POPULATION ECOLOGY OF THE LITTLE BROWN BAT, _MYOTIS_ _LUCIFUGUS_, IN INDIANA AND NORTH-CENTRAL KENTUCKY

By

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CHAPTER I

INTRODUCTION

Insectivorous bats in North America affect the health, welfare, and economy of man in a variety of ways (Ross, 1967; National Academy of Sciences, 1970; Constantine, 1970). They may be important in controlling populations of some night-flying insects. Many species of bats roost in buildings and produce undesirable noises and odors. Bats may transmit diseases such as rabies and histoplasmosis. To promote understanding of these secretive animals, many studies of the ecological functions of insectivorous bats have been undertaken in recent years.

The little brown bat, *Myotis lucifugus*, is one of the most abundant and widely distributed insectivorous bats in the United States and Canada. Although this species has been the subject of many life history studies (Barbour and Davis, 1969), its population ecology is poorly known. The purpose of the present study was to ascertain the ecological characteristics of the several types of populations formed by *M. lucifugus* and to determine how such populations interact.

Populations were located by an extensive publicity campaign of newspaper articles, "Bats Wanted" posters, radio announcements, and contacts with game wardens, state park superintendents, county extension agents, exterminators, and spelunkers. Populations in buildings and caves were sampled by hand, with long-handled nets, and with bottle forceps. During spring and fall bats were also captured by placing mist nets across cave entrances at night. Captured animals were examined, banded, and released. Bats were classified as immatures or adults according to the cartilaginous or ossified appearance of phalangeal epiphyses. A total of 71,706 *M. lucifugus* was banded from 1952 to 1969.

In this report the four seasons of the year are defined to represent specific phenological units in *M. lucifugus* life history. Winter, 16 October to 31 March, is the period of deep hibernation. Spring, from 1 April to 31 May, includes spring movements and most of the gestation period. Summer, from 1 June to 25 July, includes parturition, maternal care, and the first few days of flight of the young. Fall, from 26 July to 15 October, includes dispersal from the summer roosts, fall migration, and fall swarming behavior. Some phenomena overlap two or three seasons and some seasons may not be accurately defined for all parts of the study area; however, the above definitions are useful for clarity of discussion.

All data reported and cited refer to the eastern subspecies, *M. l. lucifugus*, unless otherwise indicated.

CHAPTER II

POPULATION TYPES AND HABITAT

Nursery Populations

During the warm months female and a few male M. lucifugus congregate in nursery colonies where the females bear and rear their young. Fifty nurseries were found in Indiana. Cope et al. (1961) published a map of the 38 nurseries found by the end of 1960. Twenty-three nurseries were selected for repeated sampling (Fig. 1, Appendix), based on large population size and property-owner cooperation.

Most nursery roosts were in attics of houses and churches, but a few were in barns or school buildings. Most populations occupied single buildings, but several large groups (Thorntown, Franklin, Brookville, Tunnelton, Shoals) used from two to four buildings each, such as a house and nearby barn or several houses in a small town. Movement records show that such a group behaved as a single population. One group, probably a nursery, was found unassociated with human dwellings, a few miles N of Williamsburg, Wayne Co., Indiana. An elm (Ulmus americana) was pushed over with a bulldozer by Mark Wright on 22 May 1967 and approximately 15 bats flew from under loose bark. Wright captured six and gave them to us. Three were adult female M. lucifugus and three were adult female Indiana bats, Myotis sodalis. Their reproductive status was not determined and all were banded and

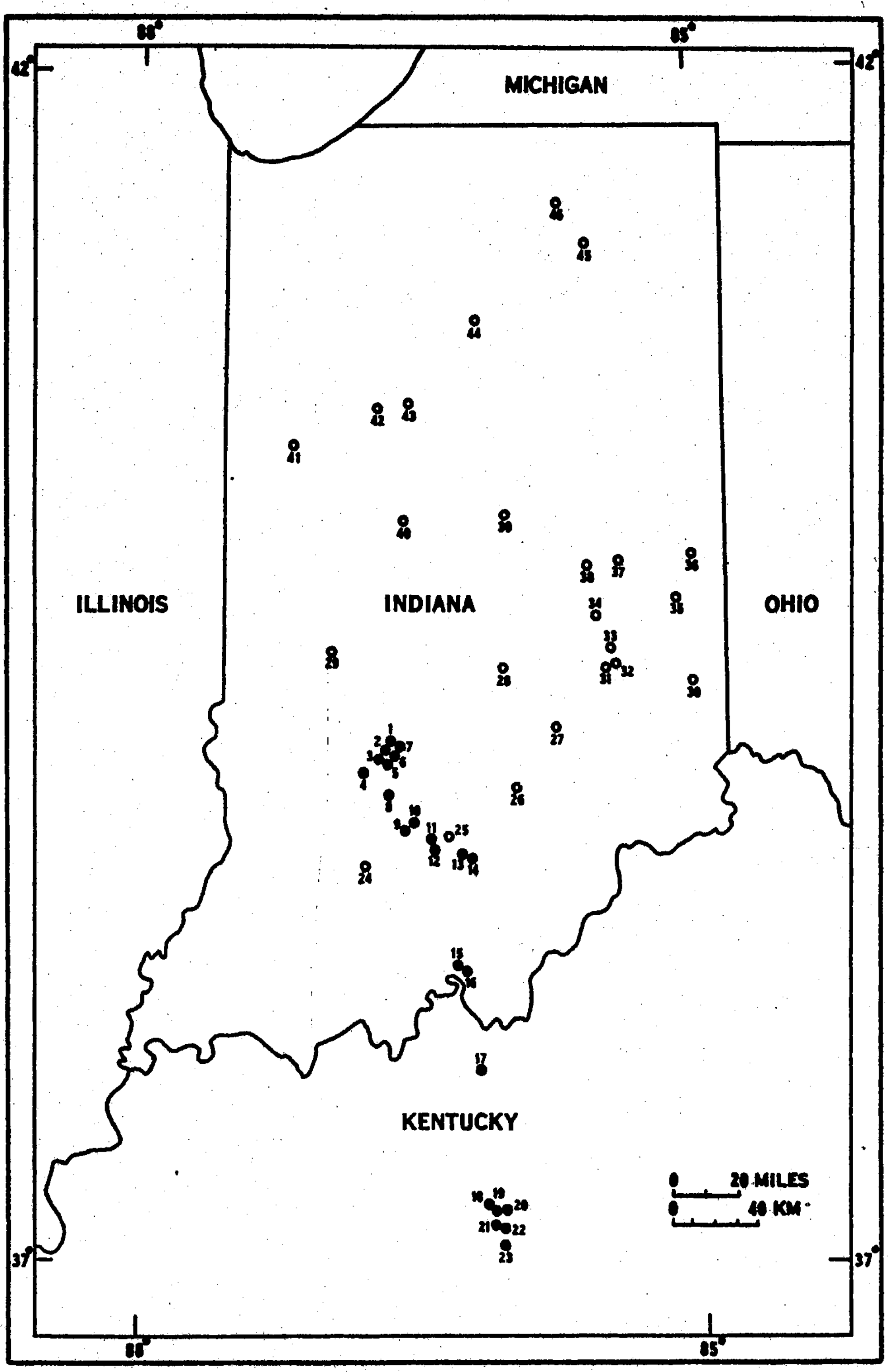

Figure 1. Distribution of Myotis lucifugus populations. Open circles are nursery populations in buildings; closed circles are winter populations in caves. Numbers refer to identity (Appendix)

released. None have been recaptured. Possibly this could have been a spring transient roost rather than a nursery. Although M. lucifugus in the wild is thought to locate nurseries in trees and rock crevices, no such roosts have been reported previously. The only other reports of nurseries not in commensal association with humans are two populations in caves in Illinois (Myers, 1964).

Most roosts were, hot, dark, and poorly ventilated, and contained several small access holes in the roof, eaves, or walls. The species sometimes occurred in the well-lighted and ventilated attics or open barns commonly inhabited by the big brown bat, Eptesicus fuscus. Davis (1967b) suggested that this species may require high nursery temperatures which promote rapid growth of the young. High nursery temperature may be a key aspect of the energetic economy of reproduction and growth. Studier and O'Farrell (1970) found that pregnant female M. lucifugus carissima and young under 10 days old were poor thermoregulators.

We commonly observed behavioral thermoregulation similar to that reported in the Yuma bat (Myotis yumanensis) by Licht and Leitner (1967) and suggested for M. lucifugus by Cagle and Cockrum (1943). On cool days we found the bats in the warmest unexposed places available, such as under shingles and flashing at the attic peak, and in eaves where they met at the peak. On hot days most of the bats hung exposed to the attic air, in loose clusters along the peak and on rafters and end walls below the peak. On very hot days most of the bats moved down the walls and rafters, many going as far as the space between the inner and outer walls of the building. The maximum vertical distance between roosting sites selected on cool and very hot days varied from 1 to 6 m, depending on the structure of the building. The sites chosen for roosting on a particular day had great influence on the proportion of the population we were able to capture.

Most nurseries were located within a few hundred meters of a pond, stream, or river, and the bats flew directly to the water when emerging in the evening. Similar observations were made by Davis and Hickcock (1965).

Shelters or Summer Male Roosts

Several authors have made non-specific reference to individuals or small groups of _M_. _lucifugus_ inhabiting rock crevices, tree hollows and loose bark, and small openings in buildings during the warm months (Griffin, 1940b; Smith, 1954; Cope _et al_., 1961; Krutzsch, 1961; Fenton, 1969b). Specific records of such shelters include house shutters (Sherman, 1929; Miller, 1955; Fenton, 1970), cottage flashing (Hitchcock, 1940; Fenton, 1970), clapboard siding of houses (Glass and Ward, 1959; this study), under rocks (Fenton, 1970), under a shale ledge (Baker, 1964), a stone quarry (Jones, 1964; Kunz, 1965), a copper mine (Stones and Oldenburg, 1968), and caves (Krutzsch, 1961; Davis and Hitchcock, 1965; Heltsley, 1965). Building shelters found in this study were in barns or picnic pavilions of Turkey Run State Park in Parke Co., Jackson County State Park, Shades State Park in Montgomery Co., and Ferdinand State Park in Dubois Co. No major cave shelters were found but intermittant use of Donnehue's, Ray's and Wyandotte Caves was noted. Animals found in these situations were mostly males seeking daytime shelter separate from nursery roosts.

While some of these were transient roosts, other had long histories of regular use. Droppings indicated repeated occupancy of two building shelters (Hitchcock, 1940) and a cave (Krutzsch, 1961). Sherman (1929) observed M. lucifugus at a building shelter from 1915 to 1928. Miller (1955) reported 10 years of observations of a shelter between 1942 and 1954. Collections and sample data were taken for six years between 1954 and 1969 at another shelter (Glass and Ward, 1959; this study). Such observations are frequent and widespread enough to justify the conclusion that substantial numbers of M. lucifugus, mostly males, roost in shelters in the warm months.

Winter Populations

M. lucifugus hibernates in caves and mines during the winter. Thirty-six caves in Indiana and 18 in Kentucky were examined for winter populations. This species occurred in 27 of the Indiana caves and six of the Kentucky caves. Six Indiana caves and two Kentucky caves were selected for repeated sampling (numbers 1, 2, 4, 10, 12, 15, 17, and 20 in Fig. 1 and Appendix) because of large population size.

The winter roost sites chosen by M. lucifugus were relatively uniform and stable in microclimate. The selected sites were cool and humid and (except at Wind Cave) had almost no air flow. Because small caves in the study area were usually either warm or variable in temperature, M. lucifugus occurred in large numbers only in the larger caves where cool, stable conditions existed far from any entrance. Although measurements of M. lucifugus hibernaculum microclimate are available (e.g., Myers, 1964), apparently no one has examined wither roosts for seasonal (October to April) variations in temperature, humidity, and air flow which might mediate winter population changes.

CHAPTER III

MOVEMENT PATTERNS

Since extensive bat banding programs have begun in North America M. lucifugus has become well known as a migratory species. Migratory movements were recorded in the eastern United States and Canada by Griffin (1940a, 1945), Gifford and Griffin (1960), Davis and Hitchcock (1965), Hitchcock (1965), and Fenton (1970). Less extensive information on M. lucifugus migration is available for the midwestern United States, although several field projects are in progress. Humphrey and Cope (1964) reported winter recaptures of bats banded at a single nursery in Indiana. Davis et al. (1965) and Barbour and Davis (1969) presented migration data from nurseries and hibernacula in several areas of Kentucky. Myers (1964) documented migration from hibernacula in Missouri.

In the present study 895 bats or 1.25% of the banded M. lucifugus were recaptured away from the banding site. Of these, 845 first recaptures at each location were enumerated by season. The records originating in fall and spring were almost all banded while flying through cave entrances rather than roosting. All movement records reported here are partial histories of movements. In no cases are the details of night-to-night movement known, and probably none of these movements are straight through space and regular through time as simple maps and tables imply.

Fig. 2 illustrates fall migration from one of the northernmost nurseries to caves in southern Indiana and central Kentucky. The longest movement, to Colossal Cave, was 455 km. Figs. 3-7 show fall migration from other nurseries and indicate some variations in movement patterns. Except in Fig. 2, only fall-banded bats are considered because too few were banded in summer to adequately illustrate the full range of movements which occurred. Fall data are less satisfactory than summer data because they are confounded by other phenomena, as discussed below. However the movements shown are fairly representative of nursery-to-hibernaculum migration. The net distance of fall migration was as short (Fig. 6) as 10 km. Most fall migration flights were from north to south but some movements occurred in all directions, depending on nursery location. Specific migration records (Table I) show that movements may take from 2 to 14 days. Possibly sampling designed to measure minimum movement time would show quick movements to be typical. Nursery flight counts and fall netting at caves provide further insight into fall migration (see Chapter IV). Migration and associated phenomena began in the last week of July and continued to the third week of October.

Fall migration was often quite different from simple linear movement. Several other types of movement occurred before, during, and after migration, viz. fall dispersal or wandering, transient visitation of non-home nurseries, fall swarming at caves, secondary dispersal, and secondary migration.

Fall dispersal and transient nursery visitation differed primarily in the way we detected them. Dispersal was exhibited by 61 *M. lucifugus* banded at nurseries in summer or fall and reported as citizen recaptures

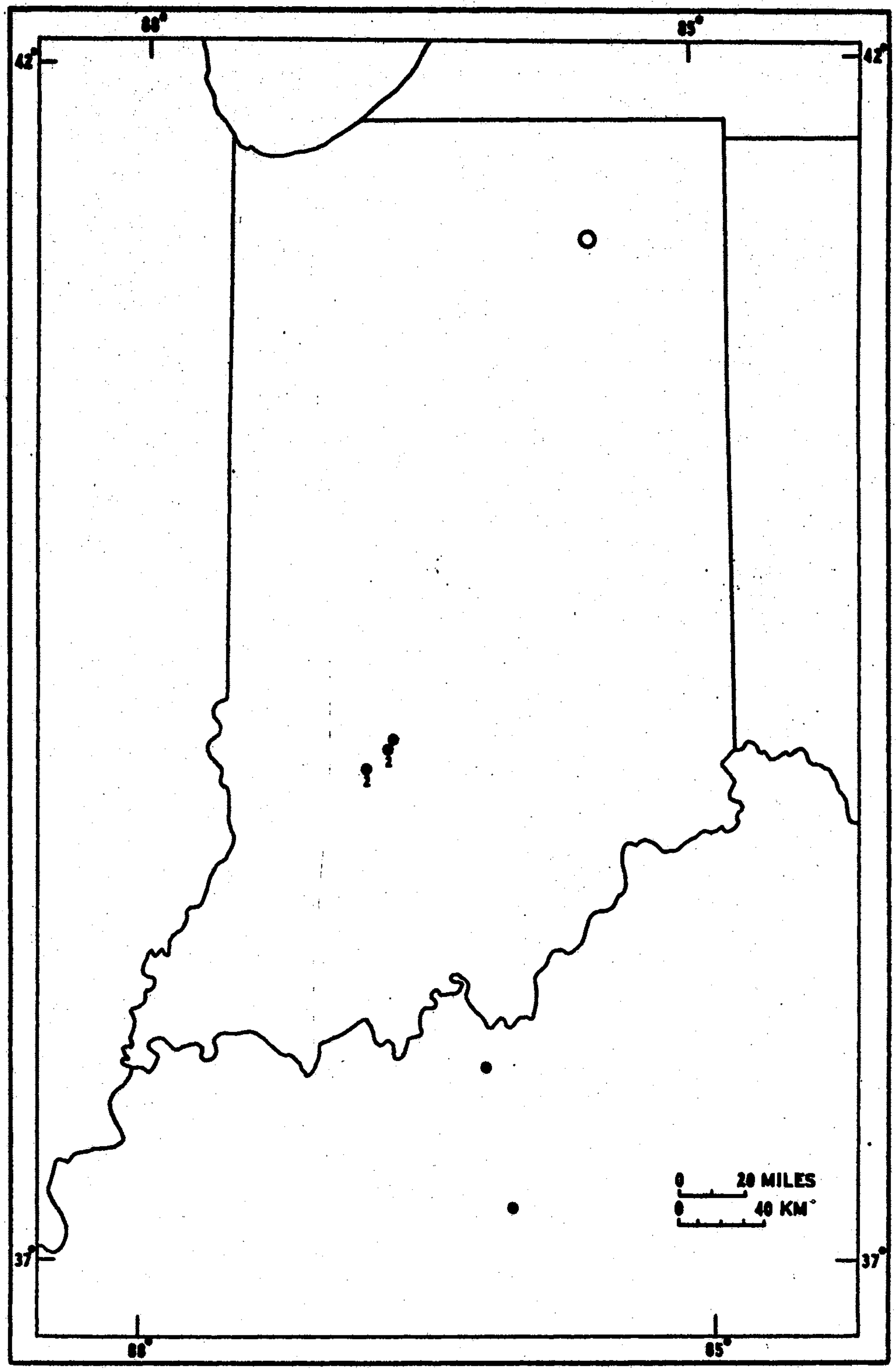

Figure 2. Foreign recaptures in any winter of female M. lucifugus banded at the Etna nursery (open circle) in summer. Numbers indicate more than one such movement

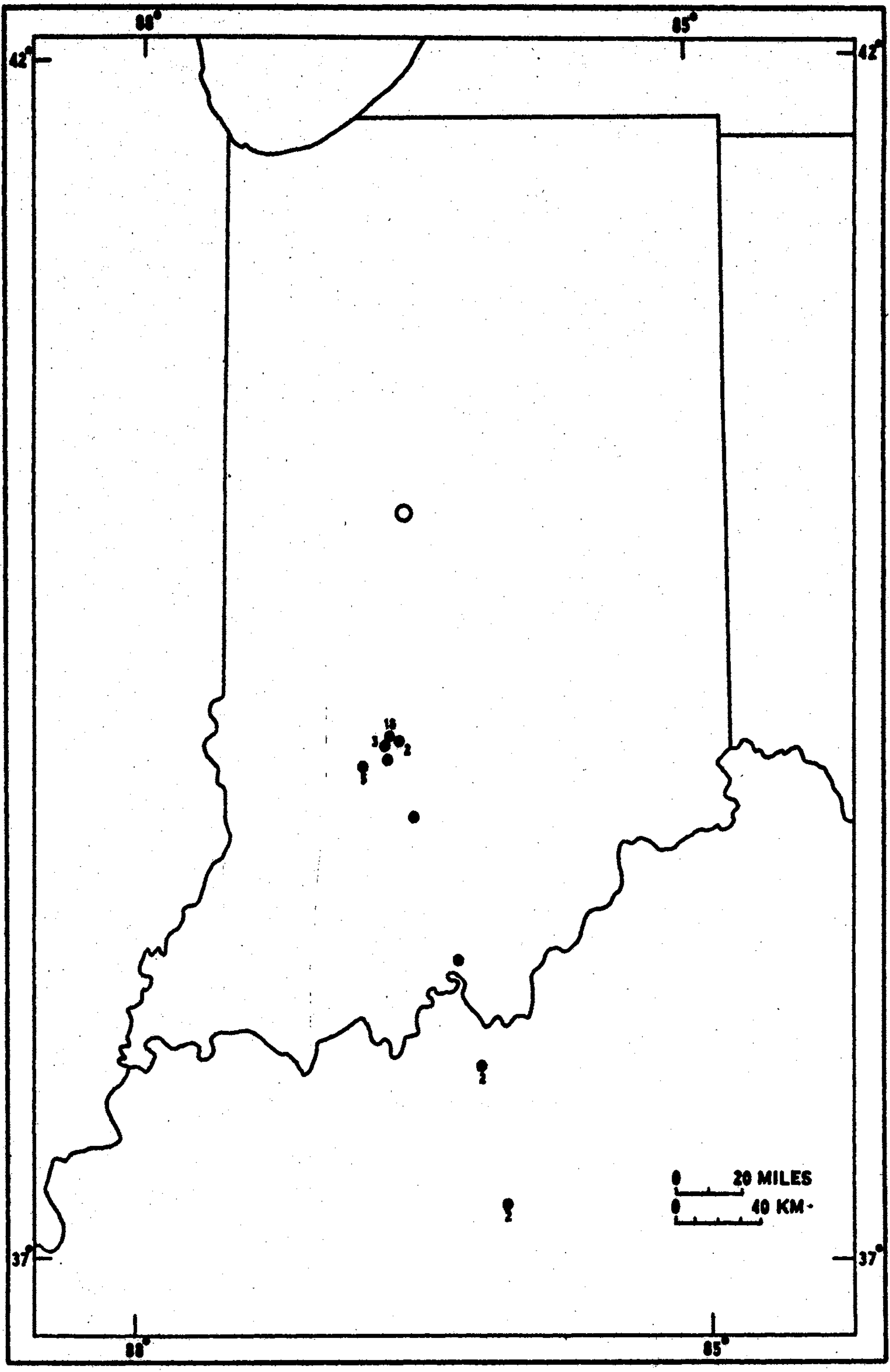

Figure 3. Foreign recaptures in any winter of both sexes of *M. lucifugus* banded at the Thorntown nursery (open circle) in fall

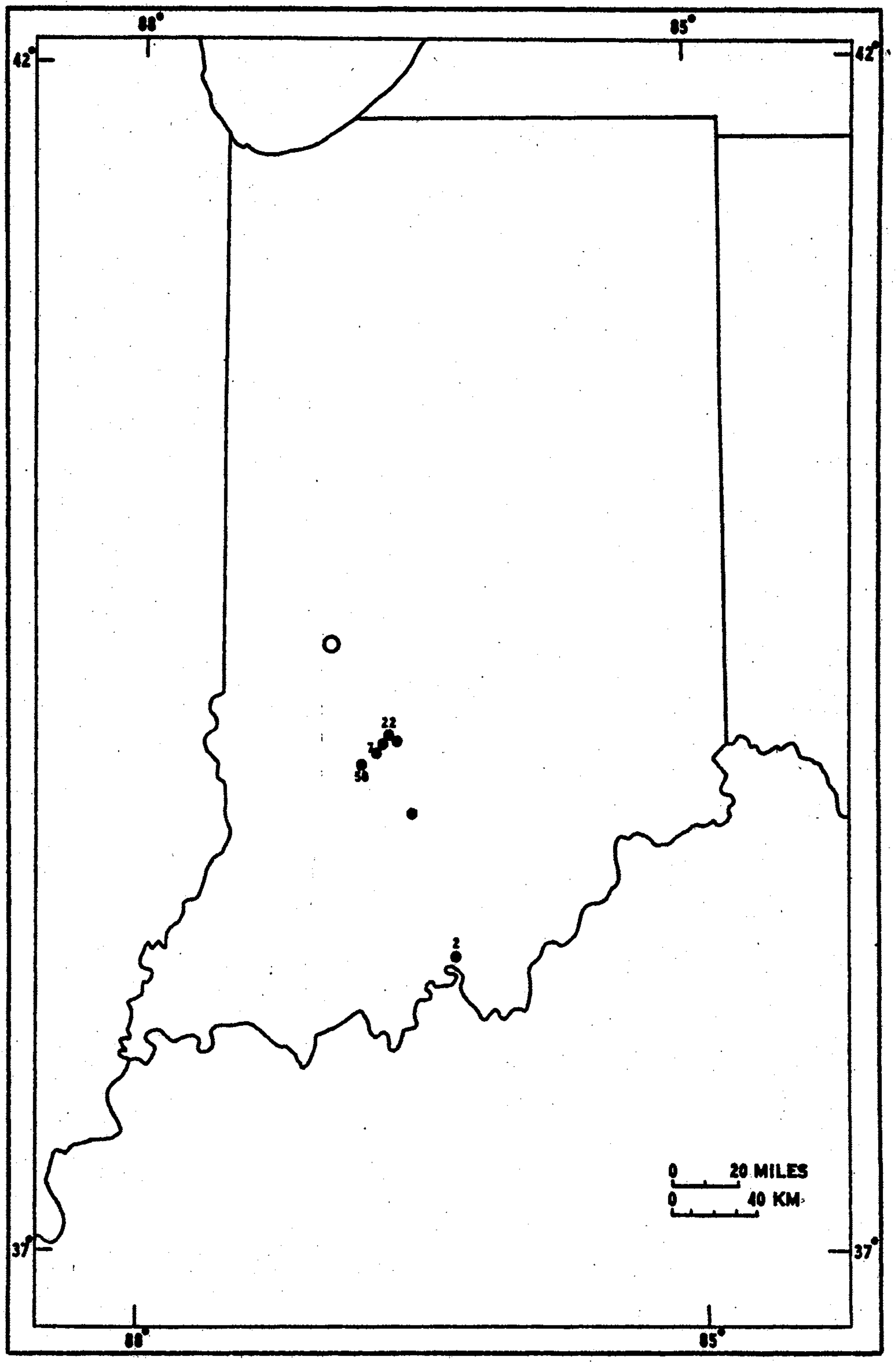

Figure 4. Foreign recaptures in any winter of M. lucifugus of both sexes banded at the Reelsville nursery (open circle) in fall

