shea and Vaughan, 1977, Pipistrellus pipistrellus—Racey and Swift, 1983).

In the present study, too few adult males were captured as they emerged from their roost sites to test for differences in emergence times between adult sexes. Our comparison of emergence times between young males and females indicates that there are no significant sex differences among young bats. There is evidence to suggest that emergence activity of adult sexes is indeed influenced by reproductive condition, but to what extent these differences are confounded by sex, reproductive condition, and social status, cannot be determined from available observations. Brosset (1962) noted that lactating female Taphozous melanopogon emerged 15-20 min before males. Similarly, Humphrey (1971) found that adult (lactating) female Tadarida brasiliensis emerged earlier than adult males. However, in P. pipistrellus, adult males reportedly emerge from roosts earlier than adult females (Stebbins, 1968; Avery, 1986). McWilliam (1989) also found that some male Tadarida pumila emerged earlier than females and suggested that this earlier departure may be related to their polygynous-based social organization. The earlier emergence times reported for male P. pipistrellus in late summer may be influenced by social organization, since males of this species form territories and defend mating sites at this time (see Gerell and Lundberg, 1985).

Our study revealed no significant difference in emergence times between pregnant and lactating M. lucifugus. Kunz (1974), however, reported that female M. velifer in early lactation emerged later than pregnant females, and suggested that this difference may reflect the time required for lactating females to remove suckling pups and to prevent them from being dislodged at peak emergence times. O’Shea and Vaughan (1977) also suggested that variation in emergence times of lactating female Antrozous pallidus may reflect the attendance of mothers to their pups. Owing to the increased demands on lactating females for energy, water, and nutrients (Kunz, 1987; Kurta et al., 1989, Kunz et al., 1995), we would predict that the emergence times of lactating females should become progressively earlier in the evening to take advantage of peak insect activity. McWilliam’s (1989) finding that Tadarida pumila emerge significantly earlier during the first three weeks of lactation than during the preceding pregnancy lends support to this prediction.

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