Population Structure and Emergence Activity Patterns in Myotis thysanodes and M. lucifugus (Chiroptera: Vespertilionidae) in Northeastern New Mexico

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ABSTRACT: *Myotis lucifugus* arrives at the maternity roost over a period of several months, probably from several hibernacula. *Myotis thysanodes* has a rapid spring immigration and a brief span of parturition dates, indicating that the maternal population may remain as a coherent group throughout the winter. Sex ratios at birth are equal in both species. In *M. lucifugus,* adult females rapidly leave the maternity colony after weaning their young and are followed first by juvenile males, then females. In contrast, young *M. thysanodes* males, then young females, leave the maternity roost before adult females. Rain and overcast conditions lead to earlier nightly departure of the first bat, but peak rate of emergence is frequently unaffected by these variables. Time of emergence is directly correlated with time of sunset and appears to be a photoperiodic response.

INTRODUCTION

Population dynamics and activity patterns are essential information in understanding the biology of bats. A number of recent studies have comprehensively dealt with the genus *Myotis* (Wilson, 1971; Kunz, 1971). More specifically, *Myotis lucifugus lucifugus* has been studied in great detail (Davis and Hitchcock, 1965; Fenton, 1970; Humphrey, 1971a). There is little information concerning the southwestern subspecies, *M. l. occultus,* and also little concerning another western montane bat, *Myotis thysanodes.*

The purpose of this study was to determine the seasonal population dynamics and structure of *M. thysanodes* and *M. lucifugus* and relate these to the physiological-ecological information we had previously collected. In addition, we attempted to characterize emergence activity patterns and determine the factors which affect them.

MATERIALS AND METHODS

Two maternity roosts were used. One, the O'Malley roost, harbored *Myotis lucifugus* and was located in the attic of a home on the SE corner of Washington and Sixth Sts., Las Vegas, San Miguel Co., New Mexico. This roost was ideal for counting emerging bats since there were only two small exits from the attic, at the eastern and western ends of the building. Approximately equal numbers of bats exit from either end of the attic. On 48 nights from 11 May to 4 September 1970, numbers of emerging bats were counted in 2.5-min

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intervals. Time of emergence for first bat was recorded and bats were counted until visibility conditions were too poor to distinguish individuals. Rain, approximate cloud cover and wind velocity were recorded and further climatological information was obtained from hourly records of the Las Vegas weather station, located ca. 6.5 km from this study area. At the beginning of each 2.5-min interval, light intensity ($\pm$ 0.1 ft-c) was determined using a Weston Illumination Meter, Model 756.

The second roost contained *M. lucifugus* and *M. thysanodes* and was in an attic at Montezuma Seminary, Montezuma, San Miguel Co., New Mexico. Visual population estimates were made several times from May to September 1969 and then at weekly intervals from 19 April to 25 September 1970. During 1970, age and sex composition, and emergence activity were determined at weekly intervals.

Age was determined by arbitrarily assigning tooth-wear categories: 1 = adults with needle-sharp canines showing no wear; 2 = blunt canines demonstrating some wear; 3 = canines worn to approximately half initial length; and 4 = canines worn to the gum line. In addition, bats that were in category 1 were examined by epiphyseal closure and shape of epiphyses to detect juveniles (Davis, 1963).

RESULTS

Population sizes and fluctuations.—In the O'Malley roost the *M. lucifugus* population increased rapidly from late April through the middle of June, at the approximate rate of 600 bats/10 days. From mid-June to the end of July, population size remained stable. Through August and early September the population declined at the approximate rate of 600 bats/10-day period. Estimated peak population size was 4400 bats.

The *M. lucifugus* in Montezuma Seminary showed a similar trend. The first individuals arrived in the attic on 18 April and the adult population rapidly increased through June, remained relatively stable until August, then began to decline. In *M. thysanodes* in Montezuma Seminary, the first individuals were observed on 18 April and the population rapidly increased through the middle of May. The adult population remained relatively stable until September, then began to decline.