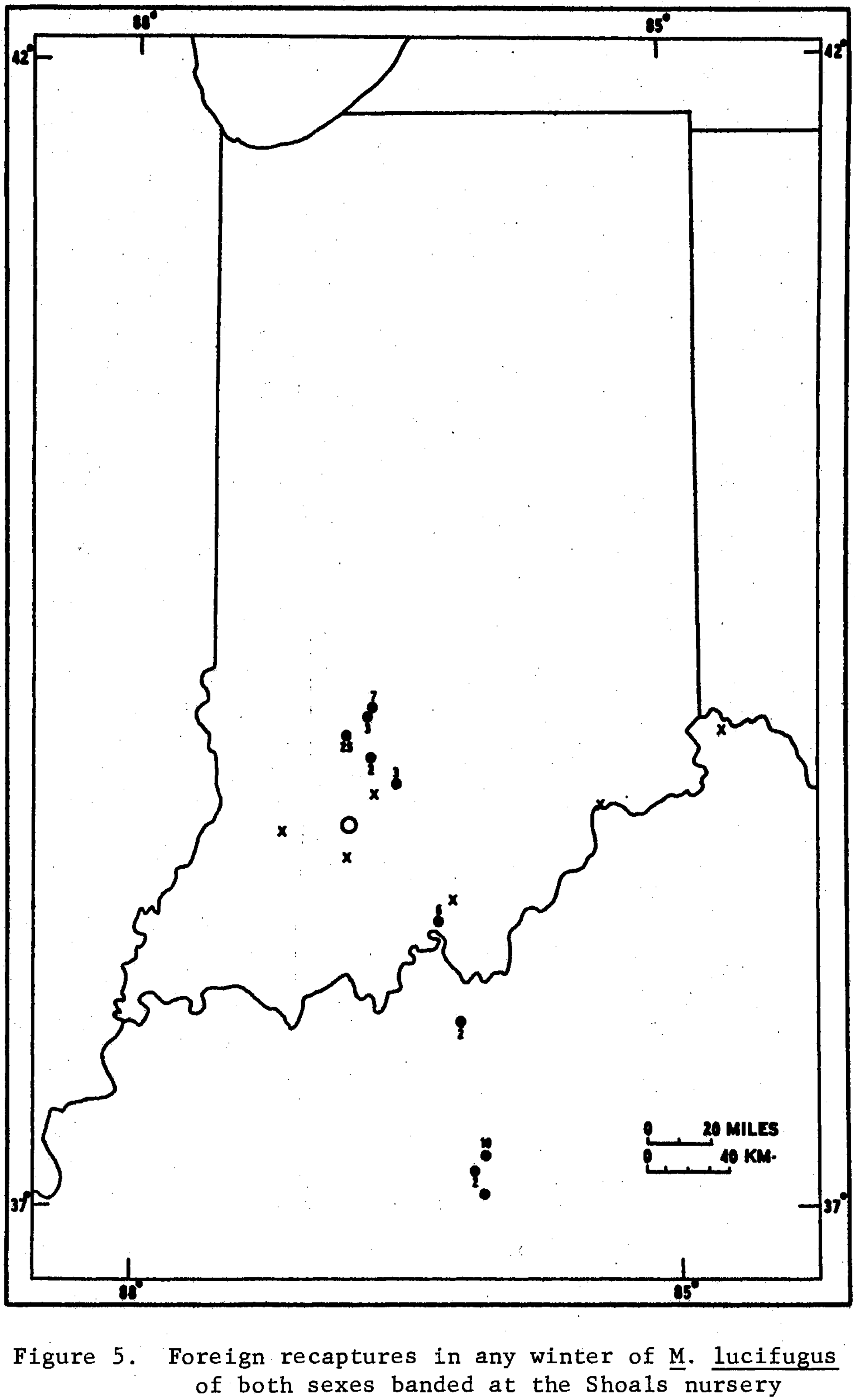

Figure 5. Foreign recaptures in any winter of M. lucifugus of both sexes banded at the Shoals nursery (open circle) in fall. "X" indicates a citizen recapture

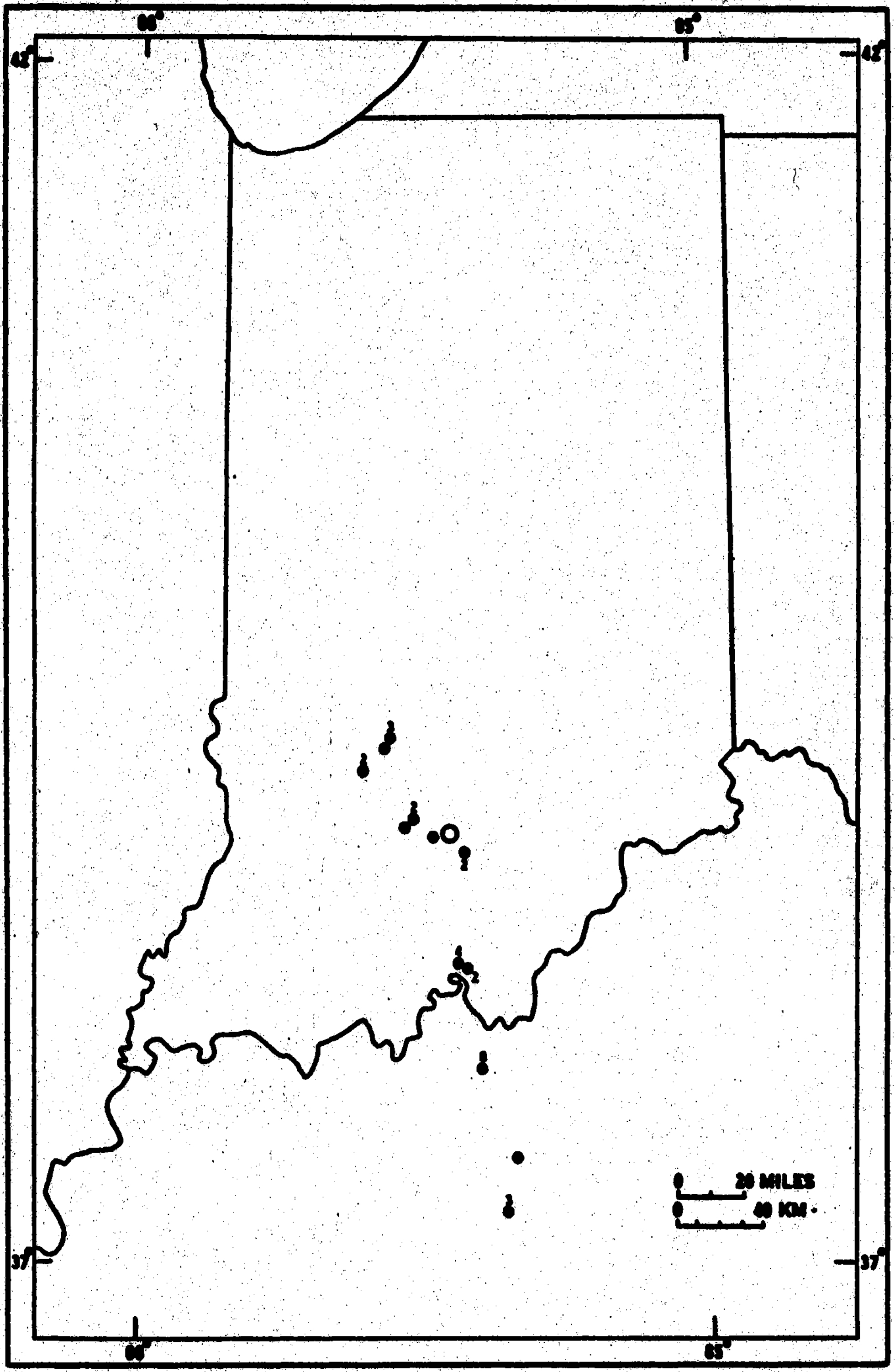

Figure 6. Foreign recaptures in any winter of M. lucifugus of both sexes banded at the Tunnelton nursery (open circle) in fall

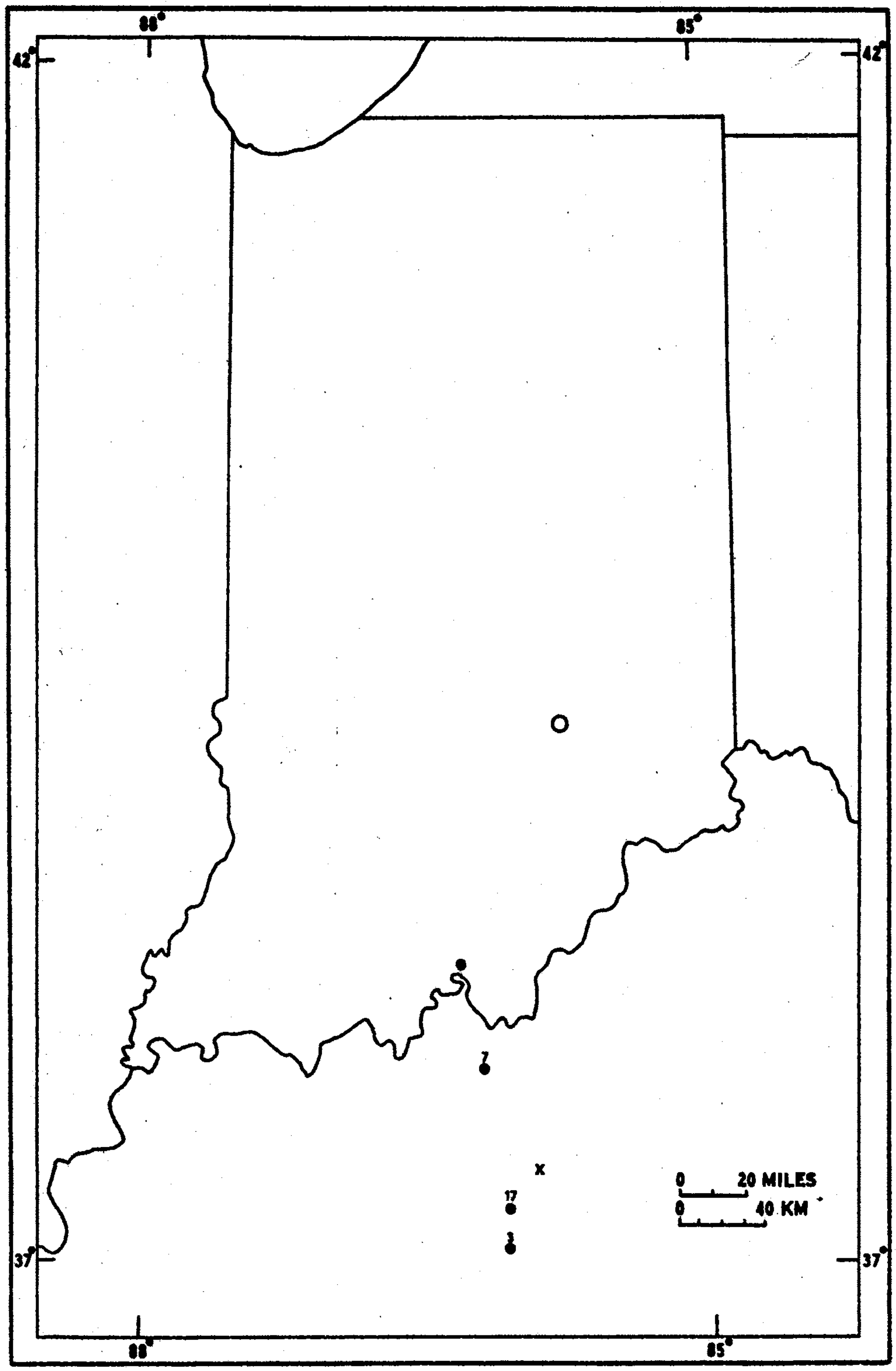

Figure 7. Foreign recaptures in any winter of *M. lucifugus* of both sexes banded at the Newbern nursery (open circle) in fall. "X" indicates a citizen recapture

TABLE I

SELECTED RECORDS OF FALL MIGRATION IN *M. LUCIFUGUS*

~~Sex~~	Banding site	Banding date	Recapture site	Recapture date	Number of days elapsed	Distance (km)
F	Newbern	14 August 1961	Colossal Cave	27 August 1961	13	227
M	Thorntown	20 August 1960	Donnehue's Cave	1 September 1960	12	140
M	Thorntown	20 August 1960	Donnehue's Cave	2 September 1960	13	140
F	Tunnelton	22 August 1961	Wyandotte Cave	24 August 1961	2	60
F	Tunnelton	30 August 1963	Dixon Cave	13 September 1963	14	174

over various time intervals. A relatively large number of these movements (17) took place within fall or from summer to fall. Age and sex identity of these were one adult female, two immature females, four unaged females, four immature males, and six unaged males. No particular directional pattern was apparent in dispersal movements. In nursery samples we recorded transient nursery visitation in the fall (Table II), which showed no strong pattern according to direction or age-sex involvement. Some of these movements may have followed secondary dispersal (see below) and thus have been quite indirect. However, the first two were probably fairly direct, since brief periods elapsed between capture and recapture (2 and 7 days, respectively).

Fall swarming is a phenomenon in which large numbers of bats of several species fly in and out of cave entrances from dusk to dawn. Similar but less intense activity also occurs in the spring. Information on movements associated with fall swarming is based on netting at Wyandotte Cave from 1961 to 1965 (8,962 _M_. _lucifugus_ banded) and at Wind Cave from 1962 to 1964 (3,701 banded). In addition, Davis (1963) handled 6,616 _M_. _lucifugus_ at Dixon Cave in the fall of 1963. When swarming activity was high in August and September, several hundred _M_. _lucifugus_ were captured at cave entrances each night but few were found roosting in the caves in the daytime.

Few _M_. _lucifugus_ were captured more than once at the same cave during a single fall season. The swarming bats left the area quickly, with individuals remaining at a cave for only a few days at most. However, as far as can be shown by these three widely separated caves, little within-season shifting from one cave to another occurred. Only one individual was taken at two swarming caves during one season: a

TABLE II

WITHIN FALL OR SUMMER-TO-FALL MOVEMENTS OF NURSERY-BANDED *M. LUCIFUGUS* TO OTHER NURSERIES

Age and sex	Banding site and date		Recapture site and date		Distance (km)	Direction
M	Thorntown	20 August 1960	Shirley	22 August 1960	87	ESE
F	Franklin	15 August 1961	Tunnelton	22 August 1961	82	SSW
F	Etna	22 July 1959	Cicero	19 August 1959	134	SSW
ad F	Tunnelton	14 June 1960	Newbern	22 August 1960	71	NE
im F	Cicero	31 July 1962	Franklin	7 August 1962	71	S
im M	Milroy-South	23 July 1962	Cortland	17 August 1962	71	SW

male netted at Wind Cave on 20 April 1963 was re-netted at Dixon Cave on 1 September 1963 and at Wind Cave on 4 September 1963. Many bats swarmed at the same cave in successive years. Small numbers of bats were found swarming at other caves during the succeeding fall. Four bats netted at Wyandotte Cave were re-netted at other caves about a year later (two at Wind Cave, one at Dixon Cave, and one at Short Cave); one netted at Wind Cave was netted at Dixon Cave about a year later.

Large numbers of _M. lucifugus_ netted at Wyandotte and Wind in fall were found hibernating in the same cave in the succeeding winter or subsequent winters. A few wintered in caves other than the swarming site. Fourteen bats banded in fall at Wyandotte were found in a subsequent winter at different caves: one at Grotto, three at Coon's, three at Ray's, one at Donnehue's, one and Endless, two at Wind, and three at Colossal Cave. One banded in the fall at Wind was found in the winter at Parker's Pit.

Netted recaptures within a season or in consecutive seasons of _M. lucifugus_ banded in Indiana nurseries showed few swarming at the two Kentucky caves. Summer-to-fall and within-fall movements of females included seventeen recaptures at Wyandotte Cave (nine from Tunnelton and one or two each from six other nurseries), two at Wind Cave (from Tunnelton), and one at Dixon Cave (from Tunnelton). Most of these movements were within a fall season; summer-to-fall records account for only two movements to Wyandotte. The four recaptures of Wyandotte-banded females at nurseries in the next summer were widely dispersed. No such movements were recorded for bats netted at Wind Cave. Bats from the Indiana nurseries apparently concentrated their swarming activity at Indiana caves, including only the northernmost of the three swarming sites examined. Most of the M. lucifugus swarming at Wind and Dixon Caves probably were summer residents of Kentucky and extreme southern Indiana. Davis (1963), in citing recaptures of our nursery-banded bats, probably overemphasized the contribution of Indiana nurseries to Dixon Cave swarming. None of the eleven bats banded at Indiana nurseries in summer or fall and recaptured at Dixon Cave were taken in the same year; five of these were banded in fall and their apparent dispersal was possibly confounded by other fall movements prior to banding.

Significant numbers of M. lucifugus netted while swarming exhibited a secondary dispersal by moving away from the swarming cave, mainly in a northerly direction. Secondary dispersal of thirteen females and seventeen males is shown in Figs. 8 and 9, respectively. Males appear to confine this movement within short distances from the cave regions, while females move farther. A strong tendency to move to the Tunnelton nursery existed in both sexes. Secondary dispersal probably includes a wider variety of nursery roosts than we recorded, since we did not sample many nurseries at the appropriate times. Trips from Wyandotte Cave to Tunnelton, 60 km away, were made in one night by several females and males. For example, a male netted at Wyandotte on the evening of 4 September 1963 was captured on the next afternoon in the Tunnelton roost. A female netted at Wyandotte on 18 August 1964 was recaptured in the Thorntown barn on 26 August 1964, 209 km to the north. Few similar records were obtained from bats netted at the two Kentucky caves, with two movements to Indiana from Wind and one from Dixon. A female netted at Wind on 1 September 1963 was 143 km to the north at Columbus, Bartholomew Co., Indiana, on 7 September 1963. A male moved

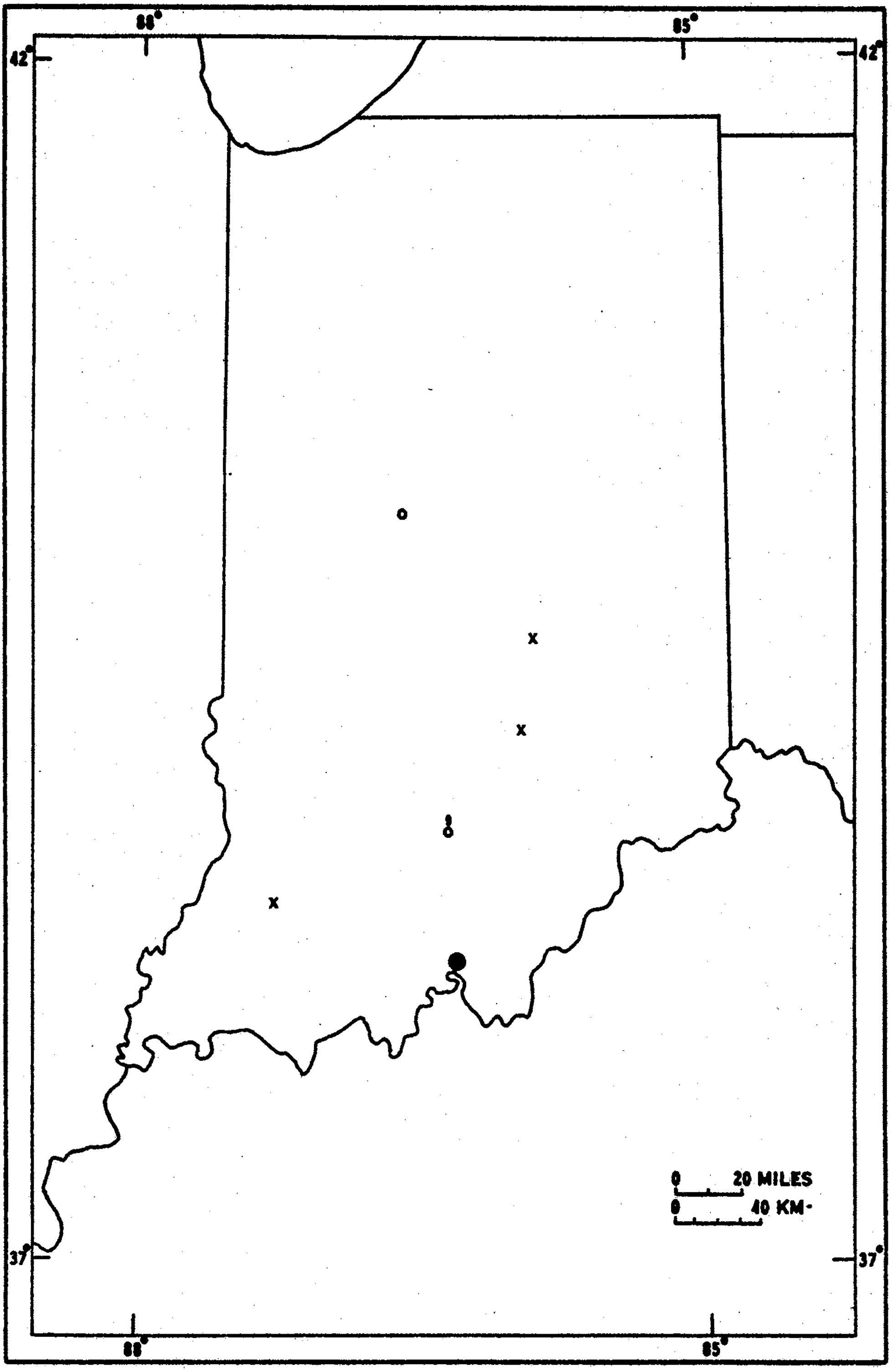

Figure 8. Secondary dispersal of female M. lucifugus banded while swarming at Wyandotte Cave (closed circle). "X" indicates a citizen recapture

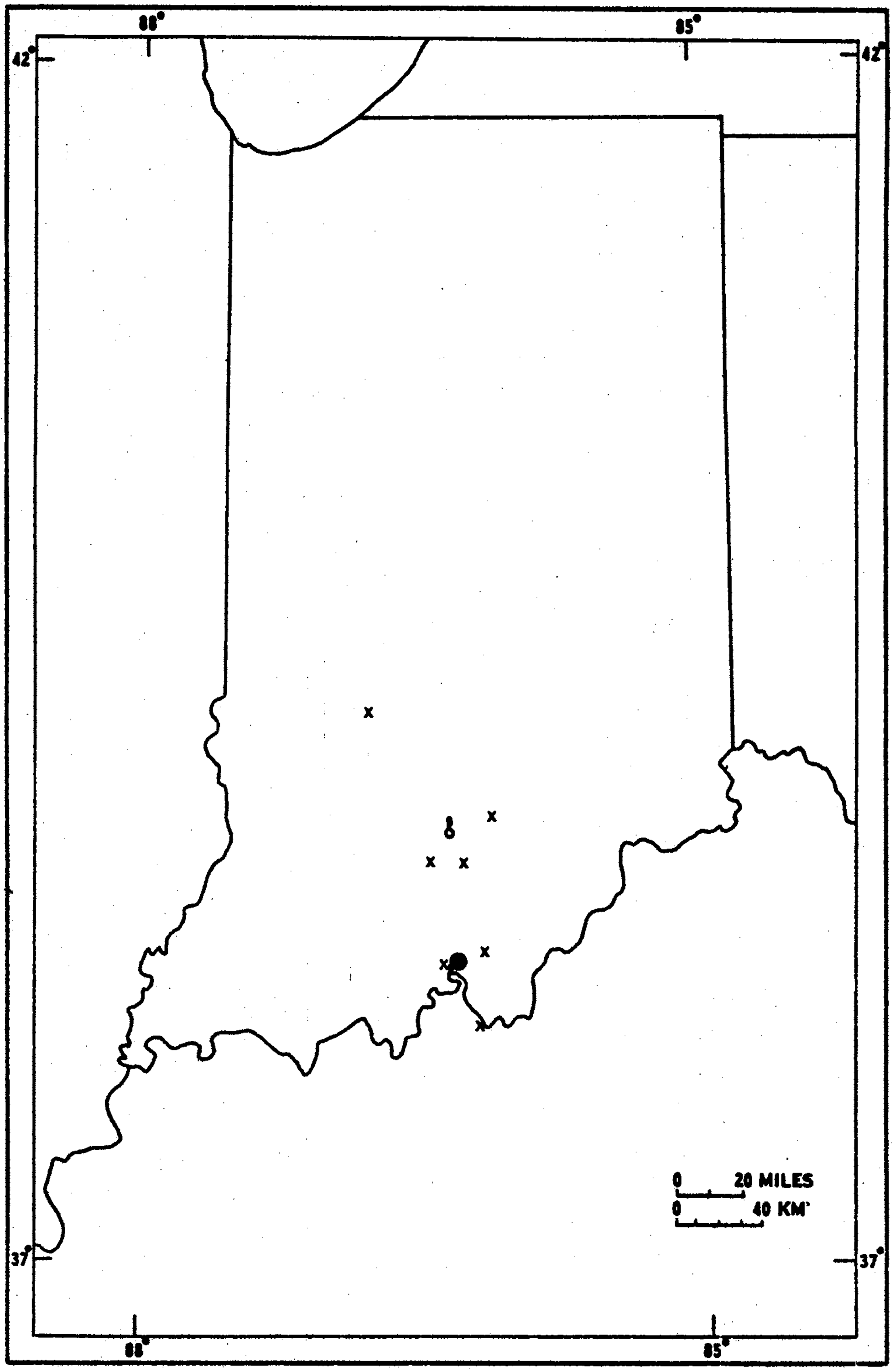

Figure 9. Secondary dispersal of male M. lucifugus banded while swarming at Wyandotte Cave (closed circle). "X" indicates a citizen recapture

109 km north from Wind on 1 September 1963 to Tunnelton on 15 September 1963. Davis (1963) cited a female which he banded at Dixon Cave on 30 August 1963 and we recaptured at Tunnelton on 5 September 1963, 174 km to the north. Bats participating in secondary dispersal presumably also undergo secondary migration before winter.

The degree to which M. lucifugus move from one cave to another during winter is not well understood. Griffin (1940a, 1945) cited two within-winter movements from cave to cave, each with the second capture in April. I suspect that April recaptures in New England should be considered spring records. In Indiana a variety of movements are associated with spring migration and swarming at caves, making cave recaptures from winter to April difficult to interpret. Hitchcock (1945) reported a 113 km, one-day movement of a male in December but suggested that the apparently anomalous datum was the result of a record-keeping error. Fenton (1970) recorded two within-winter changes of hibernaculum by males, one from October to December and one from November to March. Table III lists within-winter movements during the present study. Some were from one cave to another, but several citizen recaptures were from non-cave locations. Three other winter recaptures do not show direct movements but further reflect winter activity. A female from the Shoals nursery was recaptured in a house 14 km S of Shoals on 15 December 1963. A male from the Franklin nursery was found dead behind a house screen door on 13 January 1967 in Milltown, Crawford Co., Indiana. A female netted at Wyandotte Cave on 29 August 1963 was found dead but clinging to the south side of a house 13 km W of Columbus, Bartholomew Co., Indiana, on 20 December 1963. When this bat was found the sun was shining but the temperature was below freezing.

TABLE III

WITHIN-WINTER MOVEMENTS OF *M. LUCIFUGUS* BANDED AT CAVES

Sex	Banding site	Banding date	Recapture site	Recapture date	Distance (km)	Direction
F	Ray's Cave	21 November 1964	Clay Co.*	15 December 1964	66	NNW
F	Ray's Cave	9 January 1966	Green Co.*	14 March 1966	16	WNW
F	Ray's Cave	9 January 1966	Pulaski Co.*	21 March 1966	220	N
F	Ray's Cave	11 February 1967	Green Co.*	27 February 1967	6	N
M	Ray's Cave	15 February 1969	Green Co.*	23 February 1969	13	W
M	Grotto Cave	21 February 1965	Ray's Cave	29 March 1965	16	SW
M	Grotto Cave	28 March 1961	Coon's Cave	28 March 1961	2	NE
M	Wyandotte Cave	2 March 1957	Salt Peter Cave	9 March 1957	1	W

* Non-cave location in Indiana

These data plus those of Hitchcock and Fenton confirm that M. lucifugus move from cave to cave and from caves to cave-less areas during winter. Harsh conditions encountered during mid-winter movements apparently account for a moderate number of deaths. This species does not display enough winter activity to be classified with those species (e.g. Eptesicus fuscus, Mumford, 1958) which typically move in and out of caves repeatedly during the winter.