Over the period of observation at the Montezuma roost, both species appeared to increase; the populations in 1970 were larger than in previous years *(M. thysanodes* ca. 1000 to 1200 individuals and *M. lucifugus* in excess of 15,000). The increase in *M. lucifugus* was most impressive, since in 1970 they began using a new roost site within the attic and totally displaced the population of *Myotis yumanensis* which had been a regular resident in previous years.

A difference was observed in species synchronization of parturition which is a function of the differences in synchronization of return to the maternity roost. Parturition in *M. thysanodes* occurred over a period of about 2 weeks as demonstrated by the narrow weight distribution of juveniles (Table 1). Parturition in *M. lucifugus* (Table

1) occurred over a longer time span, as demonstrated by a wide range of weights in juveniles. In 1969 a freshly dead, fully haired *M. lucifugus* juvenile was found on 15 June. At this same time 240 adult females were brought into the laboratory (Proctor and Studier, 1970); all of these bats were pregnant and a few gave birth. In late August, 32 females were collected, and of these at least three were pregnant.

Sex ratios and age structure.—Only one adult male *M. thysanodes* was ever collected in the maternity roost. It was taken 19 April 1970 and was one of the first six *M. thysanodes* to appear that year. In *M. lucifugus,* a few adult males were always present in the maternity roost but never comprised over 5% of the population except perhaps just prior to final exodus from the maternity roost. Adult males nearly always roosted individually in cooler microclimates than females or young and, consequently, were not counted with grouped bats. Many of these adult males leave the maternity roost very late in the summer, and the percentage of adult males, therefore, increases proportionately to the small number of females remaining at that time.

About 90% of the females checked in April, May and June in Montezuma Seminary were pregnant, yielding an adult to young ratio at parturition of one. Table 2 indicates the number of young and adult bats of both sexes taken from clusters at approximate time of parturition (early) and from postlactation to late summer or autumn departure (late). Adult female *M. lucifugus* leave the maternity site soon after lactation ceases, while the young remain. In contrast, *M. thysanodes* adults remain in the maternity roost while young apparently leave soon after weaning. Results of Fisher's exact probability tests on sex distribution of young bats show a significant switch

TABLE 1.—Weight distribution of neonates randomly collected at the O'Malley roost (*M. lucifugus,* 30 June 1970; N = 27) and the Montezuma Seminary roost (*M. thysanodes,* 28 June 1970; N = 42)

Weight (g)	*M. thysanodes*	*M. lucifugus*
2 - 2.9	24	14
3 - 3.9	16	4
4 - 4.9	2	7
5 - 5.9	--	1
6 - 6.9	--	1

TABLE 2.—Numbers of adult and young bats of each sex during early and late maternity colony occupancy for Montezuma Seminary in 1970

Time	Young			Adults			
	F	M	%M	F	M	%M	%Ad.
			Myotis thysanodes				
Early	13	20	60.6	....	--	--	≅ 50.0[1]
Late	10	2	16.7	57	0	0.0	82.6
			Myotis lucifugus				
Early	18	21	53.8	....	--	--	≅ 50.0[1]
Late	55	35	38.9	17	1	5.6	16.7

[1] Estimate based on visual observation

from equal sex ratios of males and females to greater numbers of females late in the year in *M. thysanodes* ($P = 0.010$) and a similar nearly significant redistribution in *M. lucifugus* ($P = 0.084$).

Age structure of the populations of both species of *Myotis* in Montezuma Seminary is given in Table 3. In most cases the numbers of bats examined are small due to an attempt to minimize disturbance of the colony. However, we believe that these figures, obtained from clustered bats randomly collected throughout the attic, are representative of the colony.

Emergence activity patterns.—Pre- and post-solstice emergence activity of *M. lucifugus* from the O'Malley roost demonstrated a predictive linear relationship (Fig. 1). The pre- and post-solstice slopes of activity in relation to sunset, and peak emergence in relation to first bat emergence were not significantly different. Regressions were calculated for the difference between peak emergence and sunset vs. sunset, and the difference between peak and first emergence vs. first emergence. The slopes did not differ significantly from zero, indicating a constant relationship between emergence activity and sunset. Therefore, predictions can be made directly from mean values of first bat and peak emergence times (Table 4). Both the first bat and peak rate occurred earlier than expected on 2 June and 15 and 25 July; both were later than expected on 10 July. On 2, 3, 8 and 31 July and 6 August, the first bat emerged earlier than its predicted time, while peak emergence rate occurred at the time it was expected. The only consistent variable related to these abnormal emergence times was

TABLE 3.—Age structure of the population of *Myotis thysanodes* and *M. lucifugus* at Montezuma Seminary. All bats were females, excluding young of the year, and were collected during 1970

Age category	*M. thysanodes* 1	2	3	4	*M. lucifugus* 1	2	3	4
April	6	5	1	1	----	----	--	--
May	10	3	4	1	17	6	7	3
June	11	1	6	2	42	14	3	0
July	8	2	3	1	6	2	0	0
August	8	3	3	4	11	1	2	0
Sept.	36	8	3	1	----	----	--	--

TABLE 4.—Predictive values for time of emergence of the first bat and peak numbers in relation to sunset and for peak numbers in relation to the appearance of the first bat. All values pertain to *M. lucifugus* (O'Malley roost)

	First bat from sunset (min)	Peak emergence from sunset (min)	Peak from first bat (min)
$\bar{X}$	6.2	22.7	16.9
$2S_{\bar{X}}$	±0.730	±0.592	±0.646
Range	-7 to 16	12 to 32	10 to 30

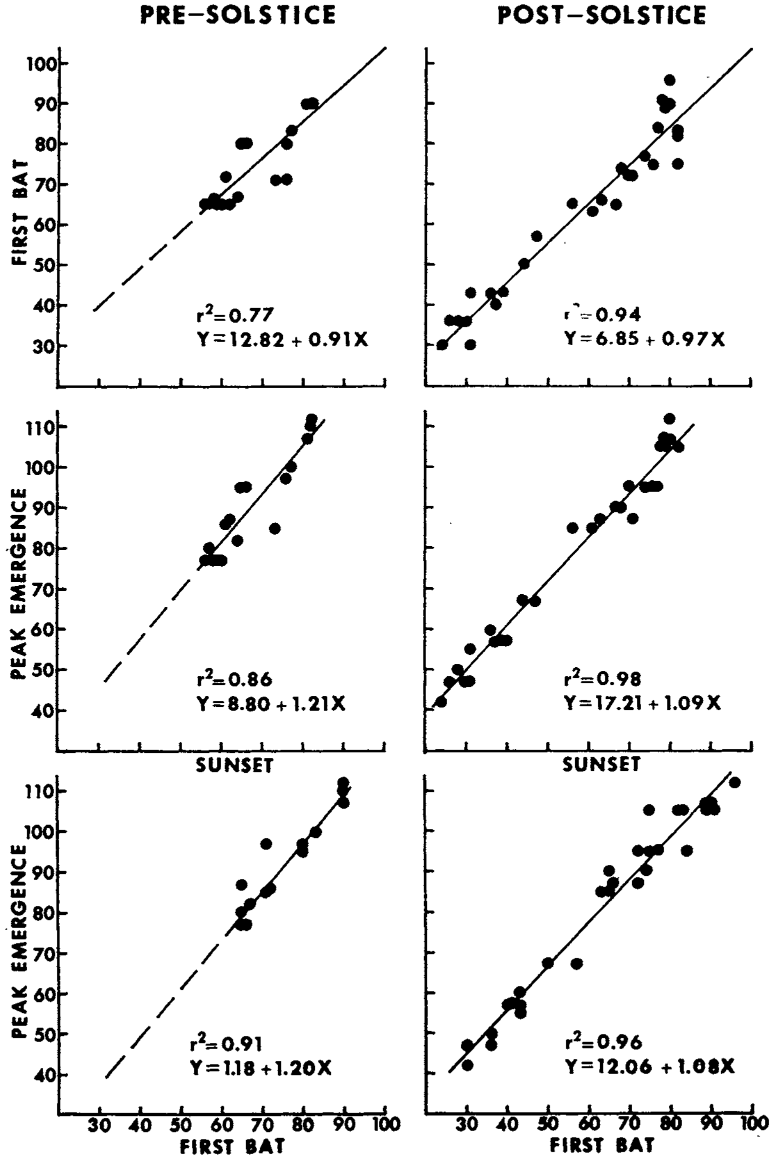

Fig. 1.—Linear regressions of emergence of first bat and peak numbers in relation to sunset and peak in relation to first bat emergence for pre- and post-solstice observations of *Myotis lucifugus* (O'Malley roost). Both axes are in minutes from 1900 hr MDST

that it was either raining or totally overcast during emergence activity on all of these nights.