Records of change of hibernaculum in M. lucifugus from one year to another are common (Griffin, 1940a, 1945; Myers, 1964; Fenton, 1970). Twenty-four such changes in hibernaculum were documented in this study (Table IV). Some of these were from one winter to the next while others were not consecutive-year recaptures. The proportions of females and males involved in these shifts were similar to the proportions banded, indicating no difference by sex.

Few data are available to elucidate spring movements. Our winter-to-spring and within-spring movements reflect spring "staging" activities, dispersal, and migration. Staging activities include marked increases and decreases in cave populations (Davis and Hitchcock, 1965), cave-to-cave movement in early spring, and nocturnal flight in and out of caves similar to fall swarming behavior. Spring dispersal is generally northward, with some divergence to the east and west. Our records of spring migration reveal a simple cave-to-nursery pattern, showing approximately the opposite of directional patterns described for fall migration. We do not know whether or not spring movements include complex patterns such as those found in the fall.

In sharp contrast to the variety and complexity of movements in fall, winter, and spring, female and male M. lucifugus exhibit a high

TABLE IV

MOVEMENTS OF CAVE-BANDED *M. LUCIFUGUS* FROM WINTER TO ANY SUBSEQUENT WINTER

Banding site	Recapture site	Number of movements female	male
Grotto Cave	Coon's Cave	0	2
Grotto Cave	Shaft Cave	0	3
Grotto Cave	Buckner's Cave	1	1
Grotto Cave	Ray's Cave	0	1
Grotto Cave	Donnehue's Cave	0	2
Grotto Cave	Wyandotte Cave	2	0
Coon's Cave	Grotto Cave	0	2
Coon's Cave	Buckner's Cave	0	1
Coon's Cave	Ray's Cave	1	2
Ray's Cave	Grotto Cave	2	0
Wyandotte Cave	Grotto Cave	1	2
Wyandotte Cave	Long's Cave	0	1
Total		7	17

degree of attachment to a nursery site in the summer. Only one female moved from one nursery to another within a summer, from Cicero on 9 June 1964 to Tipton, Tipton Co., Indiana (a citizen report), during the week of 19-25 July 1964. This recapture is so close to the date of 26 July defined as the beginning of fall dispersal that such activity may have been involved here also. Among 2,841 adult and immature females banded in summer, no recaptures occurred during any later summer other than at the home nursery. Only one male moved from summer-to-summer, from Macy on 24 July 1959 to Etna on 20 July 1960. Because only 271 males were banded in the summer, it is difficult to judge from the movement data alone whether or not males are typically restricted to a home roost.

To quantify a bat's tendency to reside year after year in the same roost, I employed a site attachment index:

$$\frac{\sum\left(\frac{Y_r}{Y_p}\right)}{n},$$

where Y_r is the number of years an individual was recaptured at the banding site and Y_p is the number of recapture-years possible in the individual's history. Samples selected for calculating index values were large, were banded early in the study, and had long histories of recapture opportunity in subsequent years. The attachment index is independent of mortality rate because it includes only the individuals recaptured at the banding site and uses as the denominator only the number of recapture-years possible until an individual's last recapture. The index is a function of the probability of the individual being at the banding site at a similar time each year and of our capture efficiency, which depended on the proportion of the population captured in each sample and the number of samples taken at the site each year. Capture efficiency was always less than 100%, resulting in underestimation of site attachment. Capture efficiency in one visit to a nursery rarely exceeded 50% but was improved by sampling repeatedly.

Nursery site attachment values are given by age and sex in Table V. Values averaged from approximately 0.64 to 0.88 and were high considering our low capture efficiency. These bats have a strong tendency to return to the same nursery year after year. The average value of 0.88 for adult males is especially high in view of the small numbers of males present and what we had assumed was a preference for separate male roosts. This high value indicates that the adult males frequenting nurseries must have strong nursery site attachment, while most males must visit nurseries seldom or never.

TABLE V

NURSERY SITE ATTACHMENT OF *M. LUCIFUGUS*

Sample type	Banding date	Sample size	Number recaptured	Maximum number of recapture-years	Site attachment value
females of all ages					
Tunnelton	30 August 1954	156	46	10	0.539
Tunnelton	1 October 1954	29	9	13	0.639
Tunnelton	7 August 1957	288	98	10	0.810
Tunnelton	14 August 1957	228	59	7	0.723
Franklin	30 July 1959	365	176	4	0.813
Franklin	22 August 1960	219	107	3	0.846
$\bar{x}$					0.780
males of all ages					
Tunnelton	30 August 1954	73	11	11	0.589
Tunnelton	1 October 1954	151	25	8	0.786
Thorntown	19 August 1959	33	11	5	0.670
$\bar{x}$					0.712
adult females					
Tunnelton	20 April 1955	278	127	8	0.594
Etna	20 July 1960	60	7	3	0.809
Pine Village	28 July 1960	57	9	2	0.889
Thorntown	3 August 1961	125	36	4	0.708
$\bar{x}$					0.640

TABLE V (Continued)

Sample type	Banding date	Sample size	Number recaptured	Maximum number of recapture-years	Site attachment value
adult males					
Tunnelton	4 July 1956	54	15	9	0.887
Tunnelton	29 May 1958	17	3	5	0.800
Thorntown	3 August 1961	17	6	3	0.889
$\bar{x}$					0.877
immature females					
Etna	20 July 1960	73	8	3	0.896
Camden	25 July 1960	17	4	2	0.875
Thorntown	3 August 1961	89	12	5	0.611
Tunnelton	25 July 1962	175	34	6	0.787
$\bar{x}$					0.772
immature males					
Tunnelton	25 July 1962	151	15	6	0.689
Tunnelton	30 July 1964	96	2	4	0.625
$\bar{x}$					0.681

CHAPTER IV

POPULATION SIZE AND FLUCTUATION

Nursery Populations

The 50 nurseries examined varied in size from about 20 to 3,000 adult females and young, but most populations ranged from 300 to 1,200 bats. Nursery populations farthest from the hibernacula, in the northern part of the study area, contained relatively few bats, and the largest nurseries were near the caves. At most nurseries we estimated population size while obtaining samples from the roost sites, by estimating the total number of bats present or adding the sample size to an estimate of the number which escaped sampling. Such visual estimates were not accurate because some bats were inaccessible between boards and shingles, behind beams and rafters, or down in the walls of the building. The proportion of bats which were inaccessible depended on roost temperatures at the time of sampling and on the frequency of disturbance in previous weeks or months. In addition, even experienced observers demonstrated fairly consistent individual bias in estimating numbers. Despite these difficulties, visual estimates give a general view of relative nursery size and form the basis for later discussion of population declines.

Accurate measurement of nursery population size was important for detailing phenological changes and for evaluating sample data so as to determine the actual numbers of animals undergoing various processes.

We obtained more accurate data by counting bats as they left their roosts at dusk. Flight counts have been applied to bats infrequently in the past; pertinent references were listed by Humphrey (1971).

We conducted flight counts at the Thorntown and Pennville nurseries, where vision was not obstructed by trees surrounding the exits and two observers could see almost all bats which flew. Bats flew from the Thorntown house and barn directly to a pond; 3% (n=1) did not go to the pond and were not included in the counts. Bats flew from the Pennville house to a stream. A few bats resided under the roof of an addition to the house and when exiting were not visible to the usual two observers. These comprised 3 to 7 ($\bar{x}$=5.6, n=3)% of the total population and were seldom included in the counts. Evening emergence patterns (Fig. 10) were more or less normally distributed but showed irregularities resulting from brief bursts of activity between short inactive periods. Flights were of short duration and few bats were missed because of darkness. The low exit rate caused no difficulty in counting individuals. Post-flight checks of the roosts in early June, late July, and August showed that few volant individuals failed to fly. We did not check during or shortly after the parturition period. Post-flight sounds suggested that flights were not complete during this time, so some bias is expected.

In 1964 visual estimates at the Thorntown nursery (Fig. 11) showed no readily interpretable pattern until mid-August when they were adjusted to the approximate magnitude of our first flight counts. In 1965 we made flight counts about once a week to perceive changes in population size. Immigration occurred from April to mid-May, when the population stabilized at about 400 adults. A decline to about 380 bats began in

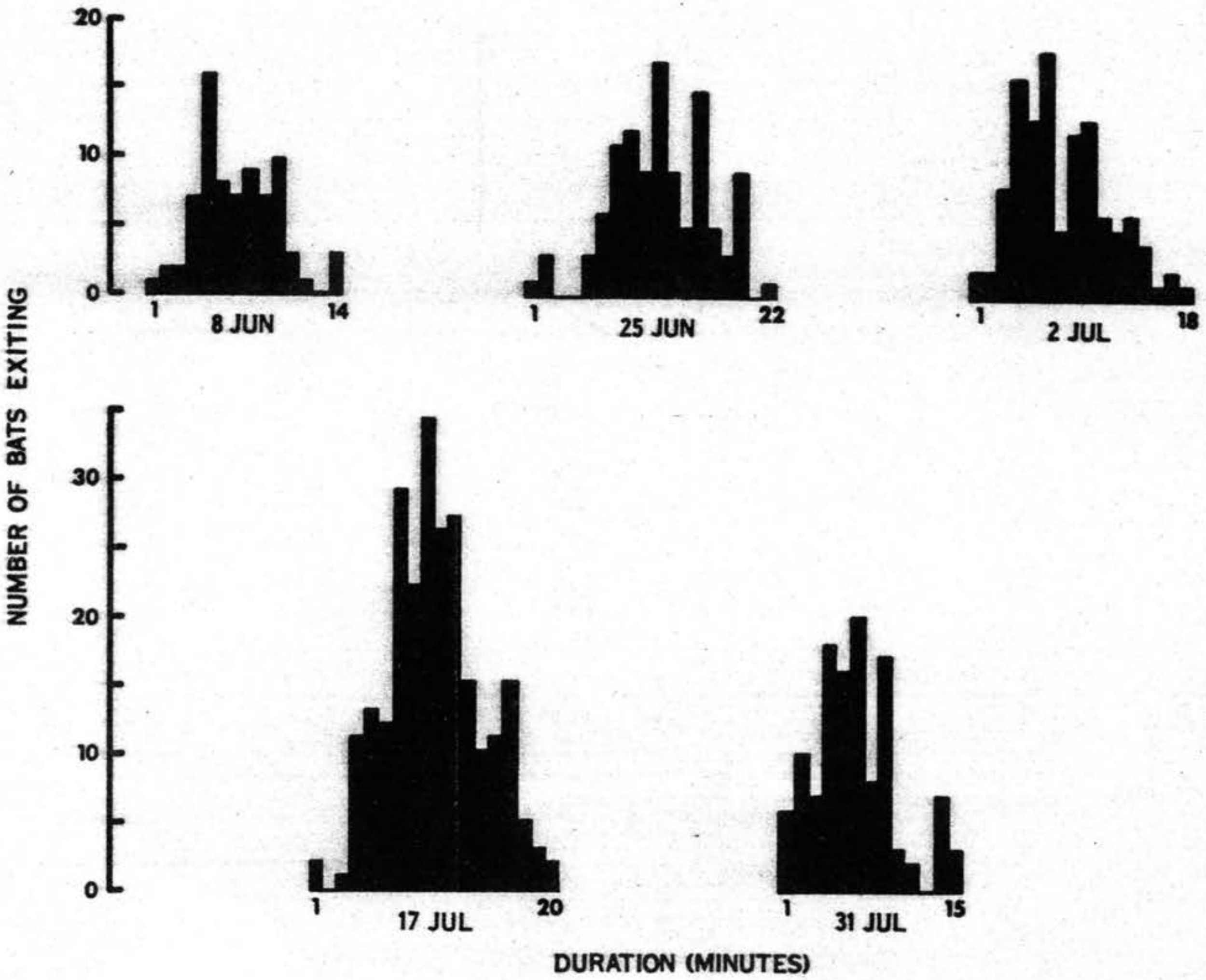

Figure 10. Evening emergence patterns of M. lucifugus from the Thorntown house in 1964

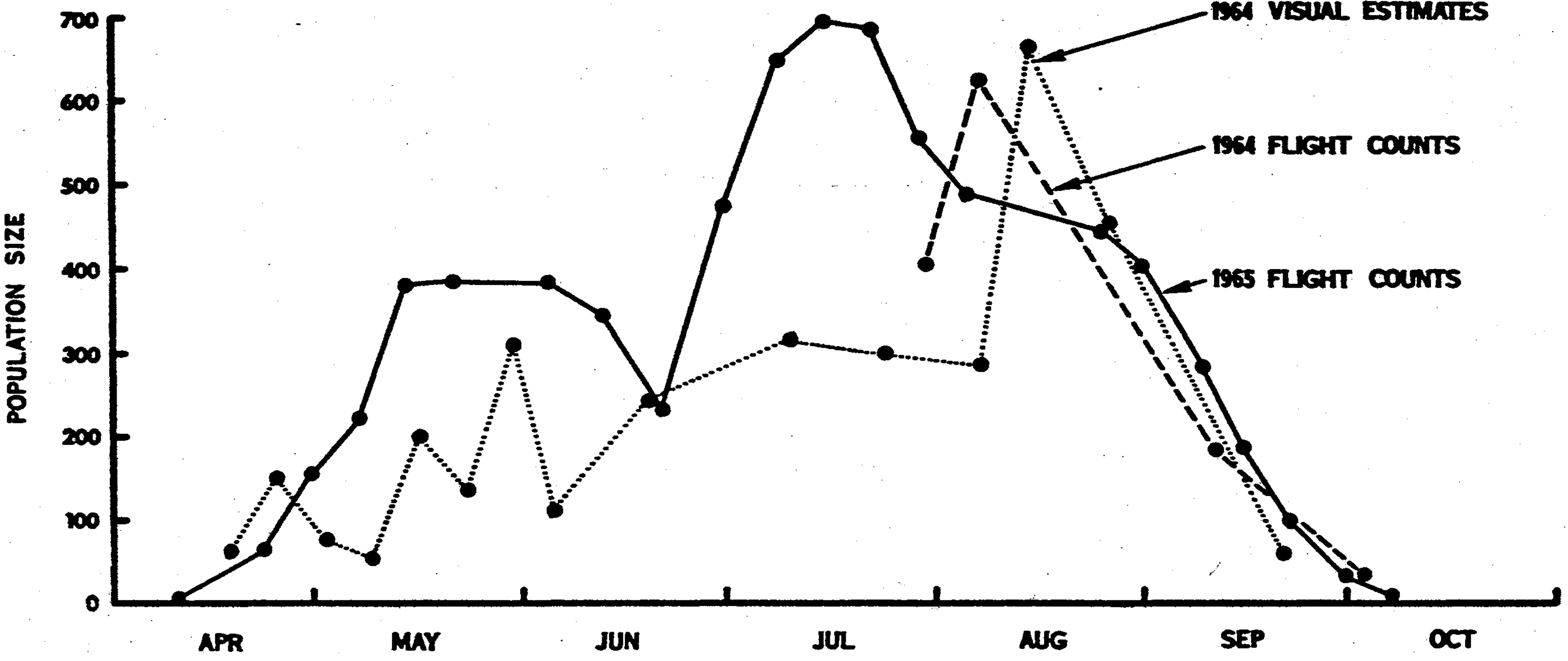

Figure 11. Changes in M. lucifugus population size at the Thorntown nursery

early June just prior to parturition, possibly because transient animals moved out. The lowest count in June was probably biased by cool and windy flight conditions. The increase corresponding with recruitment of young into the volant population began in early July and peaked in mid-July. This was followed by a decline in late July, a plateau in August, and steady emigration in September, terminating in October.

We made weekly counts at another nursery (Fig. 12) in 1965 and found approximately the same pattern. A stronger decline occurred following the May build-up, suggesting that more transient animals moved through this colony. To see if we were missing day-to-day variation the 1966 counts here included consecutive-day counts in June, July, and August. The 1966 peak was brief and could have been missed by weekly counts. The early July low of 570 could not have accounted for the subsequent peak of 1360 even with 100% reproduction, suggesting that in the parturition period some females did not join the early evening flight. Marked daily variation occurred, especially during migration, raising questions about group movement. If these changes do represent movements, then the assumption of population stability needed to estimate variance from consecutive-day counts is not valid.

These counts are sensitive to disturbance effects. The 1965 curve (Fig. 12) shows declines after sampling in early June and mid-July. Declines were to be expected at these times, but disturbance appeared to bring on premature declines of greater than usual magnitude. A sample was also taken in early July when an increase due to the flight of young was expected and did occur. Weekly sampling disturbance in the Thorntown house in 1964 caused most of the bats to move to the barn roost. When sampling frequency was reduced, many of the animals

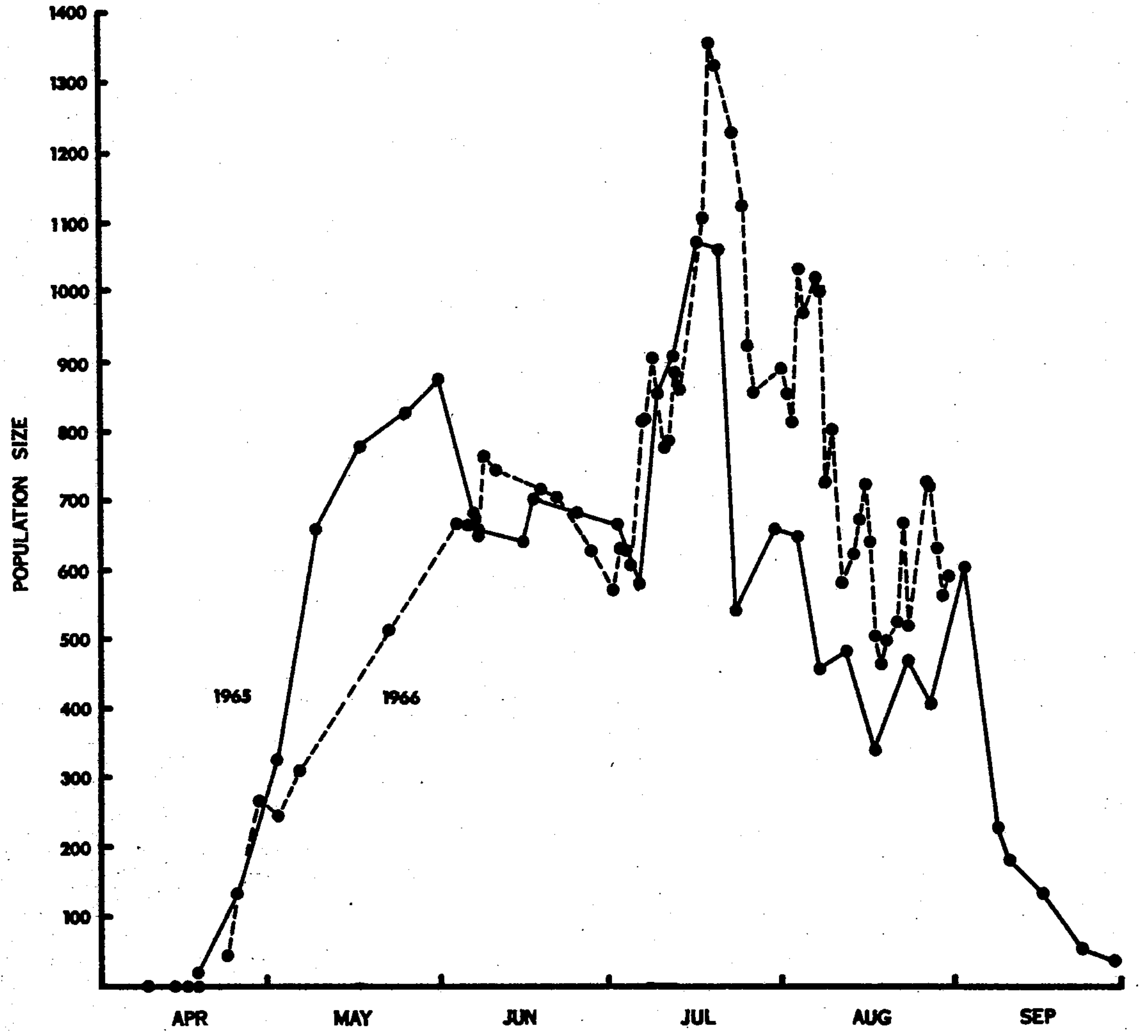

Figure 12. Changes in M. lucifugus population size at the Pennville nursery

returned to the house. Such disturbance effects could be minimized by sampling less often (not more than once a month) or possibly could be avoided by using exit traps in the evening (Griffin, 1940a; M. D. Tuttle and T. H. Kunz, personal communication).

By applying the Thorntown population size curve to pooled sample data, we approximated changes in population structure (Fig. 13). These data suggest that about 350 adult females stayed in Thorntown in June. With a litter size of one and an average pregnancy rate of 98%, we expected about 343 young to be born. Counts of about 695 bats in mid-July, associated with low postpartum mortality, coincided with our expectations. They further indicate that the females did not leave the nursery as soon as their young were weaned. Adult females began to leave in late July and young of both sexes in early August.

Swarming Groups

One part of the migratory activity pattern of M. lucifugus was monitored by mist-netting at cave entrances. Entrance netting does not provide data which can be related to nursery or hibernaculum population sizes. The number of bats captured simply reflects the number of bats which are participating in swarming phenomena at that particular time and place. The scanty spring netting data from Wind, Wyandotte, and Donnehue's Caves show that activity is low in the third week of March (Wind), moderate in the second week of April, high in the third week of April and the first week of May, moderate in the second and fourth weeks of May, and low in the first week of June. Activity is classified by comparison to the high levels of activity in the fall. In the fourth week of July, at the time adult females begin to leave the

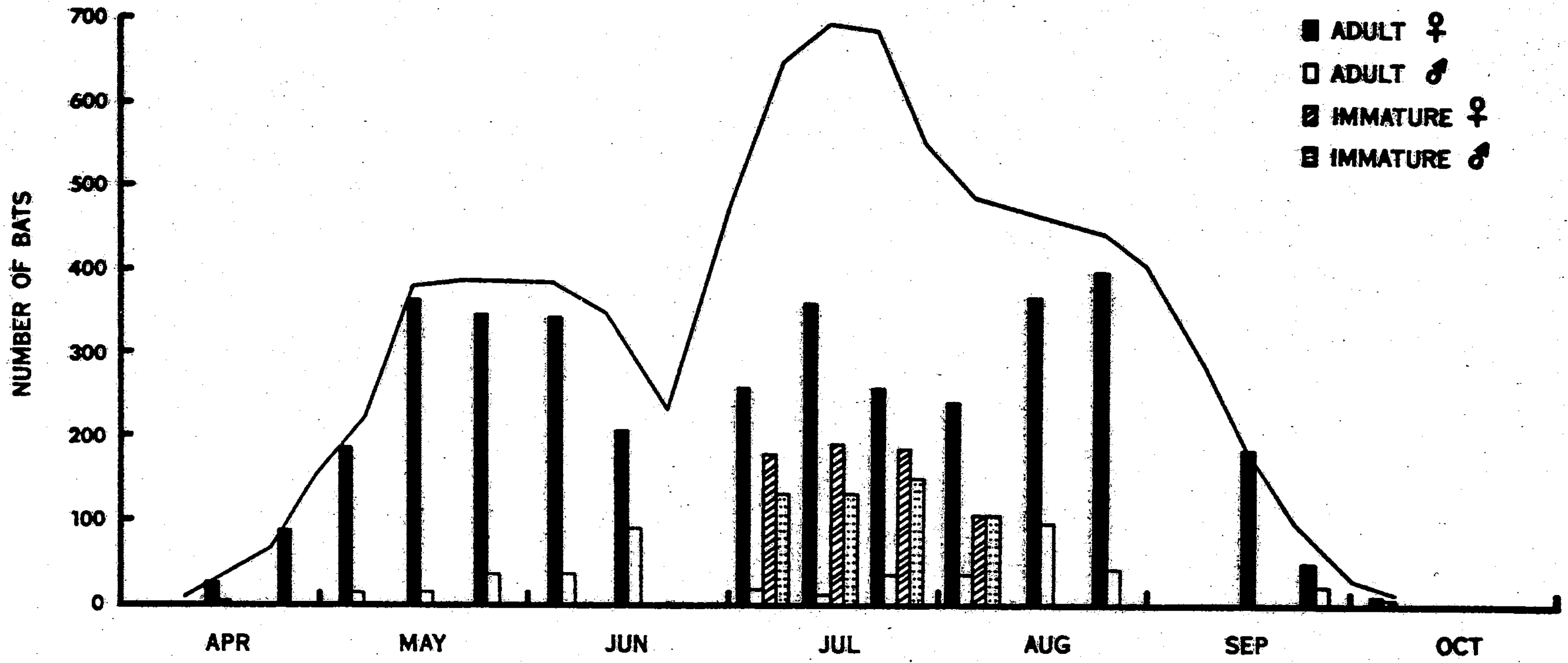

Figure 13. Changes in population size (line, from Fig. 11) and structure (pooled samples, 1958 to 1969) of *M. lucifugus* at Thorntown nursery

nurseries, activity was moderate at Wyandotte Cave.

August and September data at Wyandotte and Wind Caves are summarized in Fig. 14. Here the number of M. lucifugus caught nightly exhibited rapid and marked change. Further, activity at the two caves was apparently synchronous. Peaks of activity occurred at both on 6 September 1962, 19 August 1964, and 2 September 1964. A low level of activity was reached at both caves on 3 September 1963. The data suggest that activity may follow a similar phenological pattern each year. There were always more bats caught at the entrance than could be found in the cave either earlier that day or on the following day. Thus many of the bats moving through the cave entrances were spending the day roosting in the surrounding area or were arriving from more distant sites. A substantial decrease of the overall activity rate occurred at Wind Cave after the flood of March 1964 (DeBlase et al., 1965), indicating that the majority of M. lucifugus swarming at Wind Cave also winter there or perhaps at other caves which flooded. Later in the fall, activity at the entrance of Wyandotte Cave was moderate in the second week of October and light in the third.

Winter Populations

Visual estimates of torpid bats in winter were based on samples plus estimates of numbers of animals too high or too deep in crevices to be reached. Error included individual estimation bias and the difficulty of distinguishing distant Myotis sodalis from M. lucifugus. When we recognized that M. lucifugus usually formed loose clusters and M. sodalis formed dense ones the latter source of error diminished.