When the first bat emerged earlier than expected, the rate of increase in numbers of bats emerging builds slowly to a peak, yielding peak emergence rates at expected times (Table 4). Although the first bat to emerge is frequently affected by rain or overcast, the time most bats exit, as exemplified by peak emergence rates, is generally unaffected. However, on several nights when it was raining or totally overcast, bats exited at their normal times. Although wind affected flight characteristics, it had no effect on emergence times, nor did daytime high ambient temperature or low ambient water vapor pressures. At Montezuma Seminary, when bats were in late pregnancy and lactation, wind, high water vapor pressure and rain had no effect on the overall activity.

During early counts at the O'Malley roost, most of the first 10 bats to leave the roost returned within a few seconds, while by mid-June only one or two of the first bats to leave returned to the roost. During rains more bats than expected returned to the roost within a few seconds of leaving. In early summer, much squeaking was heard from the roost just prior to the exit of the 1st dozen bats, after which the noise level dropped significantly. In August and September, however, few sounds were heard just prior to the exit of the first bats or at any other time.

Light intensity was examined as a factor affecting time of emergence, since emergence throughout the summer is correlated with time of sunset. Our data show extreme ranges for absolute level and rate of change of outside light intensities both when the first bat and peak rate occur (Table 5). Therefore, neither absolute light intensity nor the rate of change of light intensity appears to be the major environmental cues effecting emergence.

DISCUSSION

The opportunity to make direct counts of bats during their emergence from certain roosts greatly increases the accuracy of population estimates and allows for considerably more accurate comparative data for other demographic studies. Humphrey (1971b) discussed the value of visual counts and also presented data evaluating photographic estimates of bat populations when they are too large for direct counts. The O'Malley roost was ideally suited for direct visual counts, but Montezuma Seminary was an open roost with too many exits for either visual counts or photographic estimates.

TABLE 5.—Absolute light intensity and rate of change of light intensity at time of emergence of first bat and at time of peak rate of emergence of *M. lucifugus* from the O'Malley roost

	Absolute (ft-c)			Rate of change (ft-c/min)		
	N	Mean	Range	N	Mean	Range
First bat	43	17.0	3.9-39.0	36	2.24	0.68-4.04
Peak rate	46	0.66	0.0- 2.0	46	0.22	0.00-0.56

The initial erratic spring influx of bats into the maternity colony, such as that demonstrated by *M. lucifugus* in the present study, is typical for many vespertilionids (Humphrey, 1971a; Kunz, 1971). It appears that many or most maternity colonies serve at least a partial role as transient colonies, perhaps nearly up to the time of parturition. The *M. thysanodes* in Montezuma Seminary distinctly differ from this pattern with a rapid influx in the spring and a stable population throughout the summer. In previous studies, we have shown that rate of fetal development is profoundly affected by the previous thermal history of the individual, that time of birth is closely determined by the time of return to a maternity roost and that rate of embryo development fluctuates absolutely with the ability of the female to regulate her body temperature (Studier and O'Farrell, 1972; Studier, *et al.,* 1973). In brief, a population of bats returning from the same winter roost to the maternity roost will deliver young at nearly the same time, *i.e.,* within the same week (Table 1). This indicates further that *M. thysanodes* arrive as a relatively uniform population to the maternity roost while *M. lucifugus* return at different times of the spring and probably from different roosts. Humphrey (1971a) has shown that maternity colonies of *M. lucifugus* include residents from several hibernacula. The uniform arrival and parturition span in *M. thysanodes* implies that these bats either overwinter as a group or re-form a single population during return to the maternity colony.

There was a span of about 70 days between the time we captured pregnant *M. lucifugus* in June and August 1969. This is certainly longer than the calculated gestation period of *M. lucifugus* in this colony (O'Farrell and Studier, 1973) and suggests that some adult females may be polyestrous and deliver two young during 1 summer season. This possibility is further supported by the observation that the period of rapid fetal growth in this species requires slightly less than 3 weeks (Studier *et al.,* 1973) and that a few adult males are always present in this maternity colony. Polyestry has been reported for *Myotis,* but only from tropical latitudes (Dwyer, 1970; Wilson and Findley, 1970). A second possibility, although doubtful, is that females still pregnant in August simply arrived very late at the maternity roost from a hibernaculum or that they were not inseminated before their maternity colony arrival.

Our counts from the O'Malley roost during the middle of the summer reproductive season, unlike those of Humphrey (1971a) and Kunz (1971), show no evidence of a peak corresponding to initial outflights of young of the year. Several explanations for this observation are possible. First, development of neonatal *M. lucifugus* is spread over a considerable time period so that numbers of volant young do not reach any obvious synchronous peak. Second, volant young probably emerge from the roost too late to be counted in our normal procedure. Humphrey (1971b) has shown that *Tadarida brasiliensis* of different sexes and reproductive stages emerge at different times from the maternity roost. Third, as we have previously found (O'Farrell and Studier, 1973), volant immature *M. lucifugus* exhibit strong tendencies for "practice flight" late in the evening after most of the adults have left the roost. These practice flights often extend outside the maternity roost and occur late at night. If bats, adult or young, move away from the maternity roost as young become volant, a peak in flight counts might not be observable. This is further supported by age structure data (Table 2). Fourth, it is also possible that peak outflights might have been missed on evenings when counts were not made (Humphrey, 1971a).

The autumn decline in numbers is apparently associated with prehibernation behavior. Previous studies (O'Farrell and Studier, 1973; Ewing *et al.,* 1970; Studier and O'Farrell, 1972) have shown that *M. lucifugus* and possibly *M. thysanodes* could not enter hibernation when they leave the maternity colony. Autumn dispersal in *M. lucifugus* includes an initial departure from the maternity roost, followed by a period of nightly swarming and a redispersal prior to final hibernation (Fenton, 1969, 1970; Humphrey, 1971a). For the past several years, we have observed that *M. lucifugus* leave local maternity colonies a few weeks to a month before *M. thysanodes.* This may relate to our previous hypothesis (Studier and O'Farrell, 1972) that *M. lucifugus* overwinter in a normal hibernation pattern while *M. thysanodes* remain periodically active all winter.

The presence of a small percentage of adult males roosting solitarily within the Montezuma roost is similar to that reported for *Myotis nigricans* (Wilson, 1971) and *M. lucifugus* (Fenton, 1970). Previous authors (Humphrey, 1971a) have stated that yearling females are nearly always pregnant and we agree with that statement (O'Farrell and Studier, 1973). Our colonies, however, differ from others (Fenton, 1970) in that young are born over a broad expanse of time; therefore, females born in August probably do not reproduce as yearlings unless they copulate in late spring or early summer and are the individuals which give birth very late in the summer. The switch from an equal sex ratio to a greater number of females late in the year in young bats may be due to differential mortality or, more likely, to a rapid dispersal of young males from the maternity colony as has been described in *M. nigricans* (Wilson, 1971).

O'Farrell and Bradley (1970) summarized the effects of weather on bat activity. In small desert forms wind greatly reduces activity, but in larger species wind does not seriously affect activity. Rain usually depresses activity. In the present study, we found that wind and rain did not affect overall activity but did affect emergence time, particularly in midsummer. This may be related to nutritional requirements of these bats at this time of year (Studier *et al.,* 1973).

Gould (1961) found that *Tadarida femorosacca* did not emerge from the roost until total solar radiation reached zero. DeCoursey and DeCoursey (1964) indicated that light sampling was apparently the chief means of synchronizing daily emergence cycles. The frequent early emergence of the first bat on rainy or cloudy nights supports their statement. It is apparent that absolute light intensity is not the cue for initiation of activity; but rather emergence is a photoperiodic response directly related to time of sunset.

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