Winter population estimates were made too infrequently to give a

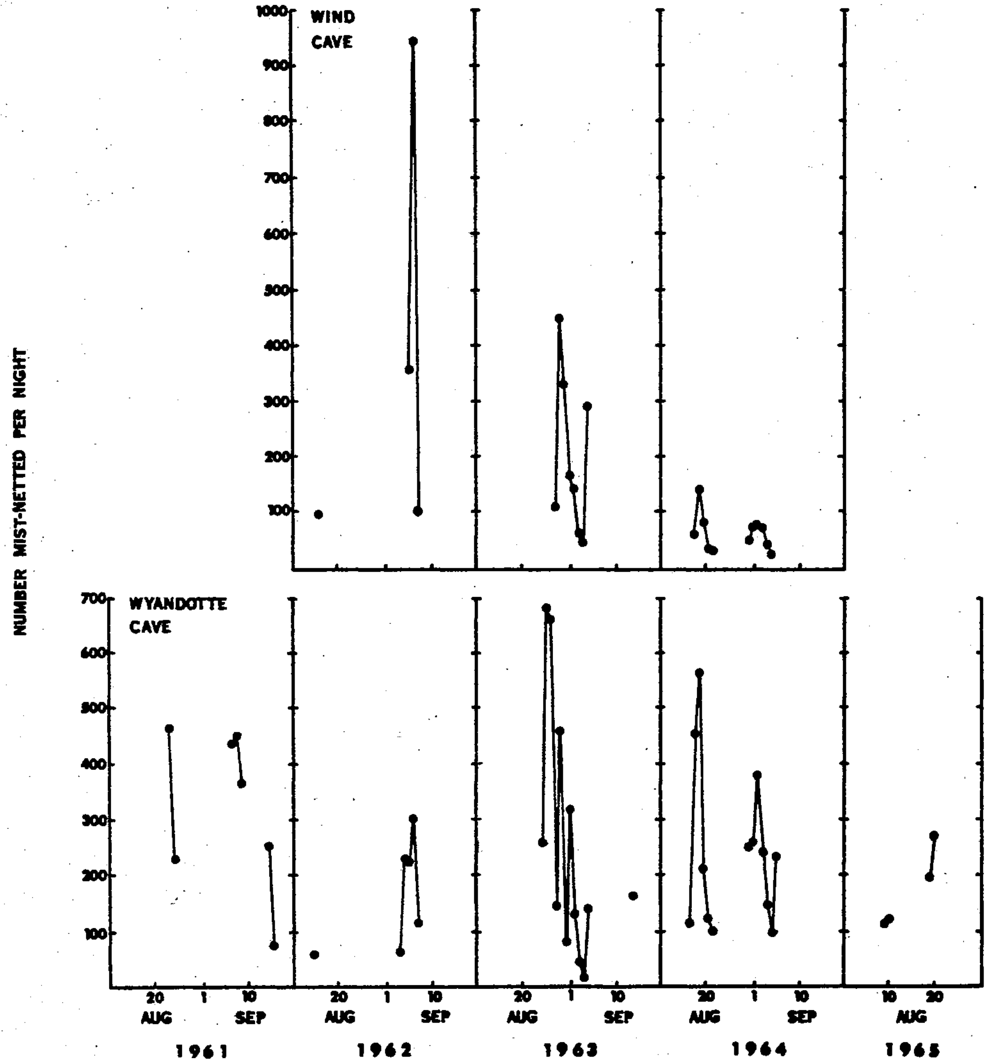

Figure 14. Number of M lucifugus mist-netted per night during fall swarming

clear picture of winter population phenomena. Because we assumed that few population changes took place in winter and wished to avoid arousing torpid bats any more than needed to obtain recapture data, usually only a single population estimate was taken for a cave per winter. An array of these values (Fig. 15) suggests that hibernating populations change markedly during the winter. Populations appear to increase from November through March and decrease in April and May.

Few authors have presented data on M. lucifugus population changes during a single winter. At Tyendinaga Cave, Ontario, Hitchcock (1965) observed 58 on 17 January 1941 and 125 (including only 13 from the previous group) on 17 April 1941. Folk (1940) found that a population at Indian Oven Cave, New York, increased until January, fluctuated in January and February, and decreased in late February. Although almost all of the bats he examined were M. lucifugus, he did not separate three other species in reporting bat numbers. Davis and Hitchcock (1965) reported a large and stable population in mine "B", New York, in February and March, followed by a decline in May. At Aeolus Cave, Vermont, Griffin (1945) reported no specific data but stated that a fall hibernating population of several hundred M. lucifugus was reduced by freezing temperatures in the roost area to fewer than 50 by mid-winter. Extremely cold roost temperatures were not found in the present study. Davis and Hitchcock (1965) reported several hundred M. lucifugus in the Aeolus Cave roost site at various dates from September to March during several winters. In April and May they documented a population buildup and decline involving 2,500 to 3,000 M. lucifugus; these observations involve spring arousal and migration phenomena to which the data of the present study are not sensitive.

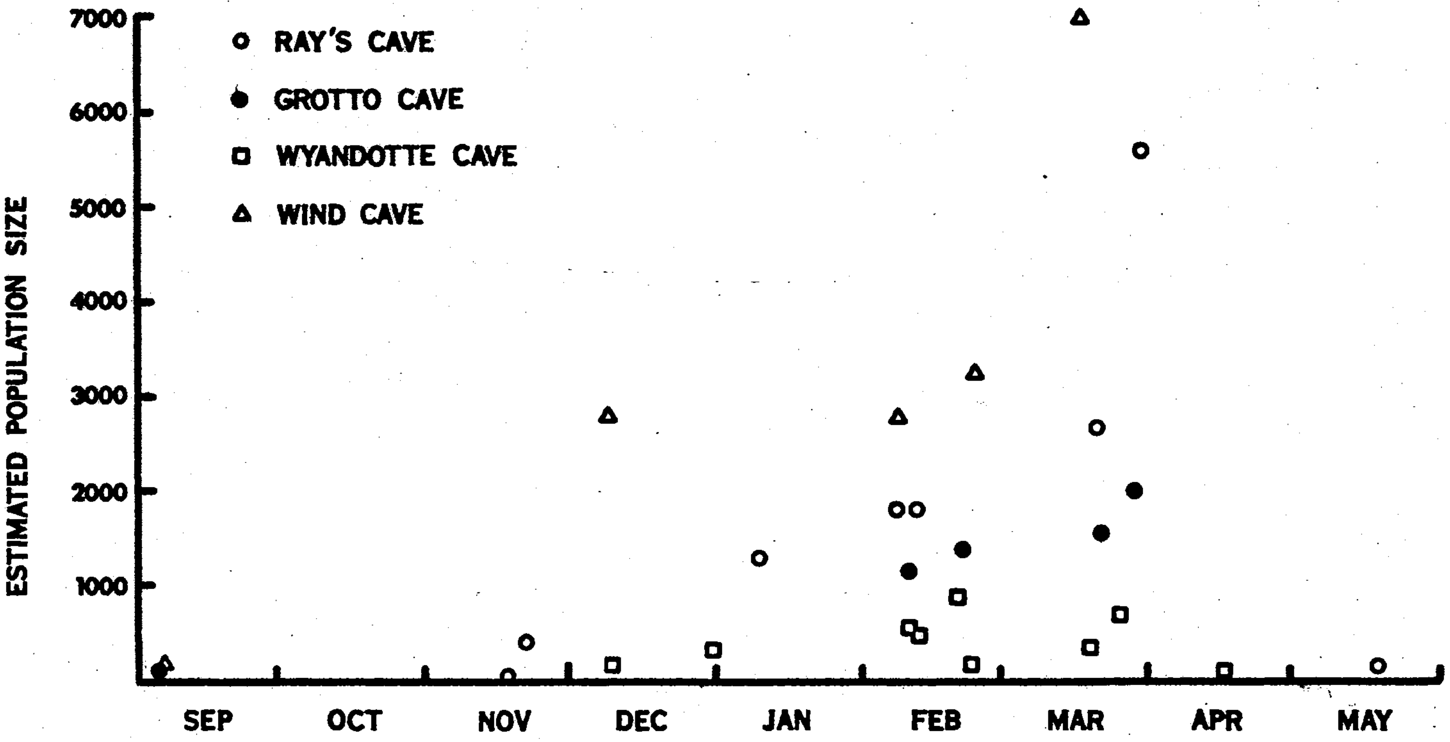

Figure 15. Population size estimates of hibernating M. lucifugus

Probably these phenomena accounted at least in part for the change noted by Hitchcock.

If, as our data suggest, major changes in population size occur throughout the winter, large numbers of *M. lucifugus* must spend portions of the winter undetected. Based on changes of cave populations in spring, Davis and Hitchcock (1965) thought numbers increased in April because bats emerged from inaccessible parts of the cave. All caves in the present study contained such sites, including recesses and passages too small to investigate by conventional means. Davis and Hitchcock presented arguments for rejecting the contention that this species winters in heated buildings. In the present study no bats were found in winter in warm nursery buildings (Pennville, November; Tunnelton, January; Thorntown, early April). Our band returns from buildings in winter all apparently involve transient animals, not hibernating ones. Bats also may find caves unfamiliar to the investigators or may be hardy enough to spend part of the Indiana-Kentucky winter in rock crevices or hollow trees. There is no evidence to support the latter suggestion. Although Griffin (1940a) cited Mearns (1898) as finding dormant little brown bats in hollow trees in winter, Mearns' reference was to *Vespertilio subulatus*, which then referred to the species now called *Myotis keenii* and *M. leibii*.

CHAPTER V

SEX RATIOS

To smooth sex ratio data so that time trends are discernible, sample data from all years and populations were pooled into 10-day intervals unless specified otherwise. For winter data, 10-day intervals did not show readily interpretable patterns so 30-day intervals were used. When a 1:1 sex ratio was expected, significant difference was tested with X^2. If $25 \leq n < 200$, a correction factor was applied to the test (Sokal and Rohlf, 1969). No test was made if $n < 25$.

Nursery Populations

Maturing of the young precluded accurate age determination of some individuals in samples as early as 22 July while age of all individuals was reliably judged as late as 7 August in other samples. This variation probably reflects population differences in birth dates and rates of development. These dates dictate the time intervals for which sex ratios of adult, immature, and unaged samples can be analyzed. Sex ratio values for these three types of samples are summarized in Fig. 16.

Samples of prevolant young did not differ significantly from 50% female (Table VI). The same is true of volant young in early July, but in late July and early August the proportion of females rose significantly. At this time young males were leaving the nurseries earlier

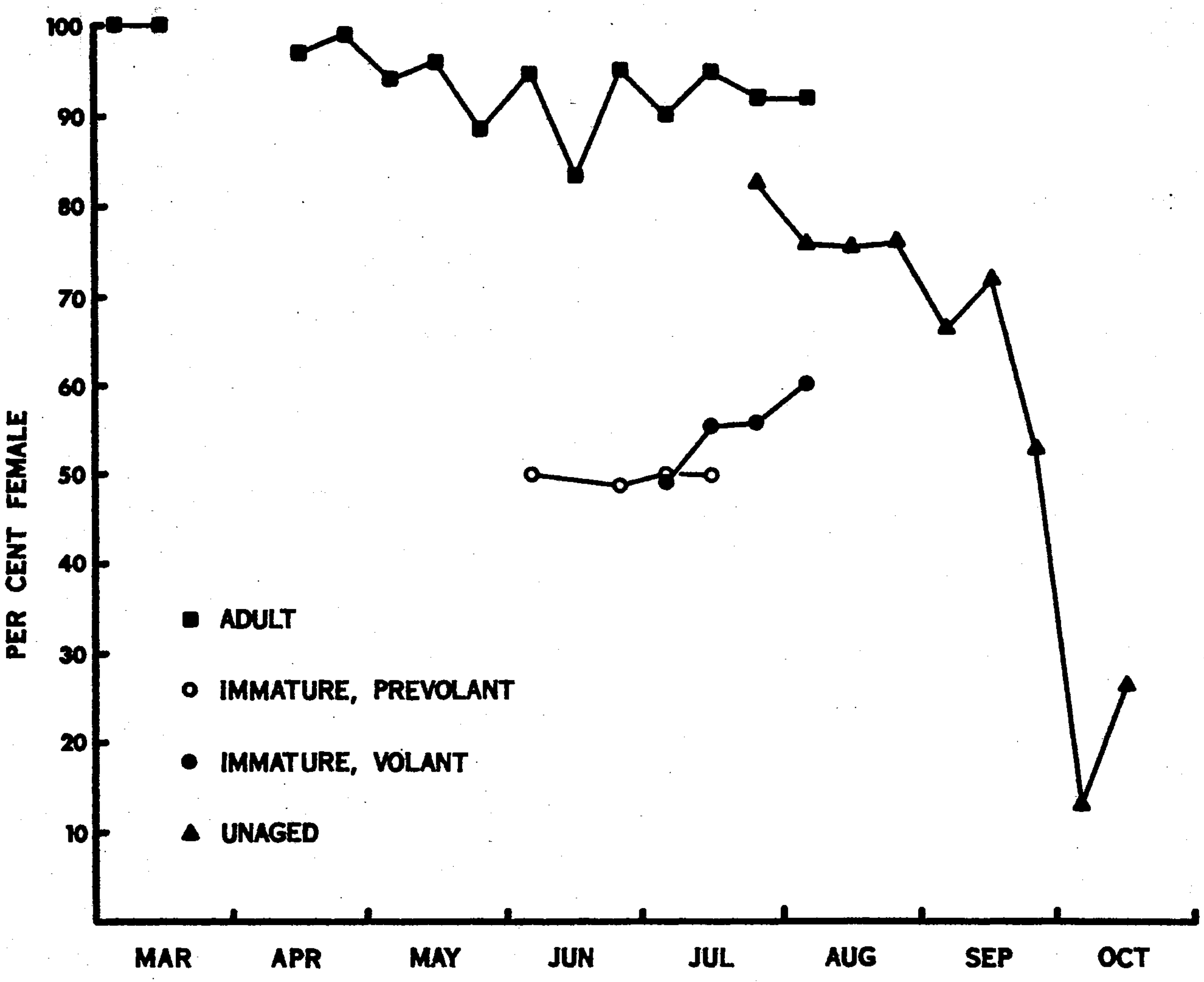

Figure 16. Average per cent female of M. lucifugus in Indiana nurseries

TABLE VI

PER CENT FEMALE OF IMMATURE *M. LUCIFUGUS* IN INDIANA

Date	Number of samples	Pooled sample size	Number of females	Per cent female	X^2	P
Prevolant samples						
1-10 June	1	8	4	50.0	-	-
11-20 June	0					
21-30 June	1	169	82	48.5	0.580	<0.05*
1-10 July	2	240	120	50.0	-	-
11-20 July	1	492	245	49.8	0.008	<0.975
Total	5	909	451	49.6	0.054	<0.9
Volant samples						
1-10 June	1	4	3	75.0	-	-
11-20 June	1	1	1	100.0	-	-
21-30 June	1	1	0	0.0	-	-
1-10 July	7	504	248	49.2	0.179	<0.5
11-20 July	6	269	149	55.4	3.126	<0.1
21-31 July	22	2,203	1,227	55.7	28.598	<0.01**
1-10 August	16	1,406	845	60.1	57.366	<0.01**
Total	54	4,388	2,473	56.4	70.958	<0.01**

* Significant
** Highly significant

and at a more rapid rate than females. Differential mortality of remaining young is also possible. Published sample data (Table VII) show the same pattern for prevolant young but the opposite trend (with rather small samples) for volant young. Further examination of our data suggests that either the departure pattern shown may be heavily dependent on the sampling schedule used or departure patterns differ from one population to another. For example, at Thorntown (Fig. 13) no prevolant samples were taken, so the basic ratio is not known. By early and mid-July the volant young were predominantly females, so perhaps males had begun departure earlier than females. But in late July the departure rate of females began to overtake that of males, and a 1:1 ratio occurred in early August.

Although the immature sex ratio data of Smith (1954, 1957) extend farther into fall than other data, these values are of doubtful reliability because Smith determined age by tooth wear. Hall _et_ _al_. (1957) considered tooth wear an unreliable age indicator for _M_. _lucifugus_ because the canine teeth of four 18-19 year-old bats were only slightly worn. We observed canines with little or no wear in banded _M_. _lucifugus_ up to 14 years old. The sex ratio difference in the 11-20 June samples in Table VIII, although not statistically significant, suggest that tooth wear ageing may frequently misclassify adult males. It seems likely that in June and July bats were classed as immature if obviously small and dark in pelage; most sex ratios in this period were similar to those in Indiana. The increased proportion of males in mid-September possibly corresponds with the influx of adult males noted in late September in the Indiana nurseries.

Samples of adults in nurseries (Table IX) consisted almost

TABLE VII

PUBLISHED DATA ON PER CENT FEMALE OF IMMATURE *M. LUCIFUGUS*

Reference	Date	Sample size	Number of females	Per cent female	X^2	P
Prevolant or probably prevolant						
Allen, 1921	5 July 1907	101	53	52.5	0.257	<0.9
Cagle and Cockrum, 1943	18 May - 12 July 1940	153	80	52.3	0.327	<0.5
Total		254	133	52.4	0.567	<0.5
Probably prevolant and volant						
Griffin, 1940b	summer	890	440	49.4	0.112	<0.9
Volant or probably bolant						
Davis and Hitchcock, 1965	7 - 8 July 1960	119	64	53.8	0.689	<0.5
Dymond, 1936	7 - 13 July 1934	54	19	35.2	4.759	<0.05*
Dymond, 1936	17 July 1933	25	6	24.0	6.800	<0.01**
Stegeman, 1954a, b	14 - 15 July 1949	257	123	47.9	0.471	<0.5
Benton and Scharoun, 1958	22, 30 July 1955	108	53	49.1	0.046	<0.9
Smith and Goodpaster, 1956	18 August 1955	27	4	14.8	13.407	<0.01**
Total		590	269	45.6	4.583	<0.05*

* Significant

** Highly Significant

TABLE VIII

PER CENT FEMALE OF IMMATURE *M. LUCIFUGUS* IN NORTHEASTERN OHIO (SMITH, 1954)

Date	Number of samples	Pooled sample size	Number of females	Per cent female	X^2	P
11-20 June	3	61	23	37.7	3.705	<0.1
21-30 June	8	218	107	49.1	0.073	<0.9
1-10 July	3	68	30	44.1	0.956	<0.5
11-20 July	7	204	104	51.0	0.078	<0.9
21-31 July	7	196	108	55.1	2.046	<0.5
1-10 August	7	141	91	64.5	11.929	<0.01**
11-20 August	3	70	50	71.4	12.871	<0.01**
21-31 August	6	96	75	78.1	30.385	<0.01**
1-10 September	4	105	85	81.0	40.248	<0.01**
11-20 September	7	43	29	67.4	5.256	<0.025*
Total	55	1,202	702	58.4	33.947	<0.01**

* Significant
** Highly significant.

TABLE IX

PER CENT FEMALE OF ADULT M. LUCIFUGUS IN INDIANA NURSERIES

Date	Number of samples	Pooled sample size	Number of females	Per cent female
1-10 March	1	1	1	100.0
11-20 March	1	1	1	100.0
21-31 March	0			
1-10 April	0			
11-20 April	2	452	438	96.9
21-30 April	3	80	79	98.8
1-10 May	4	394	370	93.9
11-20 May	3	138	132	95.7
21-31 May	3	280	247	88.2
1-10 June	8	769	726	94.4
11-20 June	2	107	89	83.2
21-30 June	2	480	456	95.0
1-10 July	10	908	815	89.8
11-20 July	5	609	577	94.7
21-31 July	22	2,200	2,016	91.6
1-10 August	16	1,804	1,652	91.6
Total	82	8,223	7,599	92.4

entirely of females. Adult males were never found in large numbers. Almost none were present in early spring but their proportion increased through May and June to 8.4% in late July and early August. The pooled samples do not indicate population variation which apparently occurred. At Tunnelton, a large southern nursery, the proportion of males was generally higher, reaching an average of 18.2% in four samples in July (Table X). Since Tunnelton samples made up a large portion of the adults examined in certain 10-day intervals, actual proportions of males in more northerly nurseries may be much lower than suggested by Table IX. Possibly most males do not move as far away from the cave area in summer as do females.

Similar seasonal patterns in adult sex ratios at nurseries occur in published data. In most studies the influx of males appears strongest in June and July. Few reliable August data are available because of the difficulty of determining age. June and July averages from this study and published records (Table XI, Fig. 17) illustrate regional differences in adult sex ratios. Few adult males were present in samples near the center of the species' range but incidence increased in nurseries closer to the southern limits of distribution. Perhaps fewer suitable summer shelters for males are available toward the southern periphery than in the north.

The proportion of males was higher in the late summer and fall samples for which age could not be determined (Table XII). The average level of 24.4% males maintained through August consisted mostly of immature males, as before. Although both adult and immature females were leaving the nurseries, the proportion of immature males did not rise because of the more rapid departure of males discussed above.

TABLE X

PER CENT FEMALE OF ADULT M. LUCIFUGUS AT THE TUNNELTON NURSERY

Date	Number of samples	Pooled sample size	Number of females	Per cent female
1-10 March	1	1	1	100.0
11-20 March	1	1	1	100.0
21-31 March	0			
1-10 April	0			
11-20 April	2	428	415	97.0
21-30 April	1	51	50	98.0
1-10 May	1	296	277	93.6
11-20 May	0			
21-31 May	1	205	179	87.3
1-10 June	2	195	167	85.6
11-20 June	1	74	66	89.2
21-30 June	0			
1-10 July	2	702	600	85.5
11-20 July	0			
21-31 July	2	729	570	78.2
Total	14	2,682	2,326	86.7

TABLE XI

AVERAGE PER CENT FEMALE OF ADULT *M. LUCIFUGUS* IN NURSERIES IN JUNE AND JULY

Reference	Location	Number of samples	Pooled sample size	Number of females	Per cent female
Dymond, 1936	Ontario	3	64	64	100.0
David and Hitchcock, 1965	Vermont	4	880	831	94.4
Stegeman, 1954a, b	N New York	2	353	353	100.0
Benton and Scharoun, 1958	SE New York	1	62	62	100.0
Allen, 1921; Wimsatt, 1945	W New York	2	185	177	95.7
Smith, 1954	NE Ohio	42	1,109	1,081	97.5
this study	Indiana*	49	5,073	4,679	92.2
this study	S Indiana	7	1,700	1,403	82.5
Davis *et al*., 1965	E Kentucky	6	2,379	1,827	76.8
Davis *et al*., 1965	SW Kentucky	1	94	62	65.6
Cagle and Cockrum, 1943	S Illinois	6	288	225	78.1

* Includes values from single population denoted "S Indiana".

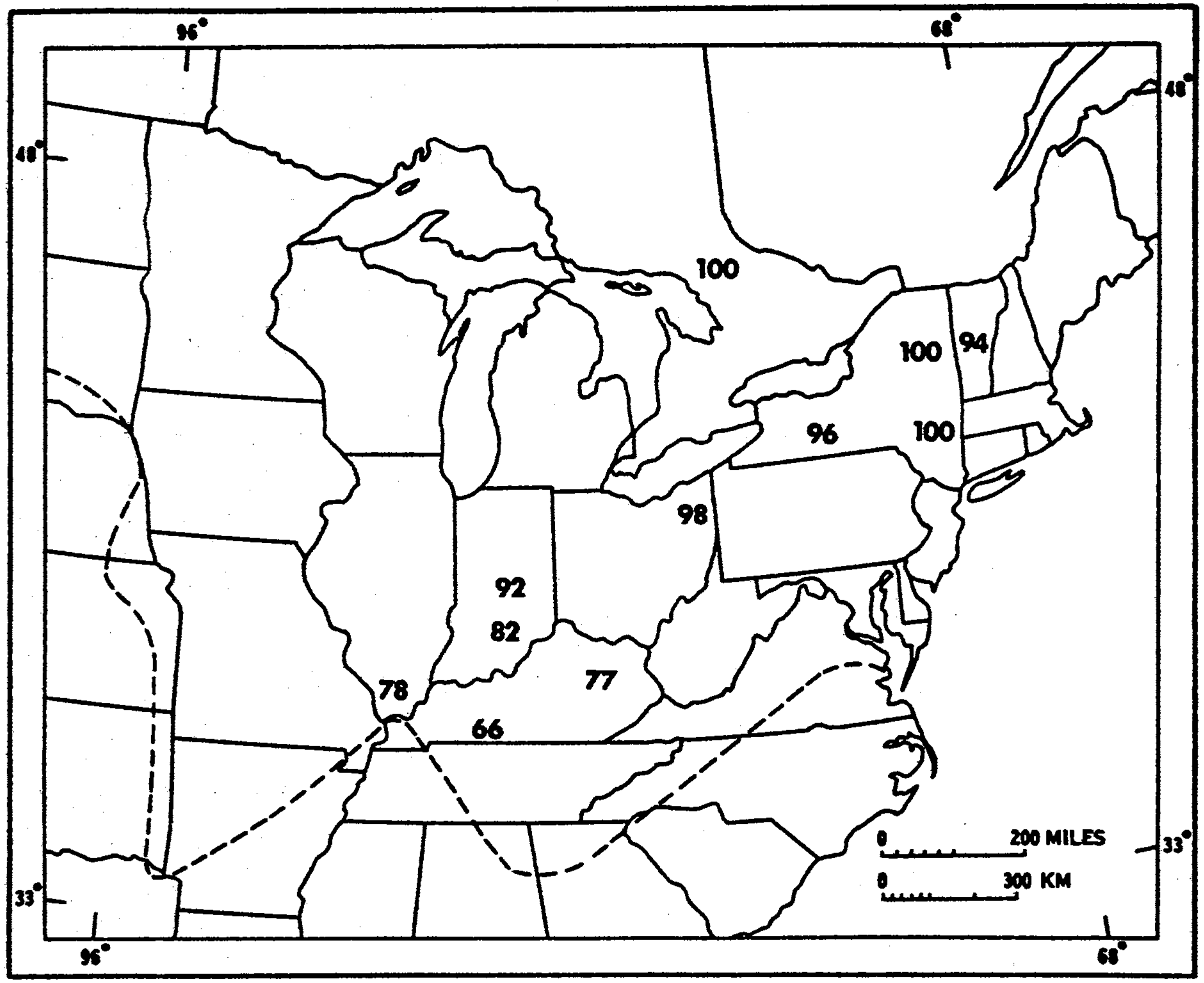

Figure 17. Average per cent female of M. lucifugus in nurseries from this and other studies, adult samples pooled for June and July. Dashed line is southern limit of distribution

TABLE XII

PER CENT FEMALE OF UNAGED M. LUCIFUGUS IN INDIANA

Date	Sample size	Number of females	Per cent female
21-31 July	2,425	1,995	82.3
1-10 August	6,076	4,598	75.7
11-20 August	14,638	11,028	75.3
21-31 August	7,259	5,508	75.9
1-10 September	858	569	66.3
11-20 September	327	234	71.6
21-30 September	93	49	52.7
1-10 October	291	38	13.1
11-20 October	19	5	26.3

Increase in the percentage of males to means of 33.3 in September and 86.1 in October resulted from continued emigration of summer residents and ingress of adult males. Humphrey and Cope (1964) described a sample which shows this influx as a high proportion of males in the unbanded, partly non-resident group.

The mean fall sex ratios depicted in Table XII do not necessarily apply to every nursery. The two nurseries for which fairly representative samples are available (Table XIII) exhibit different patterns of sex ratio change. The main difference is that the roost near the caves shows a marked increase in the proportion of males after early September, while the one farther north never shifts from predominantly female composition. If most males never move north for the summer, perhaps nurseries near the cave area play an important part in swarming behavior not shared by northern nurseries.

Shelter Groups

Shelters housed mostly adult males in early summer, but adult females and young of both sexes appeared in late July and August. Table XIV presents sex ratios of adult *M. lucifugus* samples for June only. A few of these samples contained small numbers of females. Many farmers in Indiana commented that they occasionally observed single bats roosting in a barn or other building for a few days. While some of these were no doubt *Eptesicus fuscus*, clearly many adult male *M. lucifugus* spend the summer singly in transient roosts or in small groups at permanent sites.

TABLE XIII

PER CENT FEMALE OF UNAGED *M. LUCIFUGUS* AT TWO INDIANA NURSERIES

Date	Number of samples	Pooled sample size	Number of females	Per cent female
Thorntown (north)				
1-10 August	1	503	439	87.3
11-20 August	5	1,071	847	79.1
21-31 August	1	147	133	90.5
1-10 September	0			
11-20 September	1	4	4	100.0
21-30 September	2	49	34	69.4
1-10 October	1	3	2	66.7
Tunnelton (south)				
21-31 July	1	134	124	92.5
1-10 August	2	1,168	864	74.0
11-20 August	6	3,261	2,401	73.6
21-31 August	5	1,914	1,356	70.8
1-10 September	4	777	529	68.1
11-20 September	1	149	70	47.0
21-30 September	1	44	15	34.1
1-10 October	3	288	36	12.5
11-20 October	1	19	5	26.3

TABLE XIV

PER CENT MALE OF <u>M. LUCIFUGUS</u> TAKEN IN SUMMER SHELTERS, JUNE DATA, LOCATIONS AND YEARS POOLED FOR EACH STUDY

Reference	Location	Number of samples	Pooled sample size	Number of males	Per cent male
Davis and Hitchcock, 1965	Vermont, cave	3	648	632	97.5
Davis and Hitchcock, 1965	New York, mine	1	63	55	87.3
Krutzsch, 1961	Pennsylvania, cave	1	40	40	100.0
Myers, 1964	Missouri, cave	?	6	6	100.0
this study	Indiana, cave	2	5	5	100.0
Miller, 1955	Michigan, shutters	40	82	70	85.4
this study	Indiana, pavilion	1	3	3	100.0
Glass and Ward, unpubl.	Oklahoma, siding	1	10	10	100.0
this study	Oklahoma, siding	1	7	7	100.0
Total		51	864	828	95.8

Swarming Groups

Mist-netted samples at cave entrances showed considerable variation in sex ratio. Usually night-to-night changes in numbers caught were in the same direction and of approximately the same magnitude for both sexes, but occasionally large numbers of one sex arrived or departed with little apparent change in the other sex.

Sex ratios of swarming M. lucifugus are presented in Table XV. In middle and late April 60 to 80% of the bats active at cave entrances were females. At the same time the proportion of females torpid in caves (Table XVII) was dropping and females were arriving at nursery roosts. By mid-May few females remained in the caves and the proportion of females swarming was diminishing rapidly. At this time most females were present in the nurseries in central Indiana (Figs. 11 and 12).

Throughout the fall swarming period more males than females were active at cave entrances. The percentage of males dropped from 84 in mid-July to 60 in mid-August and then rose to 81 in mid-October. Fenton (1969a) reported a similar decline in the August values when immatures, whose sex ratio was closer to parity than that of adults, began to outnumber adults. Fig. 18 shows a tendency for a particular sex ratio (in spring and fall) to occur at Wind Cave from 4 to 10 days before occurring at Wyandotte Cave, a pattern which makes phenological sense only in the spring.

Table XVI and Fig. 19 depict fall swarming sex ratio data from other studies. Although Fenton (1969a, b) determined the age of his bats, the data for Renfrew Mine in 1967 and 1968 (n=4,376) are

TABLE XV

PER CENT MALE OF SWARMING M. LUCIFUGUS MIST-NETTED AT CAVE ENTRANCES (DONNEHUE'S, RAY'S, WYANDOTTE, AND WIND) IN INDIANA AND KENTUCKY

Date	Number of net nights	Total sample size	Number of males	Per cent male
11-20 March	2	5	3	60.0
21-31 March	1	0		
1-10 April	0			
11-20 April	4	544	184	33.8
21-30 April	5	275	103	37.5
1-10 May	2	153	118	77.1
11-20 May	3	63	53	84.1
11-20 July	1	38	32	84.2
21-31 July	3	228	180	78.9
1-10 August	2	238	159	66.8
11-20 August	12	2,371	1,430	60.3
21-31 August	24	5,386	3,411	63.3
1-10 September	29	7,340	5,569	75.9
11-20 September	4	556	415	74.6
21-30 September	0			
1-10 October	1	7	5	71.4
11-20 October	3	270	219	81.1

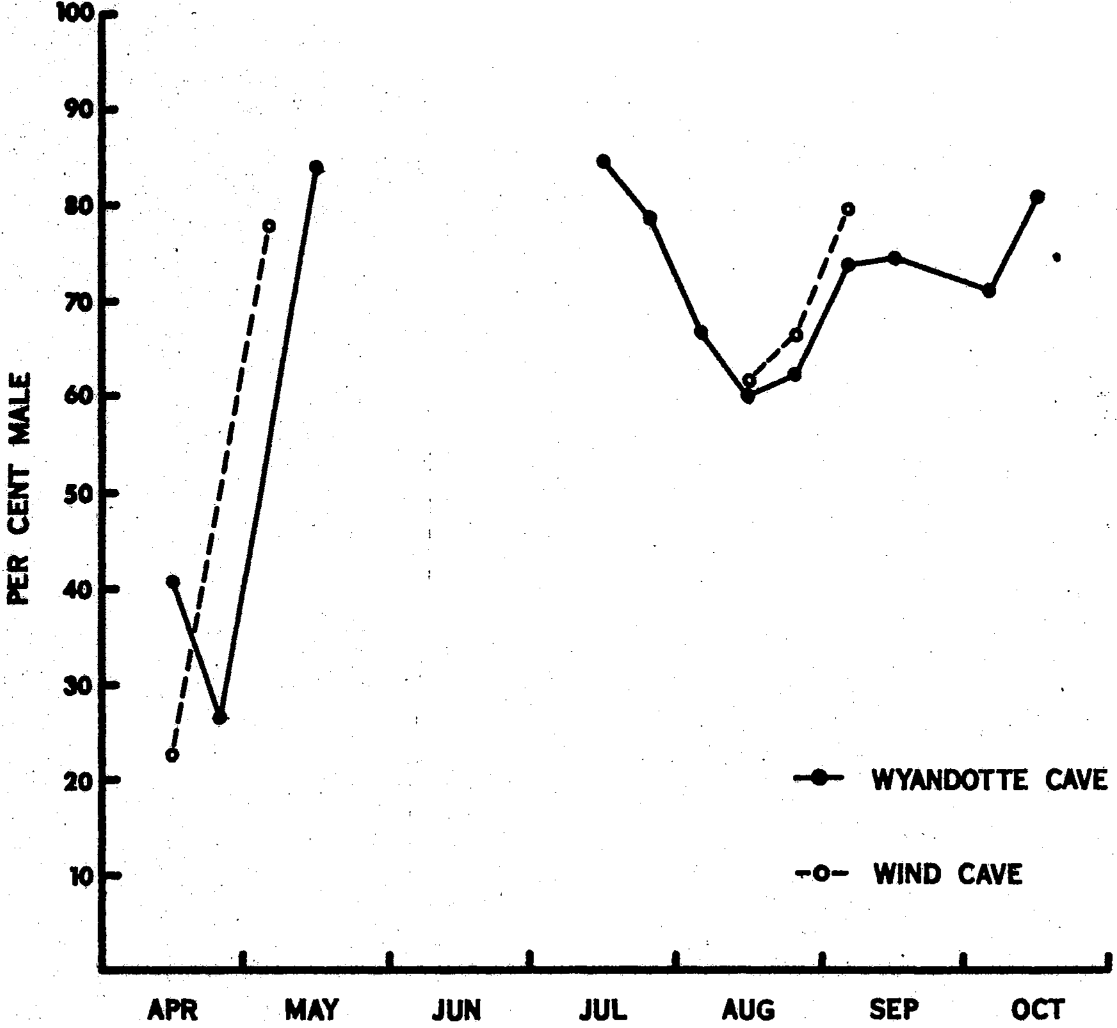

Figure 18. Per cent male of M. lucifugus swarming at cave entrances in fall, 84 mist-net nights pooled

TABLE XVI

PUBLISHED DATA ON PER CENT MALE OF SWARMING *M. LUCIFUGUS*

Date	Ontario[1]	Vermont[2]	Pennsylvania[3]	Pennsylvania[4]
1-10 July			80.0	
11-20 July			88.5	
21-31 Jyly			84.3	
1-10 August	71.1	66.7	67.2	
11-20 August	61.4	57.7	63.6	88.8
21-31 August	60.5	46.8	61.2	
1-10 September	75.0	45.2		
11-20 September	80.9		69.8	
21-30 September	78.3		74.4	
$\bar{x}$	66.7	58.4	67.3	88.8

[1] Fenton, 1969a

[2] Davis and Hitchcock, 1965

[3] Hall and Brenner, 1968

[4] Mohr, 1945

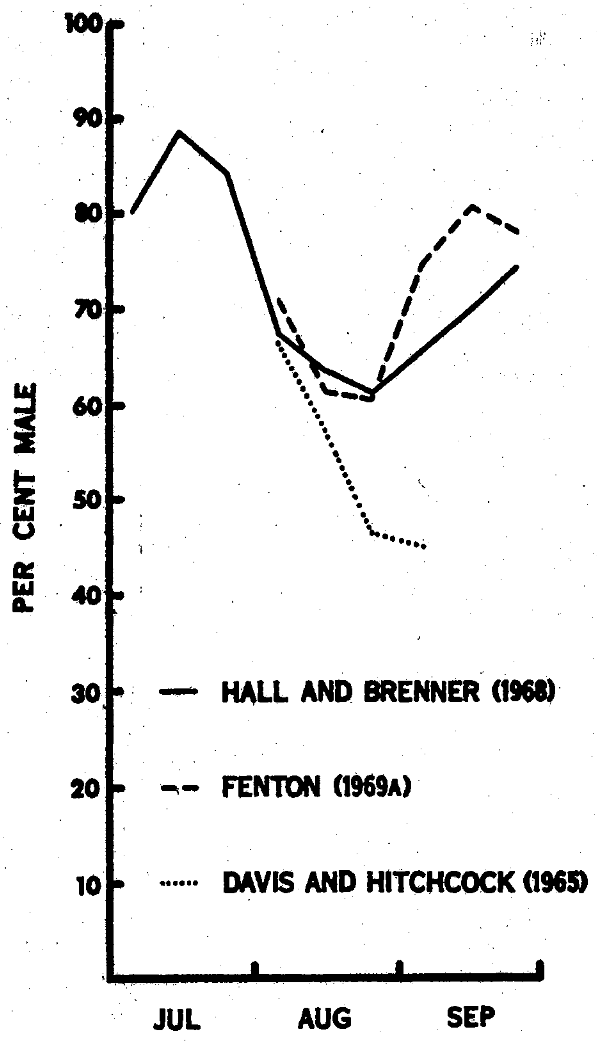

Figure 19. Published values of per cent male of *M. lucifugus* swarming at cave entrances in fall

recombined here as unaged samples for comparative purposes. The data of Davis and Hitchcock (1965; n=2,261) and Hall and Brenner (1968; n=1,060) are each from 2 years' samples at one cave. The temporal pattern in the present study agrees closely with those of Hall and Brenner (1968) and Fenton (1969a). The departure of males from the Aeolus Cave area as the swarming period progressed (Davis and Hitchcock, 1965) was a phenomenon not noted in the other studies.

Winter Populations

Sex ratios of hibernating M. lucifugus in Indiana and Kentucky caves are presented in Table XVII and Fig. 20. On the average there were always more males present than females. Sex ratios were closest to parity in mid-winter and males were most prominent in August, September, April, and May. The high percentage of hibernating males in September corresponded with a high percentage in swarming bats (Table XV) and with continued decline in the number of females at nurseries. The location of large numbers of females at this time is not known. The increased proportion of males in hibernating bats in late April corresponded with a low proportion in swarming bats and with arrival of females at nurseries. By mid-May almost no females were hibernating and few were flying in and out of the caves.

Many authors have reported disproportionate sex ratios in hibernating M. lucifugus without specifying sampling dates (Griffin, 1940b; Wimsatt, 1945; Hitchcock, 1950; Layne, 1958; Muir and Polder, 1960; Moison, 1961; Pearson, 1962; Myers, 1964; Heltsley, 1965). Their pooled data consisted of 68.1% males (n=7,880). In view of the marked within-winter changes in sex ratio found in Indiana and Kentucky,

TABLE XVII

PER CENT MALE OF HIBERNATING M. LUCIFUGUS IN INDIANA AND KENTUCKY

Date	Number of samples	Pooled sample size	Number of males	Per cent male
August	3	49	37	75.5
September	5	335	264	78.8
October	0			
November	3	527	364	69.1
December	13	4,815	3,007	62.4
January	2	1,171	700	59.8
February	33	11,596	7,877	67.9
March	19	10,730	7,073	65.9
April	4	208	158	76.0
May	3	137	132	96.4
Total	85	29,568	19,612	66.3

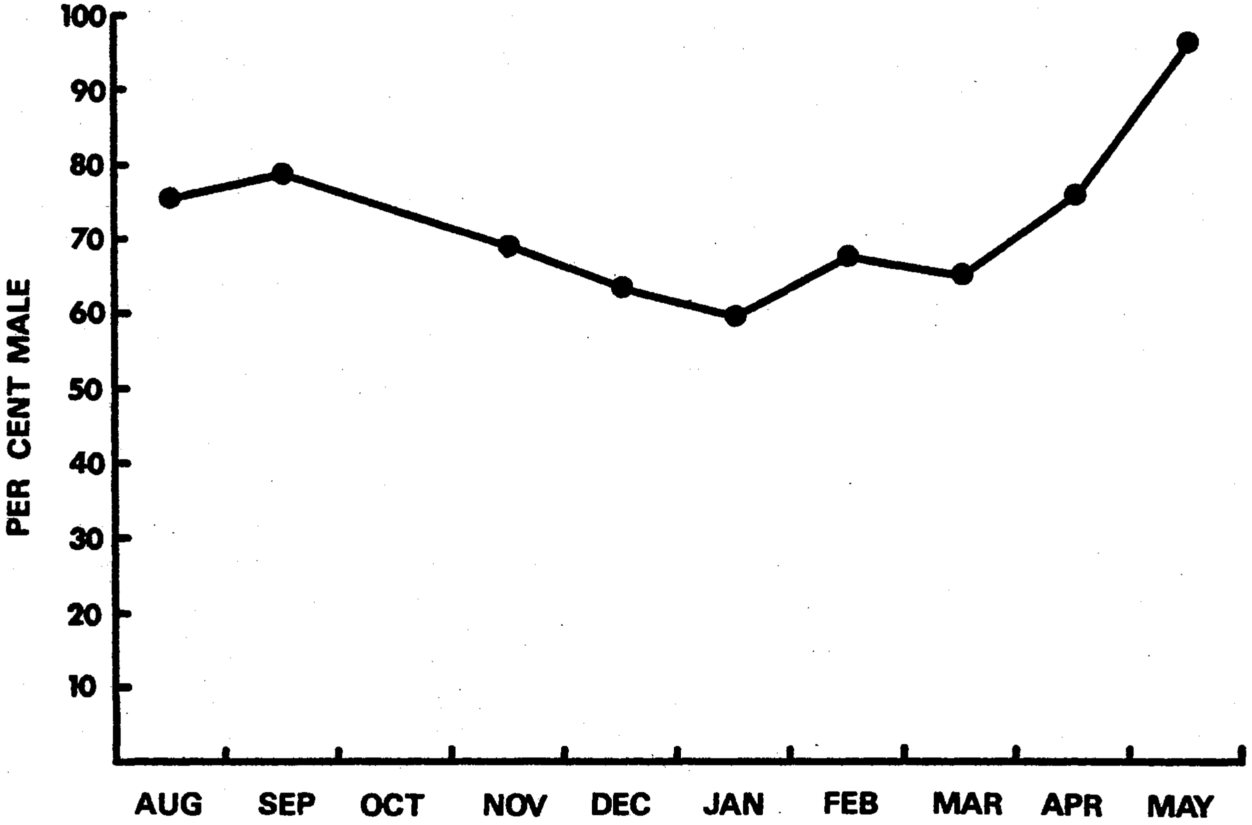

Figure 20. Average per cent male of *M. lucifugus* hibernating in Indiana and Kentucky caves

probably no small group of samples can be used to typify winter sex ratio in this species. Instead long series of samples need to be examined to ascertain patterns of winter sex ratio change. Monthly averages of five such sample series are plotted in Fig. 21. The differences shown are probably not as important as they appear, since the uneven sampling effort during the winter typical of these and the present studies yield somewhat misleading results. This is especially true of the months of August, September, October, April, and May, when rapidly occurring phenomena need to be carefully monitored. For example, all but two of the studies had small samples or none at all in April and could not have been sensitive to sex ratio changes associated with staging and departure from hibernacula. Davis and Hitchcock (1965) found rapidly shifting sex ratios from early April to mid-May. These were caused by a great increase in the number of females through April followed by a decrease in May and by an increase in the number of males in early May. Because relatively few M. lucifugus apparently occupied this roost earlier in the winter, the addition of bats of predominantly one sex had a strong impact on the sex ratio. The samples reported by Hitchcock (1949, 1965) were from both minor and major hibernacula. His samples were all from the early and middle portions of the month and showed no substantial change in sex ratio. All the studies with May samples found high proportions of males, indicating that males were typically slower to leave hibernacula in spring than females.

The other distinctive feature of major winter studies (Figs. 20 and 21) is a mid-winter period of relative stability in sex ratio. Each cave or group of hibernacula seems to have its own characteristic mid-winter sex ratio. Hitchcock (1950) and Fenton (1970) have

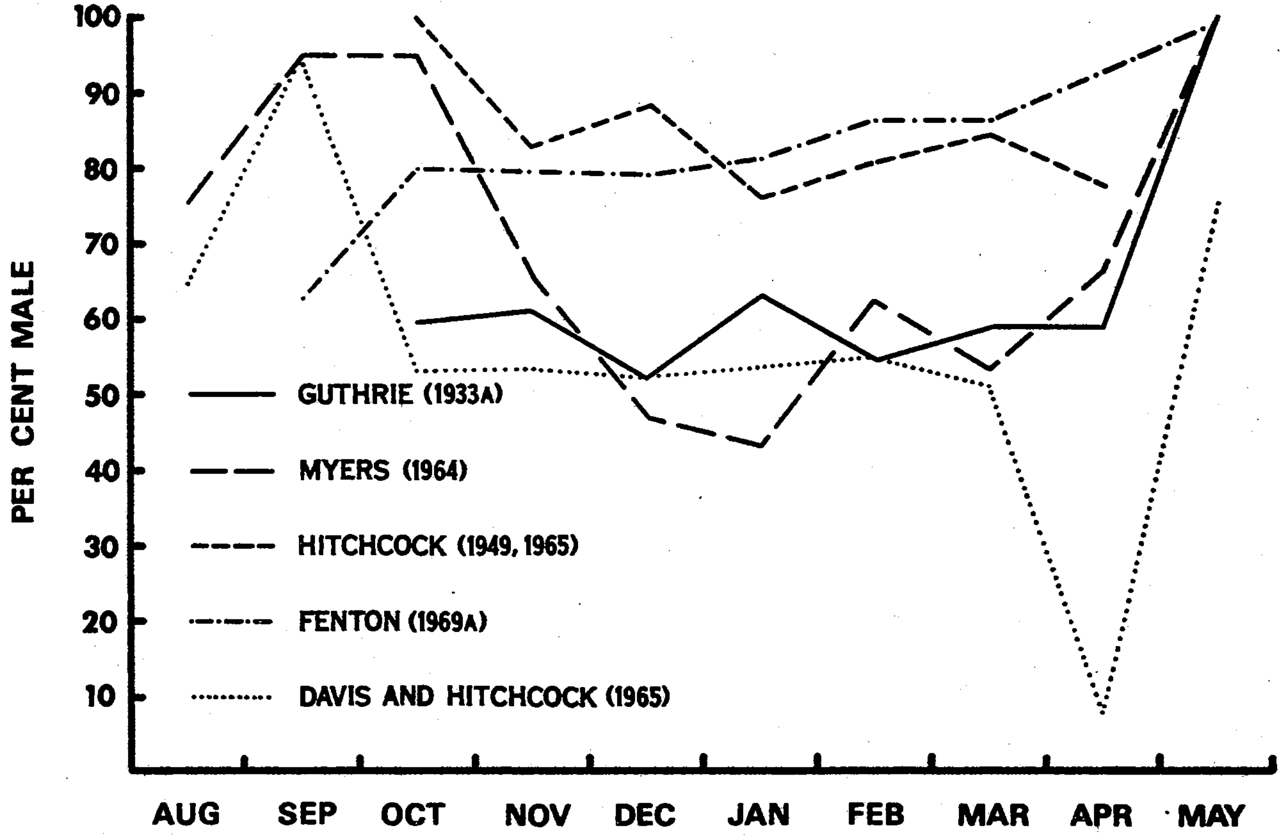

Figure 21. Average per cent male in hibernating M. *lucifugus* from published data

suggested that the more southerly hibernacula typically contain higher proportions of females than do northern ones. Table XVIII and Fig. 22 present pooled samples from November through March in each region studied. Pooled samples smaller than 50 are excluded. The interval December through February has somewhat more stable sex ratios but excludes many of the published data. Data from the present study are grouped into four north-to-south units. Northern hibernacula usually do have higher proportions of males. However, exceptions to this pattern occur, notably the large samples from Vermont and southern New York.

TABLE XVIII

REGIONAL COMPARISON OF PER CENT MALE HIBERNATING *M. LUCIFUGUS*

Reference	Location	Number of samples	Pooled sample size	Number of males	Per cent male
Moisan, 1963	Quebec	2	439	332	75.6
Hitchcock, 1949, 1965	SE Ontario	45	5,147	4,392	85.3
Fenton, 1969a	SE Ontario	?	5,192	4,246	81.8
Allin, 1942	SW Ontario	1	138	99	71.7
Hinckley, unpubl.	Michigan	2	645	534	82.8
Davis and Hitchcock, 1965	N New York	4	7,663	5,910	77.1
Davis and Hitchcock, 1965	Vermont	6	1,757	927	52.8
Davis and Hitchcock, 1964	S New York	2	2,246	1,195	53.2
Mohr, 1945; Hall and Brenner, 1968	Pennsylvania	8	2,073	1,255	60.5
Smith, 1954	W Pennsylvania	1	80	65	81.2
this study	Indiana	46	21,267	14,341	67.4
this study	S Indiana	15	2,741	1,710	62.4
this study	N Kentucky	7	3,294	1,966	59.7
this study	Kentucky	2	1,537	1,004	65.3
Mahan and Lewis, unpubl.	Tennessee	1	72	50	69.4
Myers, 1964	SE Missouri	?	4,085	1,986	48.6
Guthrie, 1933a	Missouri	10	515	288	55.9
Fitch, 1966	Kansas	?	84	55	65.5

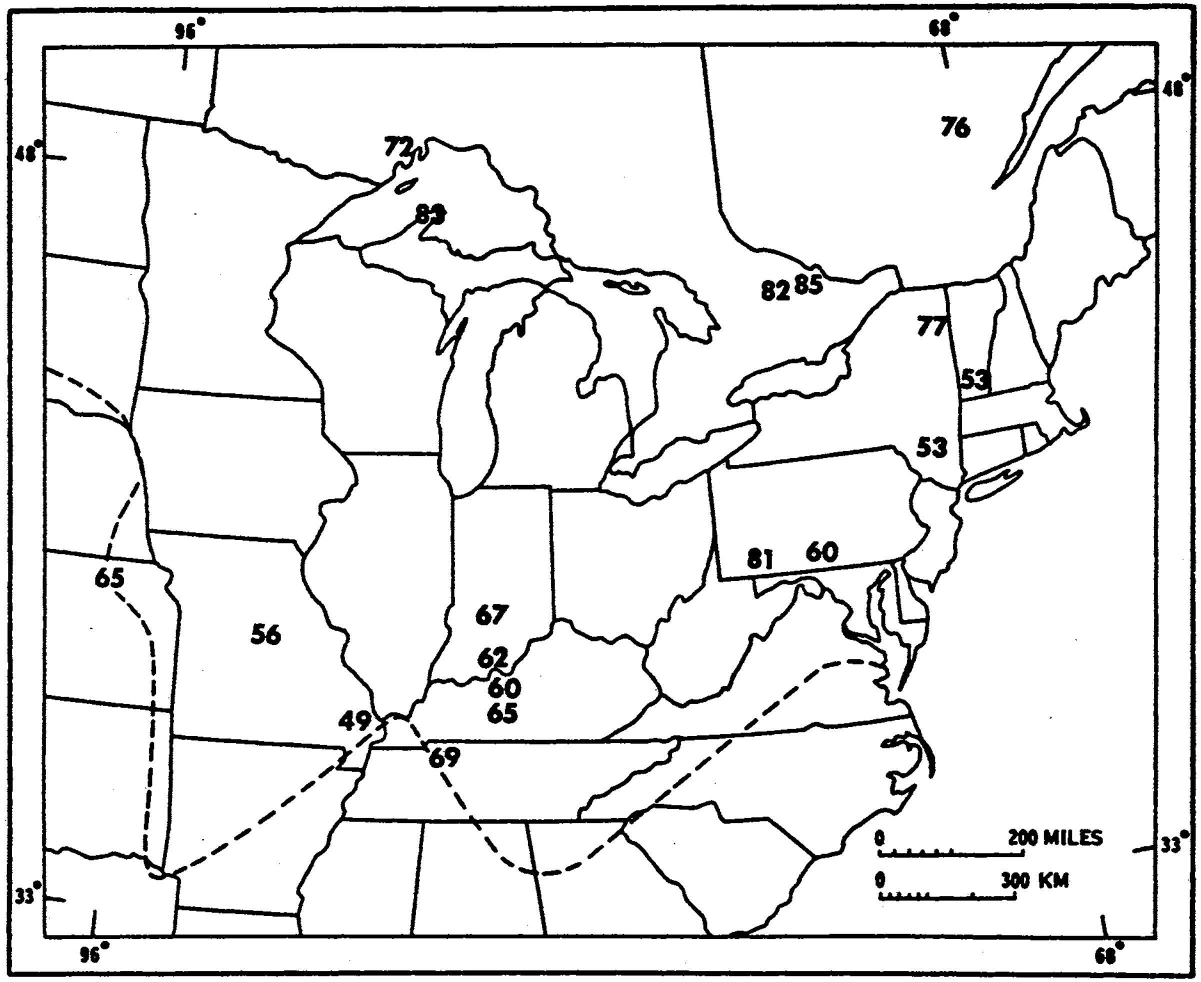

Figure 22. Average per cent male of hibernating M. lucifugus in this and other studies, pooled samples from November through March. Dashed line is southern limit of distribution

CHAPTER VI

REPRODUCTION AND DEVELOPMENT

Apparently females are sexually mature by their first fall and bear young at the age of 1 year. This view is consistent with the high reproduction rates found in all studies of M. lucifugus. At least some young males appear to be sexually mature by the first fall also. Fenton (1969b) observed young of both sexes copulating in fall. Davis and Hitchcock (1965) noted that unbanded yearling females were pregnant. Fenton and Davis and Hitchcock determined age by the shape of the finger joints up to 5 and 11 months, respectively. Although we were unable to separate all young and adults in Indiana samples after early August, when the young were 2 months old, perhaps full growth is achieved later in northern latitudes.

Unfortunately, other studies of the age at sexual maturity have relied partially or wholly on tooth wear as an age cirterion (Guthrie, 1933b; Miller, 1939; Smith, 1957). Smith (1957) recaptured pregnant bats that had been banded as young a year earlier. Judging from her sampling dates, it is likely that some of these were banded when their small size and dark pelage were unmistakably immature. Guthrie (1933b) reported the presence of sperm in "young" males and females in winter. Miller (1939) asserted that spermatogenesis did not occur until the second summer. He did not identify a method of age determination other than the sex organ development in question, but he probably relied on tooth wear since his work was directed by Guthrie. Nonetheless, it is likely that at least some of the males with small testes and inactive seminiferous tubules and accessory glands were young.

Copulation occurs in fall, winter, and probably spring. A pair of M. lucifugus was found copulating in the Thorntown nursery on 20 August 1960. All other reports on non-hibernating copulation have been from caves. Fenton (1969b) observed frequent copulation from the beginning of September through early October but none in August. Copulation has also been noted in October (Hahn, 1908; Hall, 1962), on 13 November (Griffin, 1940b), 3 January (Guilday, 1948), and at various times in winter (Wimsatt, 1945; Fenton, 1969b; this study). Winter copulation appears to be infrequent and is usually observed after hibernating bats have been disturbed by people. However, occurrence during normal winter arousal periods is likely. Guthrie (1933b) recorded copulation in the laboratory at low temperatures in late March. It is probable that insemination often occurs in spring.

Ovulation occurs after the females have left hibernation and before or shortly after they arrive at the nurseries (Wimsatt, 1944b). Wimsatt (1945) estimated the gestation period in New York at 50 to 60 days. Guilday (1950) noted a rare case of a female carrying an embryo on 31 January, the day after capture in a Pennsylvania cave.

The parturition period for this species generally begins later in the north than in the south. Fenton (1966) recorded the first nursery birth in Ontario on 9 June. In a laboratory colony he noted the first on 7 June and the last on 29 June. Davis and Hitchcock (1965) in Vermont found that one each from samples of 114 and 169 adult females on 7 June had given birth and some were still pregnant on 10 July. In

New England, Griffin (1940b) found newborn young from 13 June to 14 July. The parturition period in northeastern Ohio (Smith, 1954) extended from 10 June to 17 July. In Kentucky, Davis _et al_. (1965) found that two of 228 adult females had given birth on 21 May and 14 of 402 were still pregnant on 21 June. Oagle and Cockrum (1943) reported that in southern Illinois on 17 May two of 173 adult females had given birth while one of 46 was still pregnant on 12 July.

In Indiana at the Pennville nursery on 20 May 1969 none of the 53 reproducing females had given birth but on 5 June 1965, 246 reproducing females and eight young were sampled. One of 59 females had given birth at Pine Village on 8 June 1964. On the same date at Macy, 106 adult females and 53 young were counted. The next day at Cicero 90 adult females and 21 young were captured. At Tunnelton on 9 June 1958 one of 38 reproducing females had given birth as had one of 34 the following day. Thus the parturition period in Indiana begins in the last week of May and the first week of June, with the particular date varying from nursery to nursery.

The parturition period in Indiana ends in the first and second weeks of July. None of 114 females at Milroy-South were still pregnant on 6 July 1965, but 1 of 127 was pregnant at Pennville on 7 July 1965. On 8 July 1965 at New Castle one of 95 females was still pregnant. At Thorntown none of 33 females on 10 July 1964 and none of 38 on 12 July 1966 were pregnant. Two of 376 females were still pregnant on 13 July 1965 at Reelsville.

The interval between the first birth and the earliest flying young gives a rough measure of the period of maternal care, although the date of first flight may slightly precede weaning. Under laboratory conditions in Ontario, Fenton (1966) found the first flying young on 25 June 1965, 18 days after the first birth, and considered 3 weeks a reasonable estimate of the developmental time to flight. Griffin 1940b) captured flying young in early July in New England and judged the age at first flight at 3 weeks to a month. Cagle and Cockrum (1943) recorded the earliest flying young in southern Illinois on 14 June 1940, 29 days after the first birth. In this study young M. lucifugus began to fly at about 4 weeks of age. On 29 June 1966 a few young at Reelsville could fly. At Milroy-South on 6 July 1965, 144 of 164 young were volant. Three of 40 young were volant on 10 July 1964 at Thorntown. All of 94 young were capable of flight on 21 July 1965 at Milroy-South. On 23 July 1965 at New Castle, 73 of 75 young were volant. Fenton (1966) concluded that young had their permanent dentition at the time they were able to fly.

Although good histological evidence exists that a litter size of one is typical for M. lucifugus (Guthrie, 1933b; Guthrie and Jeffers, 1938; Wimsatt, 1944a), few authors have cited numbers of near-term fetuses in necropsied females. Mohr (1933) recorded births of single young to three females. Dymond (1936) took single embryos from each of three females and Rysgaard (1942) collected a female with a 10 mm fetus. Cagle and Cockrum (1943) examined at least 33 embryos; these were not identified as single but neither did Cockrum's (1955) review of reproduction refer to any of them as twins. Gates (1936) dissected a female with two embryos, each less than 1 mm long in February; early ovulation presumably was a result of laboratory conditions. Wimsatt (1945) found two females each with two well-developed fetuses. Davis (1967a) captured a female with two newborn young and a placental scar in each uterine born. No twins were noted in the present study; dissection of 13 near-term females revealed only single embryos. As Wimsatt stated (1945:27), twinning is probably rare in this species. No more than one litter a year has been reported for this species and no evidence of second litters was found in this study.

The proportion of females participating in reproduction each year has been consistently high (Griffin, 1940b). Published data are summarized in Table XIX. Those from this study (Table XX) are also high and consistent among nurseries. Since most values are from samples of near-term and/or lactating females, the number of reproducing females in a population is approximately equal to the annual number of births. The only deviation would be caused by stillbirths and late abortions; none have been reported under natural conditions and their incidence is probably low. Apparently few females are not residing at nurseries during the period of pregnancy and lactation. Females seldom appear at male roosts until nurseries begin to break up when the young are weaned. Miller (1955) found a few barren females at a male roost in the reproductive period. A useful check would be to compare the reproduction rates of nursery samples and samples mist-netted at feeding areas. No extensive data exist on the relation of age and fertility, but the high reproduction rate and the observations of successful reproduction in females 9 and 12 years old (Hall et al., 1957) suggest little variation with age.

TABLE XIX

ANNUAL REPRODUCTION RATES PREVIOUSLY REPORTED FOR *M. LUCIFUGUS*

Reference	Number of adult females	Number reproducing	Per cent reproducing
Cagle and Cockrum, 1943	557	541 (?)	>97
Smith, 1957	314	310	98.7
Layne, 1958	21	19	90.5
Fenton, 1966	9	8	88.9
Total	901	878	97.4

TABLE XX

ANNUAL REPRODUCTION RATES OF *M. LUCIFUGUS* IN THE PRESENT STUDY

Nursery	Date	Number adult females	Number pregnant		Number lactating	Number barren	Per cent reproducing
Tunnelton	9 June 1958	39	37		1	1	97.4
Tunnelton	10 June 1958	35	33		1	1	97.1
Pennville	5 June 1965	251	-	246	-	5	98.0
Pennville	20 May 1969	54	53		0	1	98.1
Milroy-South	5 June 1969	14	-	14	-	0	100.0
Germantown, Ohio	30 June 1969	27	0		27	0	100.0
Total		420	-	412	-	8	98.1

CHAPTER VII

SURVIVAL AND MORTALITY

Survival

Survival data are from recaptures made during annual visits to banding sites, some recaptures from other seasons, and a few citizen reports. Analysis was based on 1-year intervals. Because most visits to a population were not exactly a year apart, any recapture was considered to represent x years survival if it deviated not more than 2.5 months from a date exactly x years after banding. Thus a bat banded in mid-August was recorded as surviving 1 year if taken the next year from June to October. This procedure admits error if the accepted deviation period includes seasonal variation within the annual survival value, as would be the case in the above example if mortality rates were higher in September than in July. On the other hand, considerably more error would result from consistently recording 10-month recaptures as representing zero survival.

Recapture rates of many banded cohorts were low because of extermination, low sampling success, or failure to visit populations some years. Under these circumstances many banded bats went unrecorded for a year or more and some died before the next opportunity for recapture arose. The recapture histories of most cohorts were brief because of unexpected extermination or because they were banded only a few years before termination of the study. Data from these cohorts underestimated survival rates. Each additional sample within a year and each additional year sampled increased the probability of recapturing previously undetected cohort members, partially off-setting the downward bias of the sampling techniques. Thus the cohorts providing the best estimates of survival were those with long histories of concentrated recapture effort. Since some banded animals still may have lived undetected, the best estimates should be considered minimum values.

Recapture histories from 1953 to October 1969 of 664 banded cohorts, 386 from summer and 278 from winter, were analyzed to determine per cent survival per year. The cohorts were divided into eight groups according to age, sex, and season of banding. Some sample characteristics of these cohorts are given in Table XXI. No single cohort had a fully consistent record of recapture effort. To typify survival patterns it was necessary to select the highest value for the xth year within each type of cohort. Each of these values was supported by several slightly lower values from other cohorts, suggesting that the selected values were typical rather than abnormally high. A composite set of highest minimum values was then plotted for each type of cohort.

Semilogarithmic plots of per cent survival values (Figs. 23-26) were examined for constant rates of change. For each type of cohort the survival rate for the first year was much lower than for subsequent years. For the remaining portions of the curves no non-linear patterns were evident, so the minimum survival rates were assumed to be constant for the interval 1 to n years on each curve. The specific rate for each curve was approximated with a simple linear regression line. Because survival rates of individual cohorts were used rather than the

TABLE XXI

CHARACTERISTICS OF COHORTS FROM WHICH SURVIVAL VALUES WERE SELECTED

Cohort type	Numbers of populations with selected values	Number of cohorts selected	Cohort sample size		
			total	mean	range
WINTER					
unaged F	2	6	858	143	31-497
unaged M	2	6	1,747	291	100-1,088
SUMMER					
unaged F	13	32	12,800	400	29-1,416
unaged M	13	31	4,419	143	21-623
adult F	11	18	2,238	124	15-335
adult M	5	9	257	29	12-54
immature F	9	11	1,048	95	17-217
immature M	8	10	770	77	20-151

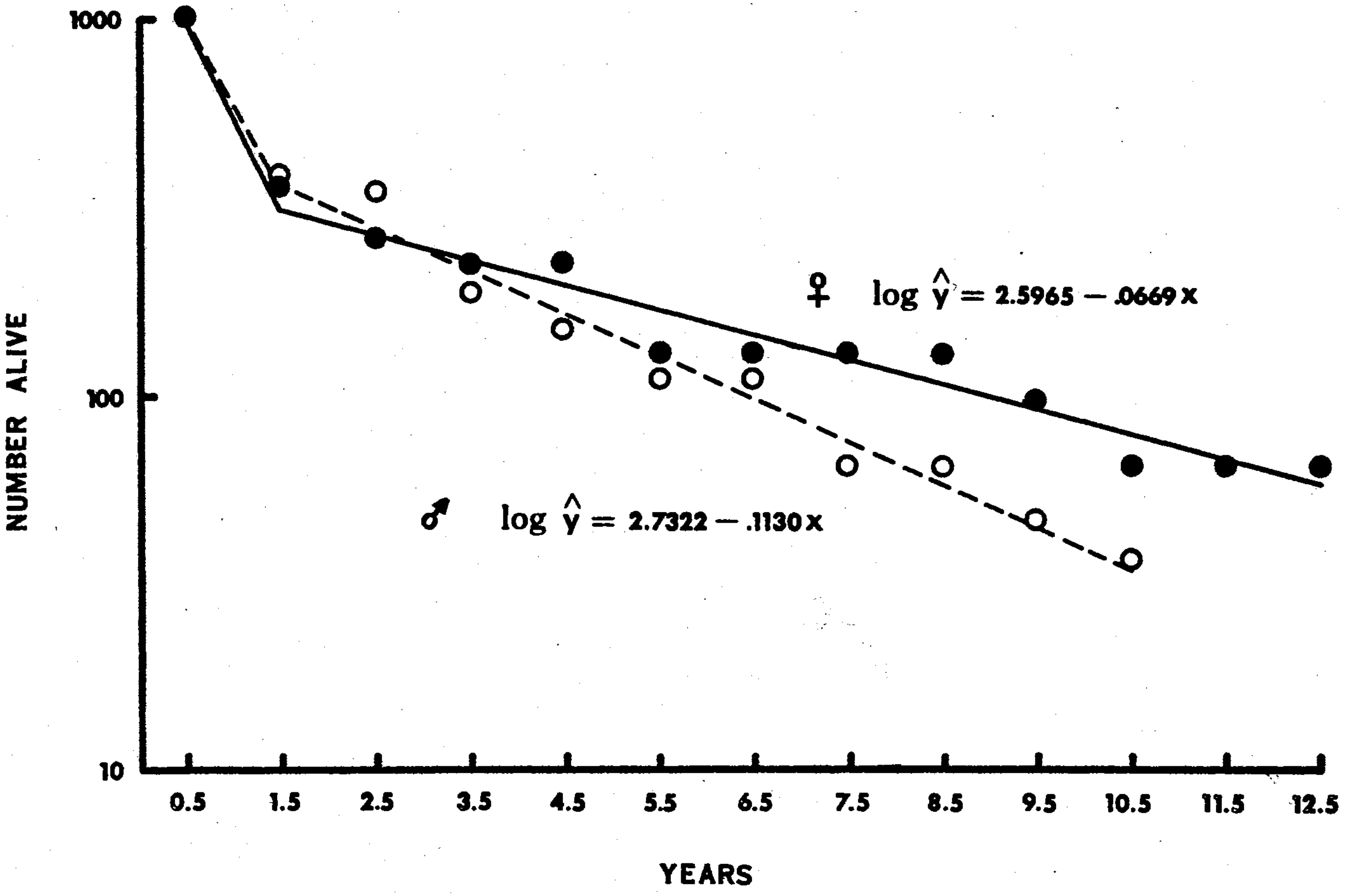

Figure 23. Survival of unaged M. lucifugus banded in winter

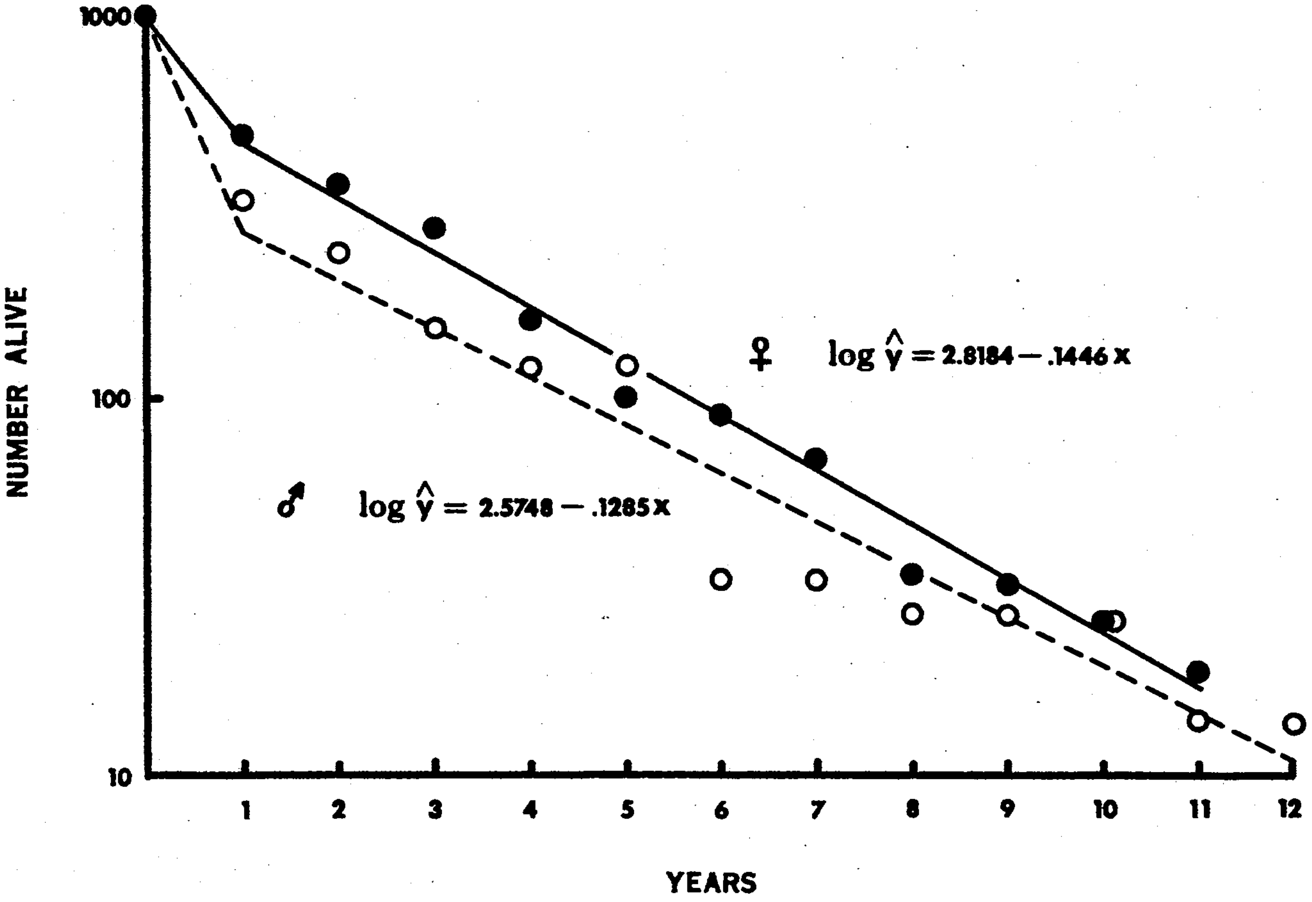

Figure 24. Survival of unaged M. lucifugus banded at nurseries

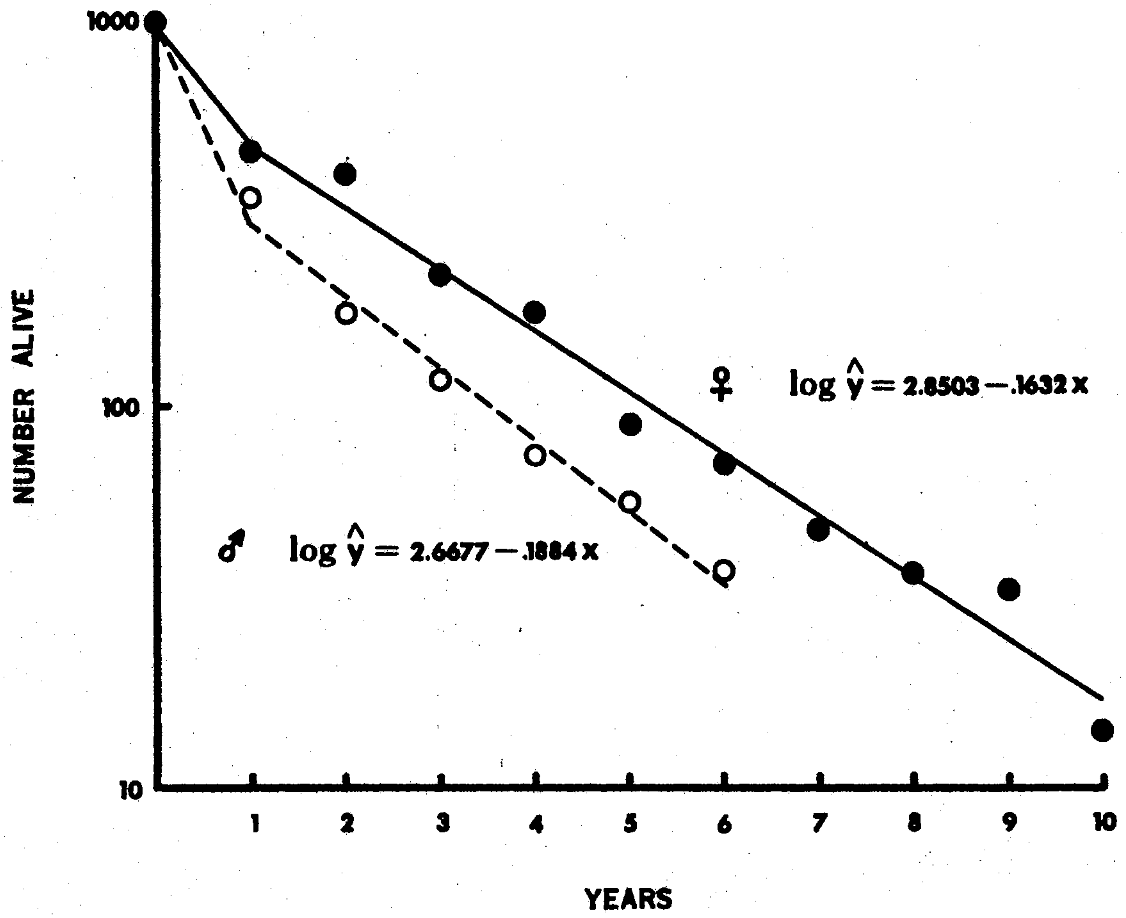

Figure 25. Survival of adult M. lucifugus banded at nurseries

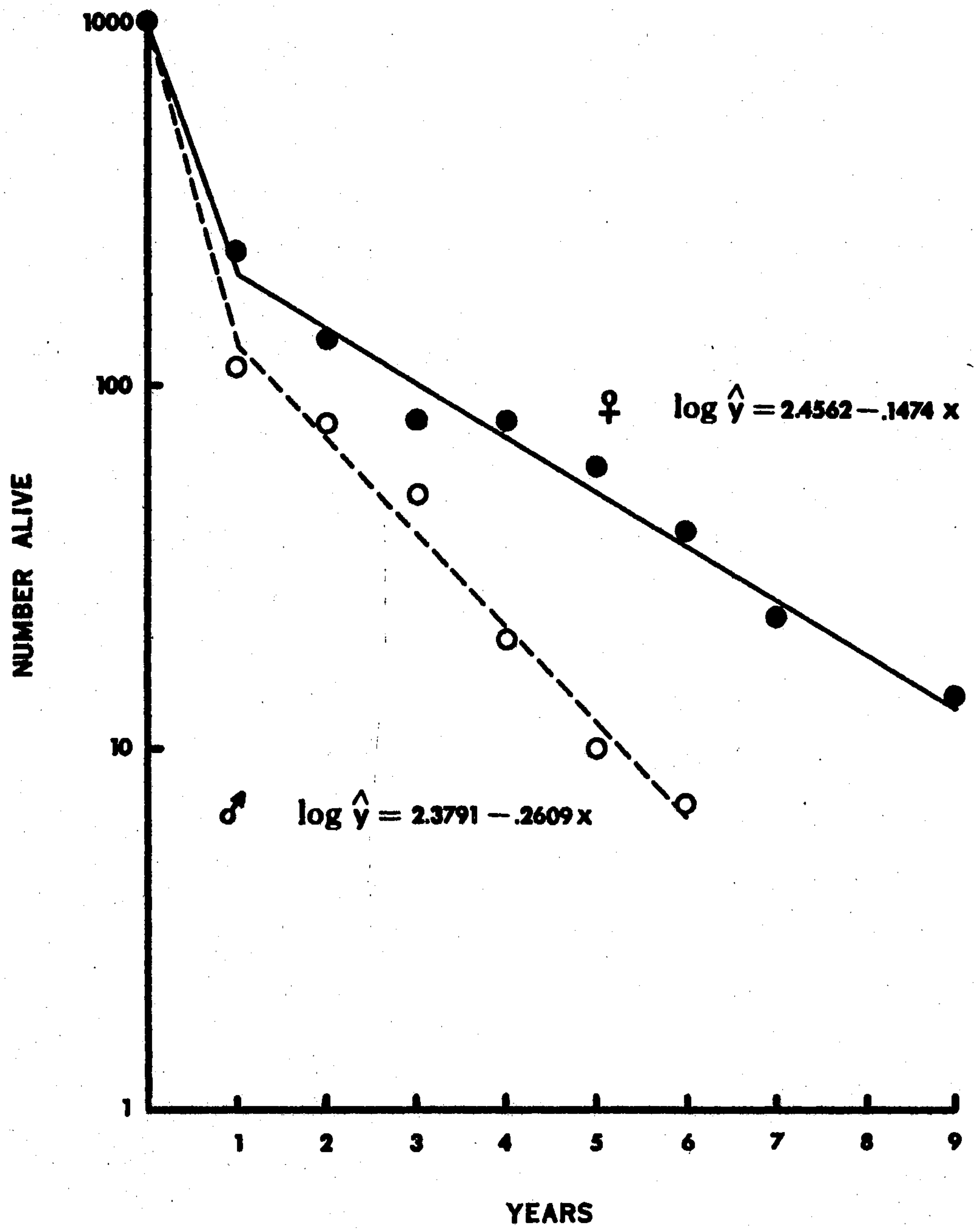

Figure 26. Survival of immature M. lucifugus banded at nurseries

less realistic mean rates, no probability statements may be made about the resultant regression equations. These data do not support statistical tests of the constancy of survival rates within a cohort type or of the equality of the survival rates of different cohort types.

Life tables (Tables XXII-XXIX) were calculated with the methods of Deevey (1947). Estimates of the number per thousand alive at the beginning of each year-interval were obtained from the regression equations. Use of the actual values for this purpose would be misleading because in some years values were no higher than in the following year, an artifact of the sample schedule giving the appearance of 100% survival.

The low survival in the first year compared to later intervals is not surprising in immature and unaged samples, which include some immatures. Such a pattern is typical of young mammals (Caughley, 1966). However, repetition of this pattern in adult samples is not expected, since the second and subsequent years of immature samples show constant rates of survival. This suggests that some individuals respond to our banding procedure in a manner that reduces apparent survival during the first year. A few loosely applied bands are undoubtedly lost, but this probably does not account for all of the difference. Bats also may be subject to increased mortality from accidental collisions or snagging in the air or roost. Several banded animals died from exposure after snagging their bands in a crack at an exit of the Pennville nursery. The possibility that some individuals move permanently to other sites is not supported by movement data.

Because immature cohorts best represent the full life history of _M. lucifugus_, they should be more useful than the other cohorts in explaining demographic behavior of these populations. Unfortunately

TABLE XXII

LIFE TABLE FOR WINTER-BANDED COHORTS OF FEMALE *M. LUCIFUGUS*

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0.5-1.5	1000	687	0.687	2.32
1.5-2.5	313	45	0.143	5.31
2.5-3.5	269	38	0.143	5.11
3.5-4.5	230	33	0.143	4.88
4.5-5.5	197	28	0.143	4.61
5.5-6.5	169	24	0.143	4.29
6.5-7.5	145	21	0.143	3.92
7.5-8.5	124	18	0.143	3.49
8.5-9.5	107	15	0.143	2.99
9.5-10.5	91	13	0.143	2.41
10.5-11.5	78	11	0.143	1.72
11.5-12.5	67	10	0.143	0.93
12.5-13.5	58	-	-	-

TABLE XXIII

LIFE TABLE FOR WINTER-BANDED COHORTS OF MALE *M. LUCIFUGUS*

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0.5-1.5	1000	635	0.635	1.96
1.5-2.5	365	84	0.229	3.49
2.5-3.5	282	64	0.229	3.38
3.5-4.5	217	50	0.229	3.24
4.5-5.5	167	38	0.229	3.05
5.5-6.5	129	30	0.229	2.81
6.5-7.5	99	23	0.229	2.50
7.5-8.5	77	18	0.229	2.09
8.5-9.5	59	14	0.229	1.57
9.5-10.5	46	10	0.229	0.89
10.5-11.5	35	-	-	-

TABLE XXIV

LIFE TABLE FOR SUMMER-BANDED COHORTS OF UNAGED FEMALE *M. LUCIFUGUS*

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0-1	1000	528	0.528	2.15
1-2	472	134	0.283	2.99
2-3	338	96	0.283	2.98
3-4	243	69	0.283	2.95
4-5	174	49	0.283	2.92
5-6	125	35	0.283	2.88
6-7	89	25	0.283	2.82
7-8	64	18	0.283	2.74
8-9	46	13	0.283	2.62
9-10	33	9	0.283	2.46
10-11	24	7	0.283	2.23
11-12	17	-	-	-

TABLE XXV

LIFE TABLE FOR SUMMER-BANDED COHORTS OF UNAGED MALE *M. LUCIFUGUS*

x	l_x	d_x	q_x	e_x
Age interval in years	Number alive at beginning of year interval	Number dying during year interval	Mortality rate of those alive at beginning of interval	Mean life left to those reaching interval
0-1	1000	720	0.720	1.55
1-2	280	72	0.256	3.27
2-3	208	53	0.256	3.23
3-4	155	40	0.256	3.17
4-5	115	29	0.256	3.08
5-6	86	22	0.256	2.98
6-7	64	16	0.256	2.83
7-8	47	12	0.256	2.63
8-9	35	9	0.256	2.36
9-10	26	7	0.256	2.00
10-11	19	5	0.256	1.52
11-12	14	4	0.256	0.87
12-13	11	-	-	-

TABLE XXVI

LIFE TABLE FOR SUMMER-BANDED COHORTS OF ADULT FEMALE *M. lucifugus*

x	l_x	d_x	q_x	e_x
Age interval in years	Number alive at beginning of year interval	Number dying during year interval	Mortality rate of those alive at beginning of interval	Mean life left to those reaching interval
0-1	1000	513	0.513	2.01
1-2	487	152	0.313	2.60
2-3	334	105	0.313	2.56
3-4	229	72	0.313	2.50
4-5	158	49	0.313	2.41
5-6	108	34	0.313	2.28
6-7	74	23	0.313	2.09
7-8	51	16	0.313	1.82
8-9	35	11	0.313	1.42
9-10	24	8	0.313	0.84
10-11	17	-	-	-

TABLE XXVII

LIFE TABLE FOR SUMMER-BANDED COHORTS OF ADULT MALE *M. LUCIFUGUS*

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0-1	100	698	0.698	1.34
1-2	302	106	0.352	2.29
2-3	195	69	0.352	2.27
3-4	127	45	0.352	2.23
4-5	82	29	0.352	2.17
5-6	53	19	0.352	2.07
6-7	34	-	-	-

TABLE XXVIII

LIFE TABLE FOR SUMMER-BANDED COHORTS OF IMMATURE FEMALE *M. LUCIFUGUS*

x	l_x	d_x	q_x	e_x
Age interval in years	Number alive at beginning of year interval	Number dying during year interval	Mortality rate of those alive at beginning of interval	Mean life left to those reaching interval
0-1	1000	796	0.796	1.17
1-2	204	59	0.288	2.78
2-3	145	42	0.288	2.70
3-4	103	30	0.288	2.59
4-5	74	21	0.288	2.43
5-6	52	15	0.288	2.21
6-7	37	11	0.288	1.90
7-8	26	-	-	-

TABLE XXIX

LIFE TABLE FOR SUMMER-BANDED COHORTS OF IMMATURE MALE *M. LUCIFUGUS*

x	l_x	d_x	q_x	e_x
Age interval in years	Number alive at beginning of year interval	Number dying during year interval	Mortality rate of those alive at beginning of interval	Mean life left to those reaching interval
0-1	1000	869	0.869	0.78
1-2	131	59	0.452	1.67
2-3	72	33	0.452	1.63
3-4	39	18	0.452	1.56
4-5	22	10	0.452	1.43
5-6	12	5	0.452	1.20
6-7	7	-	-	-

the immature cohorts and, to a lesser extent, the adult ones had brief recapture histories and thus gave underestimates of survival. Further difficulty arises because mortality of immatures in their first month of life is not accounted for, since only volant bats were banded. The unaged cohorts banded at nurseries and caves had long recapture histories. If no factor other than mortality affected survival data, the first-year survival ($1-q_x$ in Tables XXII-XXIX, or slopes of lines in Figs. 23-26) of the nursery-banded cohorts should be relatively high for adults, low for immatures, and intermediate for unaged animals. For females, survival rates of adults and unaged bats are approximately equal and much higher than that of immatures. The much longer recapture histories of unaged cohorts increase apparent survival, compensating for the inclusion of immature animals. For males, survival of unaged cohorts should be almost as low as immature survival, since most unaged males in nurseries were immature. Instead unaged survival is almost as high as that of adults, with immature survival much lower. Probably the difference between unaged and immature values is due to difference in their respective recapture histories. Perhaps in males the first-year survival of immatures is actually only slightly less than adult survival.

If, again, mortality is the only factor operating, the survival curves of nursery-banded adults, immatures, and unaged bats should have equal slopes for the second and subsequent years. For these intervals all individuals are adult. Among the females, unaged and immature cohorts have almost identical slopes and adult cohorts have slightly lower survival, having shorter recapture histories than unaged groups and less consistent recapture effort than immature groups. For males, unaged cohorts exhibited substantially higher survival than adult cohorts, which in turn showed higher survival than immature groups. This pattern corresponds with a descending order of recapture history length and sampling effort, so the unaged value is probably most realistic. Winter-banded cohorts have the longest recapture histories and most consistent sampling effort and thus should provide the best estimates of survival. Although within-winter changes in population size confound survival data, we may have avoided the effects of behavioral changes by taking most samples in late winter when populations were large. At the time of banding, winter cohorts included unknown numbers of immatures.

Based on the above reasoning, Table XXX presents the best estimates of *M. lucifugus* survival available from this study. Some of the values are in agreement but others which theoretically should be similar are not. Whether the constant rate of survival after the first year is real or an artifact of the smoothing procedure used is a vital question. Caughley (1966) reviewed mammalian survival patterns and found that the post-juvenile phase may exhibit either a constant rate or a steadily decreasing rate of survival. The pattern found in the present study needs verification by studies in which recapture effort can be quantified.

The maximum longevity recorded in this study was 14 years for a nursery-banded female. Much longer records of 20.5 years (Hall *et al.*, 1957; Hitchcock, 1965) and 24 years (Griffin and Hitchcock, 1965) exist for *M. lucifugus* in the northeastern United States.

TABLE XXX

BEST ESTIMATES OF PER CENT ANNUAL SURVIVAL OF *M. LUCIFUGUS*

Cohort type	First year	Subsequent years
immature F	$20.4 \leq ? \leq 47.2$	71.2
adult F	48.7	71.7
winter F	31.3	85.7
immature M	27.9	74.4
adult M	30.2	74.4
winter M	36.5	77.1

Agents of Mortality

The single most important non-human agent of mortality is probably the variety of accidents which *M. lucifugus* encounter while flying or seeking shelter. The disposition of citizen-recaptured bats (Table XXXI) provides some insight into such causes of mortality. Seventeen % of these bats were found dead, 14% were killed when captured, 9% were released alive, and the disposition of the remaining 59% was not specified. Most of these animals were taken in or near human dwellings or utility buildings. Most of the dead bats were found in spring and fall, many during cold weather or after cold nights. Some of the bats killed when captured were reported as appearing sick or injured. The number of recaptures did not vary strongly by season, although there were somewhat fewer reports from summer, when temperature minima were highest. The nursery-banded bats provided particularly interesting information because almost all (97.1% of 9,462) males banded were immatures. In comparison to females, males were a significantly higher proportion of the bats reported than of those banded ($X^2=45.124$, $P<0.005$). Seasonal proportions from summer, fall, and winter contributed to this difference while spring frequency did not. Thus it appears that mortality of immature males was significantly higher than mortality of unaged females (banded in proportions of approximately two adults to one immature) during their first summer, fall, and winter but was not different in their first spring. We have no records of death of hundreds of *M. lucifugus* in fall migration as reported by Zimmerman (1937) but do not doubt that similar mishaps frequently befall individuals or small groups of bats. This species sometimes dies in

TABLE XXXI

SEASONAL FREQUENCY OF M. LUCIFUGUS REPORTED AS CITIZEN RECAPTURES

Season of recapture	Number of recaptures	
	female	male
NURSERY-BANDED		
Winter	4	10
Spring	6	2
Summer	1	10
Fall	17	13
Total	28	35
CAVE-BANDED		
Winter	12	18
Spring	11	17
Summer	8	11
Fall	10	22
Total	41	68

the warm months by becoming snagged on sharp objects such as burdocks (Lyon, 1925). Cave-banded bats showed no significant disproportions between numbers banded and recaptured by citizens. Both sexes at caves included immatures and adults, and by winter much of the high immature male mortality had already occurred.

When M. lucifugus are highly clumped in nursery and winter roosts any regularly effective or catastrophic agent of mortality would easily reduce or exterminate populations. This would be especially critical at nurseries, where reproducing females aggregate. However, in this study non-human agents of mortality were not important at the nurseries. Every nursery contained a few dead immatures and adults but the number was always small. Apparently large scavengers did not enter nursery roosts and remove bat carcasses. Predation was observed at only one nursery. House cats occasionally stood on the roof of the Pennville nursery at twilight and tried to catch flying bats. Children found eight partly eaten bats or bands in the gravel driveway next to the house in 1964 and 1965. The eaves of the Thorntown nursery housed a nesting pair of sparrow hawks, but their activity period did not overlap the bats'. During evening flight counts we never saw owls or other predatory birds attack M. lucifugus, although once I observed a great blue heron attempt to catch a hoary bat, Lasiurus cinereus, in the air. Smith (1954) also noted low mortality at M. lucifugus nurseries.

A number of mortality agents operate in caves, but there is no compelling evidence that these agents are regularly effective. DeBlase et al. (1965) reported the death of approximately 2,850 M. lucifugus, virtually an entire winter population, when Wind Cave flooded in March 1964. This is the only such catastrophe known for this species and is surely a rare event. In Ray's Cave we noted occasional losses of hibernating bats to human activity, once when vandals killed about 100 M. lucifugus and M. sodalis with torches and several times when bats were collected for laboratory experiments. Hitchcock (1965) recorded loss of M. lucifugus to collectors and Fenton (1970) noted several cases of extensive mortality resulting from commercial enterprises in caves. Several miscellaneous instances of predation on this species have been reported, including house cats (Blatchley, 1896), voles (Martin, 1961), mice (Hitchcock, 1965; Fenton, 1970), and a pine martin (Fenton, 1970). Only one definite case of in-cave predation was found in the present study. At Wyandotte Cave in the fall swarming period of 1968 a house cat caught several bats, including two banded male M. lucifugus, which were flying through a very low passage of the cave entrance. We commonly observed tracks of raccoons and mink in Indiana and Kentucky caves and concluded that their prey only occasionally included bats which had fallen to the floor. M. lucifugus rarely chose roost sites within reach of such predators. Davis and Hitchcock (1965) found that many young M. lucifugus entered hibernation without storing large amounts of fat and postulated that many of these fail to survive the winter. We also observed many thin bats in late fall and early winter. Even considering the irregular visits of scavengers which remove bat carcasses from the cave floor, we so seldom saw dead bats on the floor or in roost cracks that without further evidence we are not prepared to accept this as a probable cause of significant mortality. The possibility that starving bats die by flying out to seek food before spring should not be overlooked.

Loss of Populations

Humphrey (1964) commented on destruction of _M. lucifugus_ nurseries in Indiana, and Cope and Hendricks (1970) presented a more detailed and recent account, some of which is included below. The population size figures in Table XXXII are approximate and except for Pennville and Thorntown are based on visual estimates. Because most estimates were made later in the fall than the July peak documented by flight counts at Pennville and Thorntown, it is probable that most estimates were of populations already reduced by fall migration. Thus it can be assumed that these are underestimates in most cases. The "early estimate" column total provides a conservative estimate of the number of _M. lucifugus_ accounted for in the Indiana nurseries we selected for detailed study, viz, 15,450 adult females and their young.

The Brookville colony was exterminated by application of DDT dust to the bats and roost surface. Bats failed to reoccupy the Newbern nursery after napthalene mothballs were hung in the roost sites in the spring. At Shoals, where the population inhabited four buildings, bats at one were poisoned in 1963 and their access holes were caulked in 1964. Another Shoals roost was partially exterminated in 1969 with DDT dust and automobile exhaust. Reroofing of the Reelsville roost excluded bats. Thirty _M. lucifugus_ remained in the Shirley nursery a month after it was reroofed in mid-summer. A month after reroofing of the Franklin attic about 250 bats were found in a nearby barn and fewer than ten in the house. The owner of the Etna house caulked access holes and killed many bats inside the attic with a tennis racket, but some holes and bats remained. No decrease is recorded in this case because the 1969 estimate was taken well after fall migration had begun.

TABLE XXXII

CHANGES IN *M. LUCIFUGUS* NURSERY POPULATION SIZE (ADULT FEMALES AND YOUNG) IN RELATION TO DESTRUCTIVE ACTIVITY

Nursery	Population estimate early in study	Year of known destructive activity	Population estimate after activity	Year of most recent population estimate
Benton	140	none	140	1969
Brookville	650	1968	0	1969
Camden	200	none	200	1962
Carthage	400	none	400	1964
Cicero	200	none	200	1964
Cortland	350	none	350	1964
Etna	300	1968	300	1969
Franklin	600	1964	250	1964
Macy	200	none	200	1969
Milroy-East	170	none	170	1960
Milroy-South	800	1968, 1969	275	1969
New Castle	600	?	35	1969
Newbern	850	1968	0	1969
Pennville	1,360	1969	580	1969
Pine Village	110	none	110	1966
Pittsburg	220	none	220	1962
Reelsville	1,200	1968	0	1969
Rushville	100	none	100	1968
Shirley	600	1964	30	1964
Shoals	3,000	1963, 1969	875	1969
Thorntown	700	1969	250	1969
Tunnelton	1,800	none	1,800	1969
Williamsburg	900	none	900	1969
Total	15,450		7,385	

The Pennville population was reduced 48% when examined in 1969, apparently because a door in the attic wall had fallen in, increasing the amount of light and air circulation in the roost. This probably limited the area of stable microclimate to the deepest recesses of the attic. In 1970 the house was reroofed but a reduced population continued to inhabit the attic (Hendricks and Cope, in preparation). A similar change in microclimate occurred at Thorntown when vandals broke holes in the roof of the abandoned house. The Milroy-South nursery declined from 800 to about 275 adult females and young, primarily because in 1968 and 1969 many bats, including our banded ones, were collected. We cannot explain the fairly regular decline at the New Castle colony from 600 in 1958 to 400 in 1965 and 35 in 1969.

We learned of the loss of three other Indiana _M. lucifugus_ nurseries when exterminators reported banded bats. In 1964 a man near Tipton, Tipton Co., exterminated a colony in his attic by spraying the bats and their roost with DDT solution. This was apparently a medium-sized population. A nursery of 1,500 adult females and young in Columbus, Bartholomew Co., and one of unknown size in Vallonia, Jackson Co., were destroyed by professional exterminators in 1963 and 1965, respectively. Aside from documenting additional losses, these records confirm the likelihood that many sizeable nurseries were not detected during our study.

The summed population estimates before and after destructive activity at nurseries (Table XXXII) show a drop from 15,450 adult females and young to 7,385, a 52.2% decline in about a decade. Further, eight of the 23 populations have not been examined since 1964 or earlier, and it is probable that some of these have been destroyed as well.

Recapture records document the fate of bats whose nurseries were destroyed. Only one bat was ever recaptured after poisoning at Brookville. A female banded there on 23 August 1960 was found 19 km N at a nursery in Dunlapsville, Union Co., Indiana, on 13 August 1970. The only Newbern bat taken after repellant application in 1968 was a female (banded on 28 July 1958) found in the Tunnelton nursery on 14 August 1969. None of the Shirley bats were recaptured since the post-roofing check in August 1964, when 30 were still present. Within a few days of reroofing at Reelsville in 1968, two females, banded on 12 August 1960 and 13 July 1965, were captured while trying to find shelter in separate (unsuitable) buildings in Reelsville. A female banded at Reelsville on 12 August 1960 was taken 6 km away near Lena, Parke Co., on 14 May 1969. One Franklin female, banded on 30 July 1959, was taken in the Thorntown nursery on 14 August 1964, 4 days after the post-roofing check. A male banded during this post-roofing visit was captured behind a screen door in Milltown, Crawford Co., Indiana, on 13 January 1967. No bats from these five nurseries were recaptured in hibernacula following nursery destruction. A survey of all buildings within a 1 mile radius of the Thorntown nursery during extensive sampling disturbance in the summer of 1964 revealed no movement other than to the other roost of the two-building colony. Clearly individuals sought suitable alternate roost sites after exclusion, but there is no evidence of successful or even attempted group establishment at a new roost. Perhaps a few females (each several years old) relocated in previously established nurseries. Thus it appears that virtually all bats involved in a successful extermination or reroofing disappear.

A 10-year history of winter population estimates (Table XXXIII) of M. lucifugus shows a strong downward trend. Since much variation resulted from not using a standard estimation date, the largest estimate is given when more than one estimate was made in one winter. The low estimate of 25 bats at Ray's Cave in 1962-63 was made in November without a later check for possible increased numbers. The Wind Cave flood (DeBlase et al., 1965) occurred shortly after the estimate of 2,850 was made, accounting at least in large part for subsequent low estimates there. The most marked and synchronous decline appeared between the winters of 1966-67 and 1967-68.

Several factors may be related to this decline. It correlates generally with the extermination of nursery populations or destruction of their roosts, and such loss no doubt contributes significantly. Unfortunately we do not know what proportion of the winter population is represented by the nurseries which we monitored. Another possibility is that hibernaculum disturbance by spelunkers and researchers could have caused many bats to seek caves which were less disturbed. Some species are quite sensitive to such disturbance (e.g., Myotis grisenscens, M. D. Tuttle, personal communication; Myotis velifer, Tinkle and Patterson, 1965, T. H. Kunz, personal communication, Humphrey, unpublished data; Eptesicus fuscus, Beer, 1955, Hitchcock, 1965, Phillips, 1966). However, there are no published data suggesting that M. lucifugus avoids disturbed hibernacula. Hitchcock (1965) visited two fairly large hibernacula almost annually for 23 years and found no decline in M. lucifugus populations, while a marked decline in E. fuscus occurred. In the present study a few M. lucifugus moved from one cave to another, up to 16 km away, within a winter. Several

TABLE XXXIII

M. LUCIFUGUS POPULATION SIZE ESTIMATES IN SELECTED HIBERNACULA

Year	Ray's Cave	Grotto Cave	Wind Cave	Wyandotte Cave	Coon's Cave	Total
1960-61	-	2,000	-	-	900	2,900
1961-62	2,680	1,525	-	350	-	4,555
1962-63	25	-	7,000	175	-	7,200
1963-64	1,800	-	2,850	150	225	5,025
1964-65	5,600	1,377	-	900	-	7,877
1965-66	1,300	-	116	500	350	2,266
1966-67	1,800	1,180	200	550	-	3,730
1967-68	70	-	130	140	-	340
1968-69	350	190	162	24	-	726
1969-70	575	266	84	4	-	929

banded in one cave in winter hibernated in a different cave during a later winter. This limited evidence suggests that some disturbed bats move to new caves during a winter or for a later winter, but probably not enough bats are involved to account for the observed declines. A third possible cause which has not been investigated for this species is accumulation of lethal amounts of pesticides. High levels of DDT and DDE have been implicated in a severe decline of a Mexican free-tailed bat (Tadarida brasiliensis) population in Arizona (Cockrum, 1970). The appearance of a threshold effect in the fairly distinct decline in M. lucifugus populations between the winters of 1966-67 and 1967-68 lends credence to this suggestion. This time period shows no specific correspondence with the years in which nursery destruction occurred (Table XXXII). If a general population decline did result from accumulated pesticides, reduced population estimates should appear at nurseries where no destructive activities took place. Although the visual estimates used to construct Table XXXII are not sensitive to such changes, the two nurseries for which we have accurate flight counts, Thorntown and Pennville, had substantially smaller populations in 1968 than at comparable dates in 1964-65 and 1965-66, respectively.

CHAPTER VIII

ECOLOGICAL STRATEGIES

Like other species of insectivorous bats living in temperate climates, the little brown bat has a food supply available only part of the year. When no alternate food supply is accessible, species attempting to fill this type of niche are subject to severe constraints. M. lucifugus has adopted several strategies enabling it to fill such a niche by being energetically conservative and performing all species-maintenance functions during the warm months.

Perhaps foremost in the strategies used by M. lucifugus is a pattern of thermoregulation shared, at least in general characteristics, with other temperate species of insectivorous bats (Lyman, 1970). During the cold months and when at rest in the daytime during the warm months, body temperature drops to within a degree of the ambient temperature. This allows a reduction of metabolic rate and thus in the amount of food consumed. Energy stored in adipose tissue is used during extended winter hibernation. A M. lucifugus possibly may spend the majority of its lifetime in torpor.

The proper functioning of this thermoregulation strategy requires an optimal thermal environment in the roost. M. lucifugus appears to have rather specific roost microclimate requirements, and availability of suitable roosts is probably a limiting factor. A hibernaculum must have a stable, cool microclimate compatible with deep hibernation, as well as high humidity and low air flow rates, minimizing evaporative water loss. Such sites are apparently found only in natural or artificial caves. A nursery must be stable and hot, having available at all times temperatures in the thermal neutral zone of the species (approximately 33°C, Stones, 1965). Temperatures in this zone permit daily torpor in adults and promote rapid growth of the young, which are poor thermoregulators. Suitable nursery sites are apparently found only in tree recesses and man-made structures.

The scarcity of roost sites with optimal microclimatic qualities leads to strong clumping. As a result M. lucifugus occurs in fairly large populations of one sort or another throughout the year. Winter populations are restricted to areas where caves and mines occur. Summer populations are much more widely distributed, including but extending well beyond cave and mine regions. Bats are in both types of roosts in spring and fall. Nursery populations and fall swarming aggregations are the functional units of additional ecological strategies.

One of the most important species maintenance functions occurring in nursery populations is reproduction. Although natality data from growing populations are needed for confirmation, it appears that the biotic potential of M. lucifugus is one offspring per female per year. Apparently this species regularly achieves almost all of its biotic potential. Perhaps environmental conditions in this study were optimal for reproduction. Population growth could be enhanced only by improving survival rates, while population decline could result from decreasing either reproduction or survival rates. Extremely rapid population growth could not occur because this species has no ability to respond to improved environmental conditions by increasing reproduction above the level recorded here. Nor is a notable surplus of offspring produced to allow for high or irregular mortality rates. Survival rates must be high to insure population stability or growth, so roost sites must be virtually free of mortality agents.

The mean life expectancy of females (e_x for year interval 0-1, Tables XXII, XXIV, and XXVI) is slightly more than 2 years. This means that on the average each female will produce exactly two offspring, one female and one male (Table VI), during her lifetime. Thus a female just replaces herself and populations should be stable. This expectation is generally supported by our data on size of undisturbed nursery populations. Restriction of the annual single-birth pulse to a fairly precise date causes a peculiar interaction of natality with survival. An increase in mean life expectancy from, for example, 2.3 to 2.8 years will have no effect on natality because mean life expectancy must increase to 3.0 (plus a month for maternal care) to allow production of a third litter. Only a substantial increase in survival rate will permit population growth to begin.

Thus density-dependent factors which limit nursery population size by reducing survival should be examined. A new population must achieve a mean life expectancy of at least 3 years to grow and then would double about every 4 years. Survival rates high enough to produce that long a mean life expectancy would indeed be remarkable for such a small mammal. A stable population must have a mean life expectancy of at least 2 years but less than 3, and this reduced survival may be some function of density inside the roost or in the feeding area. Whatever the reason, limiting reproduction to one young a year seems to be an effective strategy of self-regulation for this sort of bat. The same rate is found in 13 of the 14 species of *Myotis* in the United States. The one commonly having twins is the southeastern bat (*M. austroriparius*), which does not hibernate in Florida winters and is subject to warm-weather mortality agents all year long (Rice, 1957).

Another vital maintenance function is food-gathering, which has not been studied in *M. lucifugus*. Aside from the obvious importance of acquiring energy for individual metabolism, production of young, and storage of fat, future studies of food habits may help answer questions on limiting factors and the distinctness and location of nurseries. Do individuals compete for food or are enough insects available even in cool weather to justify the expenditure of foraging energy regardless of population density? Competition for food (or space) could explain why newly established populations become stable rather than continuing to increase. Competition could share the influence of roost site scarcity on the lack of summer inter-colony movement and on the high degree of natal site fidelity exhibited by females. Competition could also share with roost site scarcity the responsibility for wide dispersal of *M. lucifugus* in summer colonies.

The distribution of populations shown in Fig. 1 is no doubt greatly biased by our searching procedures. A much better view of the total yearly distribution of the animals we studied is given by citizen reports (Fig. 27). The functional unit whose distribution is outlined is a deme of *M. lucifugus*, a distinct population of interbreeding animals. Existence of demes is apparently quite common in temperate zone bats, although they have not been clearly identified by this term. Roer (1960) concluded that two distinct populations of *Myotis myotis*

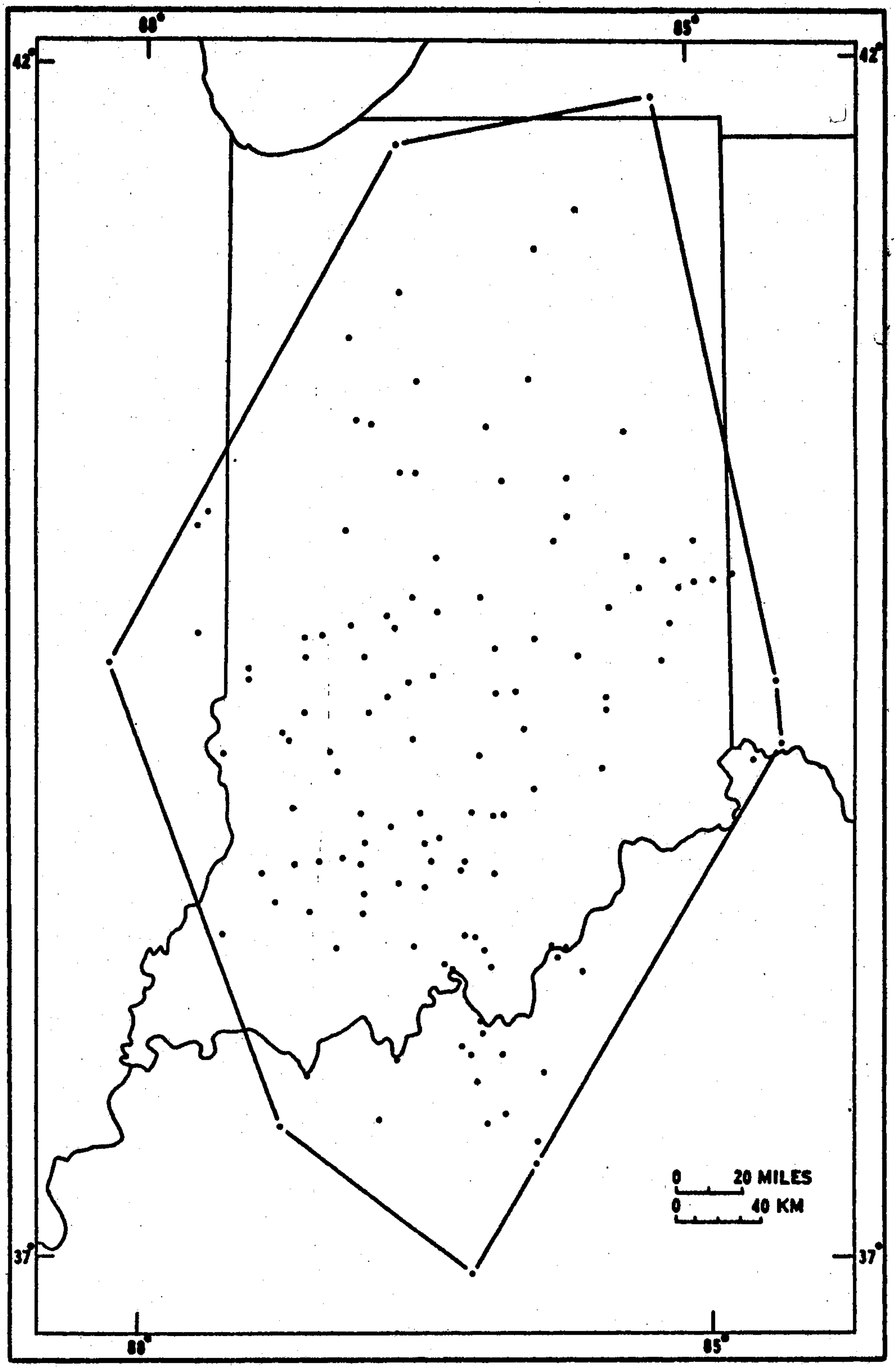

Figure 27. Distribution of the Indiana M. lucifugus deme based on citizen recaptures of banded animals

exist in northern Europe. Hall (1962) stated that Myotis sodalis have "populational ranges" which restrict gene flow. Deme distribution is probably equivalent to the "familiar area" recognized by Davis (1966). Hall and Wilson (1966) discussed a large "populational home range" of Myotis grisescens. Dwyer (1966) described for Miniopterus schreibersii three "partially discrete breeding populations, occupying specific population ranges," "within which gene flow would be at a high level but between which gene flow would be more or less restricted." Dwyer (1969) suggested that such populations "may approach deme status." Cockrum (1969), in reviewing data on migration of Tadarida brasiliensis, concluded that "four or more behaviorally (and possibly genetically) separate populations" exist in the western United States. Barbour and Davis (1969) illustrated distributions of what appear to be two demes of Myotis sodalis. Much of the eastern subspecies of M. lucifugus seems to be organized into demes. Deme distributions (Fig. 28) have been documented in central Missouri (Myers, 1964), western Illinois (Myers, 1964), northern Illinois (Walley, 1971), Indiana (Humphrey and Cope, 1964; Barbour and Davis, 1969; this study), southwestern Ohio (Barbour and Davis, 1969; R. S. Mills, personal communication), southeastern Pennsylvania (Hall and Brenner, 1968), southeastern New York (Davis and Hitchcock, 1965), New England (Griffin, 1940a, 1945; Davis and Hitchcock, 1965), and Ontario (Fenton, 1970).

These deme ranges will become more clearly defined as recapture data accumulate. Ascertaining the degree of overlap or distinctness will clarify patterns of gene flow. Movement data from bats banded at boundaries between demes would be especially instructive. Of our foreign recaptures, only two go beyond the boundaries shown in Fig. 27.

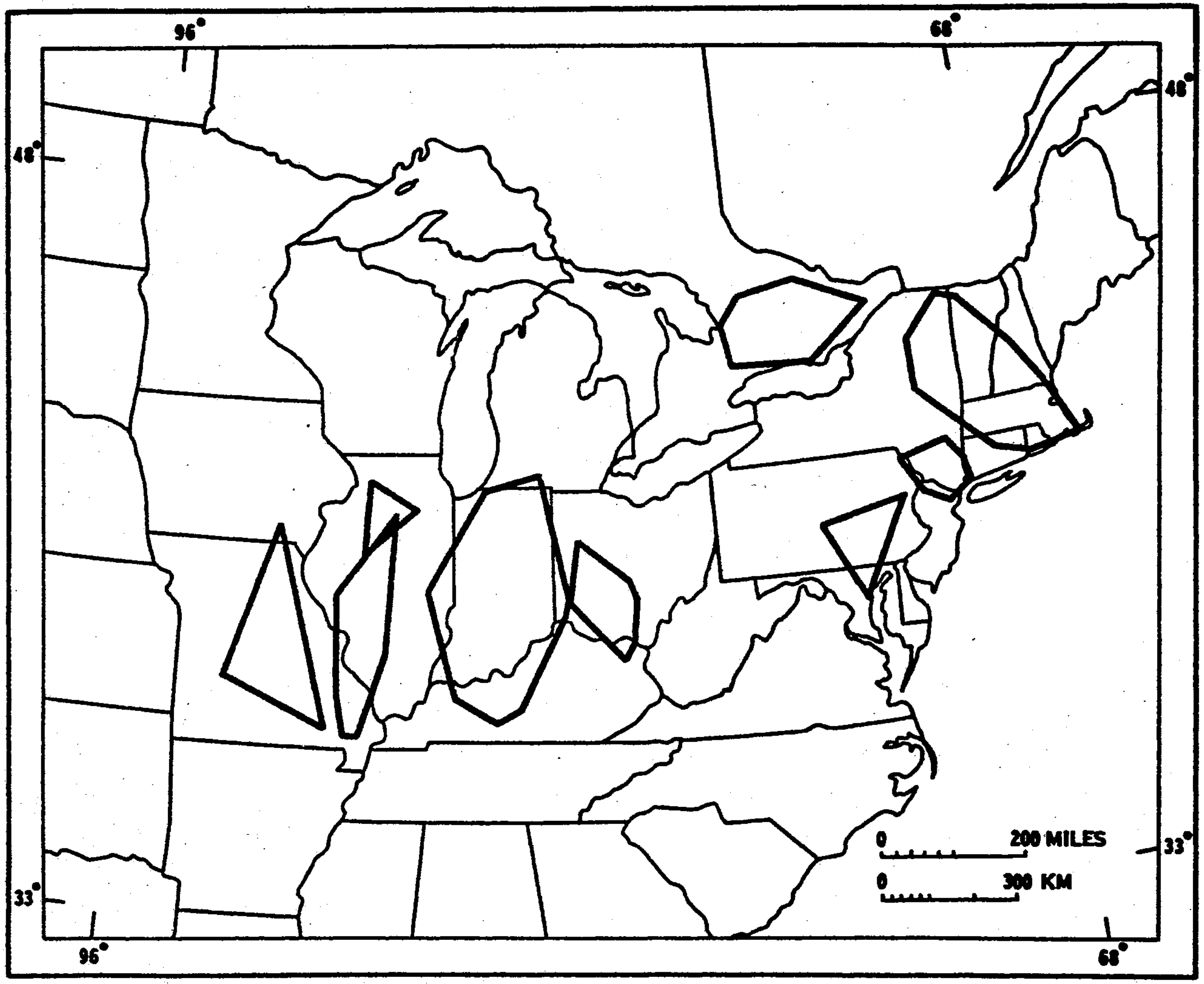

Figure 28. Distribution of *M. lucifugus* demes based on published movement data

A female banded at Grotto Cave on 8 February 1964 was found dead on 26 June 1966 in Chandlerville, Cass Co., Illinois, 319 km (198 miles) WNW. Another female banded at Grotto Cave on 21 February 1965 was recaptured on 2 August 1966 at Merton, Waukesha Co., Wisconsin, 465 km (289 miles) NNW. Of thousands banded in north-central Illinois, H. D. Walley (personal communication) has one similar record of overlap, a M. lucifugus recaptured in the fall in Indianapolis, Marion Co., Indiana. Perhaps these bats became disoriented during migration. Such wanderers probably account for little gene flow between demes. Probably most of the extralimital records of M. lucifugus (summarized on a distribution map by Barbour and Davis, 1969) also represent disoriented individuals, as all are within normal movement distance of areas with established populations. Overlap of the groups in western and northern Illinois as drawn in Fig. 28 is based on a single movement; interpretation as typical movement or atypical wandering must await publication of Myers' data. Based on current information, I believe that gene flow between M. lucifugus demes could be low enough to promote genetic divergence. Examination of morphological and physiological characteristics might reveal variation between demes.

Although the Indiana group of M. lucifugus populations is rather distinctly isolated from others, justification of the claim of deme status demands consideration of the functional properties of such a geographical unit. Probably the most important functions of the unit relate to fall movement and in particular to swarming. Davis and Hitchcock (1965) and Fenton (1969b) suggested that fall swarming functions in the selection of a winter roost site. Our evidence of the lack of movement between caves during the swarming period leaves open a possible function of enabling immatures to learn (and adults to re-learn) the location of one winter roost but does not support the view that swarming provides bats an opportunity to examine several caves. Perhaps the latter function may occur at the northernmost Indiana caves at which we did not study swarming behavior.

Fall swarming appears to perform a very important gene flow function. Swarming is a behavior by which M. lucifugus (and probably other species) dispersed over a wide geographical area in nurseries and male roosts come together to breed. This prevents both failure to find a mate and the local inbreeding which would occur if a nursery population was its own gene pool. It is tempting to speculate that delayed fertilization was adopted as a mechanism to allow plenty of time for moving to and mixing at a common breeding area when food is abundant. Then in spring females could move quickly to nurseries, and early birth and rapid development would permit the young to participate in breeding during their first year of life. Swarming probably does not produce a completely homogeneous mixture of breeding animals, judging from the lack of cave-to-cave movement within the fall and the differences in fall visitation of Wyandotte versus Wind and Dixon Caves. Further development of this thesis depends on better information regarding the relative importance of nurseries, swarming sites, and hibernacula as centers for copulation. Detailed behavioral observations at these locations in fall, winter, and spring would provide insight into the uniformity or routes of gene flow within a deme.

Future studies of swarming should consider the possibility, inferred here from secondary dispersal records and population differences in adult and unaged sex ratios, that the familiar area of the average male

M. lucifugus may be more closely confined to the cave region than that of the average female.

Since patterns of hibernaculum use may also relate to gene flow, movements from nurseries to winter roosts may reveal regional differences within the deme. Figs. 2-7 show that nursery populations differ in the extent to which they use a given cave in the winter. Evaluation of these and other data (Table XXXIV) indicates a spectrum of differential movement from nurseries in various parts of the deme. Populations in several areas behaved similarly; three groups of such populations were pooled to increase sample size. Bats from the northwestern nurseries and Reelsville almost all moved to the northernmost caves. Shoals bats concentrated there also but showed more movement to caves farther south. Tunnelton bats moved almost uniformly throughout the cave region. Bats from the south-central nurseries almost all moved to the southernmost caves while east-central bats concentrated at both southernmost and northernmost caves. These differences may reflect partial routes of gene flow within the deme.

The differences in movement patterns also provide clues regarding possible modes of long-distance orientation in M. lucifugus. Data and speculation are rapidly emerging in literature on numerous bat species indicating (1) that bats migrate in groups (e.g., unknown species, Hammond, 1948; Tadarida brasiliensis, Constantine, 1967) and (2) that bats move in apparent relation to a variety of physiographic features (see review and supplemental data of Dwyer, 1969). Implicit have been assumptions that many bat species are capable of coordinated group movement (such as in feeding flights of T. brasiliensis, personal observation) and that they are capable of detecting landmarks from a

TABLE XXXIV

RELATIVE REGIONAL MOVEMENT OF *M. LUCIFUGUS* FROM NURSERIES TO HIBERNAUCLA. MOVEMENTS FOR BOTH SEXES, FROM SUMMER OR FALL TO ANY WINTER

Nursery of origin	Number of recaptures	Per cent recaptures in each cave region				
		Ray's[1]	Donnehue's[2]	Wyandotte[3]	Wind	Mammoth[4]
northwestern[5]	70	81	1	4	6	7
Reelsville	84	96	1	2	0	0
Shoals	61	61	5	10	3	21
Tunnelton	38	24	21	24	21	11
south-central[6]	44	5	2	5	23	66
east-central[7]	23	35	9	13	22	48

[1] Includes Ray's, Grotto, Coon's, Brinegar's, Buckner's, Shaft, Salamander, and Sullivan's Caves.

[2] Includes Donnehue's, Blue Spring, Bronson, Donaldson's, Endless, and Nymon Caves.

[3] Includes Wyandotte, Salt Peter, and Parker's Pit Caves.

[4] Includes Dixon, Colossal, Mammoth, Long's, Short, and Coach-James Caves.

[5] Includes Benton, Etna, Macy, Camden, Pittsburg, Pine Village, Cicero, and Thorntown.

[6] Includes Franklin, Newbern, and Cortland.

[7] Includes Shirley, New Castle, Williamsburg, Brookville, and Milroy-South.

distance beyond the range of echolocation. Acceptance of these assumptions may lead to another that bats learn and remember the topography of a very large geographical area. Data on _M. lucifugus_ migration are consistent with these concepts. The observation of Zimmerman (1937) shows that this species may move in groups. Our records of large numbers of individuals arriving at and leaving nurseries (Fig. 12) and swarming caves (Fig. 14) suggest coordinated group behavior. The movement patterns in Figs. 2-7 and Table XXXIV probably reflect response to physiographic features. The movement of south-central and east-central bats to the southernmost caves suggests that (perhaps low-flying) bats do not move over (nor through valleys dissecting) the eastern escarpment of the Norman Upland and Mitchell Plain, which extends from a point between Franklin and Martinsville to New Albany, Indiana. Instead they appear to move down the Scottsburg Lowland and Muscatatuck Regional Slope, across the Ohio River, along the western edge of the flat Outer Blue Grass Region and over The Knobs to the Kentucky caves. For maps of relief and physiographic regions refer to _The National Atlas_ (1970), Schneider (1966), and Lobeck (1929). Hall's (1962) view that _Myotis sodalis_ migrates by following water bodies is not applicable to this _M. lucifugus_ deme. It would invoke unnecessarily long and circuitous routes along the Wabash, White, Ohio, and Greene Rivers. It would require bats from extreme northwestern Indiana to move west along the Kankakee River, south along the Illinois and Mississippi Rivers, and east along the Ohio, while bats from the Benton nursery would fly along the St. Joseph River to Lake Michigan. Nonetheless it does seem reasonable to suggest orientation in response to a combination of waterways, escarpments, and other topographic features (perhaps even including major highways). Special orientation conditions may exist where M. lucifugus is found in the Great Plains, as indicated for northern Illinois by Walley (1971). There the restriction of recaptures to river valleys also coincides with the distribution of belts of forest, caves, and very old houses.

Little is known about the duration or importance of the commensal relation of little brown bats and humans. Owners of some nursery buildings in Indiana thought that their attics had been inhabited by bats for at least 70-80 years. A large number of the Indiana nurseries occupied houses of an architectural style popular from about 1850 to 1920, brick structures with wooden eaves and black slate roofs. Davis (1962) speculated that the ageing of houses and clearing of forests have increased the amount of habitat suitable for M. lucifugus and that the species is more abundant now than before settlement of North America by Europeans. Fenton (1970) suggested that buildings might be more satisfactory places to rear young than natural structures and that extensive logging operations may have promoted assumption of the house-dwelling habit.

Although further evidence is needed, this study suggests that M. lucifugus does indeed roost in trees in the warm months. Probably most valuable in this regard are over-mature, senescing, and standing dead trees which contain hollows, cracks, and large sheets of loose bark. Whether the house-dwelling habit developed before or after large-scale removal of such timber and whether abundance is favored more by man-made structures or by widespread stands of climax forest seem to me to be moot points. More certain is the probability that little brown bats in Indiana will continue to decline in abundance in the near future.

We observed that as people's standard of living rose and they became more aware of bats' potential for creating unpleasant odors and carrying rabies and "bugs" they decided to expend money or effort on extermination or major repair that would not have been undertaken otherwise. New styles of architecture are less suitable for bat habitation, and clearing and selective logging have eliminated most potential roost sites in forests. I expect a general decrease in availability of the preferred nursery microclimate in the study area and a corresponding decrease in the abundance of this species. Studies of *M. lucifugus* food habits would be very useful as measurements of the cost of this loss in terms of reduced control of night-flying insects.

CHAPTER IX

SUMMARY

1. Female M. lucifugus spent the warm months in nursery populations, where they bore and reared their young. Nursery roosts were located in buildings and were typically hot, dark, and poorly ventilated. Most males spent the warm months in separate roosts, either individually or in small groups. M. lucifugus hibernated in caves during the winter. Air in winter roosts was cool, humid, and almost completely still.

2. Migration from nurseries to hibernacula was mostly from north to south. Distance of migration ranged from 10 to 455 km.

Several other types of movement were associated with fall migration. Bats dispersed from the nurseries in all directions. Some bats visited nurseries other than their natal ones during fall dispersal. Bats arriving at the caves participated in a fall swarming behavior in which flight in and out of a cave occurred all night long. During this period few bats roosted in the cave in the daytime. Most individuals swarmed at a cave for only a few nights, but their subsequent fall movements apparently did not include other caves. Bats usually used the swarming cave for winter hibernation and for swarming in the next fall, but a few moved elsewhere. M. lucifugus from the Indiana nurseries concentrated their swarming activity at Indiana caves while most of those swarming at the Kentucky caves were probably summer residents of Kentucky or extreme southern Indiana. Many swarming bats underwent a secondary dispersal, moving generally northward away from the caves to nurseries and other sites; females went farther than males.

Most M. lucifugus spent each winter in the same cave, but changes of hibernaculum from one year to another were common.

In spring M. lucifugus began "staging" activities, including cave-to-cave movement and nocturnal flight similar to fall swarming behavior. Spring dispersal from the caves took the form of movement to the north, east, and west. Bats returned to the nurseries in spring migration.

In contrast to the substantial mixing of bats from different populations in fall, winter, and spring, both sexes showed a high degree of nursery site attachment. Nursery populations were distinctly separate units. Movements from one nursery to another during summer were very rare, and females always spent each summer at the nurseries where they were born.

3. Immigration at nurseries began in mid-April and continued to the middle or end of May. Small declines in early June suggested departure of transient animals. Nursery population size virtually doubled when the young were born. Peak numbers of flying bats occurred in mid-July when all immatures were flying but migration had not begun. During fall migration (or at least from late July through August) nursery population size fluctuated markedly, with several hundred bats leaving or arriving at a roost in one night. Distinct emigration began in early September and almost all bats were gone by early October.

4. Swarming activity at caves occurred at low or moderate levels from the third week of March to the first week of June. Low to high levels of activity were monitored from the last week of July to the

third week of October. Numbers of M. lucifugus swarming in August and September varied considerably from one night to the next. Peaks and lows of activity occurred on the same night at two distant caves and activity appeared to follow similar phenological patterns from year to year.

5. Size of hibernating populations appeared to change markedly during the winter. Large numbers of M. lucifugus must have spent portions of the winter undetected, either in parts of caves inaccessible to humans or at unknown sites.

6. The sex ratio of immatures was 1:1 shortly after birth and throughout the prevolant period. After learning to fly males apparently left the nurseries earlier than females.

Adults in nurseries were mostly females. Adult males were always scarce but more were present in June and July than in the spring. A large southern nursery contained more males than did northern nurseries; possibly most males remain relatively near the cave region in the summer.

Increased proportions of males in September and October resulted when males moved into the nurseries. This change was most prominent at a nursery near the caves.

7. In hibernating populations there were almost always more males than females. Sex ratios were closest to parity and most stable in mid-winter and the highest proportions of males occurred in fall and spring. Each cave or group of hibernacula appeared to have its own characteristic mid-winter sex ratio. Northern hibernacula tended to have higher proportions of males than southern caves.

8. Females bear their first young at the age of one year. Litter

size is almost always one, and there is only one litter per year. The reproductive rate per female was 0.98 offspring per year. No variation in age-specific fertility is known or suspected.

9. Highest minimum survival rates were relatively low in the first year after banding but were much higher and apparently constant in subsequent years. Mean life expectancy of females was slightly more than two years. Maximum longevity was 14 years.

The most important non-human agent of mortality was a variety of accidents encountered while flying or seeking shelter. Natural mortality was negligible within nursery and winter roosts, except for rare cave flooding. Extermination or bat-proofing of nurseries resulted in loss of at least 52% of the _M_. _lucifugus_ in a decade. The decline as measured in winter populations appeared even more serious, perhaps as high as 80%. Continued declines in abundance are expected .

10. Successful occupation of a niche with only seasonally available food depends on being energetically conservative and performing all species maintenance functions during the warm months. _M_. _lucifugus_ must find roost sites with stable microclimates suitable for deep hibernation in winter and for both daily torpor of adults and rapid growth of immatures in summer.

11. Females regularly achieved almost all of their biotic potential of one offspring each per year. Since the average female produced one female offspring during her lifetime, populations appeared to be stable. Populations would have had to greatly increase survival rates in order to grow. The existence of density-dependent factors which limit nursery population size by reducing survival is suggested.

12. Animals in the populations included in this study are members

of a deme since they interbreed and are genetically isolated from individuals in outlying populations. Other studies indicate that much of the eastern subspecies of M. lucifugus is organized into similar demes. Swarming behavior brings together bats dispersed throughout the deme range to breed in a smaller region near the hibernacula, apparently preventing both local inbreeding and failure to find a mate.

13. Differences in summer-to-winter movement patterns are consistent with the view that these bats may migrate in groups and orient themselves by recognition of physiographic features.

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APPENDIX

LOCATIONS OF *MYOTIS LUCIFUGUS* POPULATIONS MAPPED IN FIGURE 1

WINTER POPULATIONS

1. Grotto Cave, 6.8 miles W, 1.7 miles S of Bloomington, Monroe Co., Indiana.
2. Coon's Cave, 7.2 miles W, 2.2 miles S of Bloomington, Monroe Co., Indiana.
3. Brinegar's Cave, 6.9 miles W, 3.4 miles S of Bloomington, Monroe Co., Indiana.
4. Ray's Cave, 3.9 miles W, 2.2 miles N of Cincinnati, Green Co., Indiana.
5. Buckner's Cave, 6.8 miles W, 2.6 miles S of Bloomington, Monroe Co., Indiana.
6. Shaft Cave, 6.7 miles W, 1.7 miles S of Bloomington, Monroe Co., Indiana.
7. Salamander Cave, 6.4 miles W, 1.5 miles S of Bloomington, Monroe Co., Indiana.
8. Sullivan's Cave, 4.0 miles W of Springville, Lawrence Co., Indiana.
9. Blue Spring Cave, 4.4 miles S, 4.4 miles W of Bedford, Lawrence Co., Indiana.
10. Donnehue's Cave, 2.2 miles S, 1.7 miles W of Bedford, Lawrence Co., Indiana.
11. Bronson's Cave, 3.6 miles E, 0.4 mile S. of Mitchell, Lawrence Co., Indiana.
12. Donaldson's Cave, 3.2 miles E, 1.0 miles S of Mitchell, Lawrence Co., Indiana.
13. Endless Cave, 2.9 miles N, 0.3 mile E. of Campbellsburg, Washington Co., Indiana.
14. Nymon Cave, 2.7 miles E, 1.7 miles N of Campbellsburg, Washington Co., Indiana.
15. Wyandotte Cave, 3.8 miles E, 2.1 miles N of Leavenworth, Crawford Co., Indiana.
16. Parker's Pit, 1.3 miles W, 1.3 miles S of White Cloud, Harrison Co., Indiana.

17. Wind Cave, 2 miles W, 1 mile S of Big Spring, Breckinridge Co., Kentucky.

18. Dixon Cave, 0.3 mile W, 0.3 mile N of Mammoth Cave, Edmonson Co., Kentucky.

19. Mammoth Cave, 0.1 mile W, 0.1 mile N of Mammoth Cave, Edmonson Co., Kentucky.

20. Colossal Cave, 2.4 miles E, 0.2 mile N of Mammoth Cave, Edmonson Co., Kentucky.

21. Long's Cave, 4.2 miles S, 1.0 mile E of Mammoth Cave, Edmonson Co., Kentucky.

22. Short Cave, 1.8 miles W, 1.6 miles N of Park City, Barren Co., Kentucky.

23. Coach-James Cave, 2 miles S of Park City, Barren Co., Kentucky.

NURSERY POPULATIONS

24. Shoals (attics of a house, a school, and two churches), Martin Co., Indiana.

25. Tunnelton (two house attics), Lawrence Co., Indiana.

26. Cortland (house attic), Jackson Co., Indiana.

27. Newbern (church attic and belfrey), Bartholomew Co., Indiana.

28. 3 miles E of Franklin (house attic and barn), Johnson Co., Indiana.

29. Reelsville (church attic and belfrey), Putnam Co., Indiana.

30. Brookville (school attic, church steeple), Franklin Co., Indiana.

31. 2 miles S of Milroy (house attic), Rush Co., Indiana.

32. 3 miles E of Milroy (house attic), Rush Co., Indiana.

33. 4 miles S of Rushville (house attic), Rush Co., Indiana.

34. Occident (house attic), Rush Co., Indiana.

35. 2 miles S of Pennville (house attic), Wayne Co., Indiana.

36. Williamsburg (house attic), Wayne Co., Indiana.

37. 3 miles W of New Castle, Henry Co., Indiana.

38. 4 miles N of Shirley (house attic), Henry Co., Indiana.

39. Cicero (warehouse eaves), Hamilton Co., Indiana.

40. 4 miles E, 2 miles S of Thornton (house attic, barn wall), Boone Co., Indiana.

41. 6 miles E, 2 miles S of Pine Village (garage loft, stack of shutters), Warren Co., Indiana.

42. Pittsburg (house attic), Carroll Co., Indiana.

43. Camden (house attic), Carroll Co., Indiana.

44. 3 miles W of Macy (ceiling beams in ground floor of barn), Fulton Co., Indiana.

45. 1 mile N, 1 mile E of Etna (house attic), Whitley Co., Indiana.

46. 4 miles S, 3 miles E of Benton (sliding door in barn), Elkhart Co., Indiana.

VITA 3

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Doctor of Philosophy

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