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Life History and Taxonomic Study of the Indiana Bat, *Myotis sodalis*

BY

JOHN S. HALL [1]

INTRODUCTION

e Indiana bat, *Myotis sodalis*, was described by Miller and Allen in vhen they reviewed the genus *Myotis* in North America. This species en overlooked for many years, even though it was well represented in ions. It had been confused with *Myotis lucifugus*, which it closely les. Little is known about *M. sodalis* other than its distribution in and some fragmentary life history information. A general life history udy of a species as widespread and numerous as this bat was definitely needed and such a study was begun in the fall of 1956.

e range of *M. sodalis* extends from Vermont through southern Michiid southern Wisconsin, south through Missouri and Oklahoma, and ast again to northern Florida. Field research was conducted in caves ine tunnels in Illinois, Indiana, Kentucky, and Missouri. This area center of distribution of the species. Studies were conducted during nths of the year. A total of 130 days was spent in the field from r 1956, through December 1960.

e objective of the work done in the winter was to determine the size stribution of hibernating colonies, to study factors concerning selecthe hibernating site, and to learn the habits of *M. sodalis* during the period. During the summer months information was obtained on ition, composition, activity, and habitat selection of summer colonies s. Approximately 12,000 *Myotis sodalis* were banded in an effort to ine seasonal movement, non-seasonal movement, and returns to same n winter and summer, and to begin a study of survival by band res from year to year. Other investigators have banded many thouof *M. sodalis* in the mid-west over the last ten years. This banding valuable in my studies and made possible a large number of band ies. The area of banding was large enough to define areas of movemore clearly than has been possible before. This information conmovement patterns of *M. sodalis* has implications on homing ability thods of navigation by bats.

partment of Biology, Albright College, Reading, Pennsylvania.

This has been a favorable species to study because of its limited geographic range. The intensive field work was done over a large portion of he range. This made it possible to obtain definite information on the opulational structure of the species and on factors involved in the distribuion and dispersal of the species.

Another objective of this work was to study geographic variation of *M. odalis* and to compare its morphology with several other *Myotis*. Several pecies of *Myotis* were compared as to differences in distributional patterns nd ecological relationships. Six species of *Myotis* occur in the study area nd often four are found in one cave system. This provided a fine opporunity to study differences in the ecology of these species. This informaon is important in understanding mechanisms of isolation during speciaon in the genus *Myotis*.

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I wish to thank persons in charge of various collections, who made availle to me specimens in these collections. The abbreviations following the mes listed below are those used throughout the paper for the various colctions. I extend my appreciation to:

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[2] This report is based upon a dissertation submitted in partial fulfillment of the reirements for the degree of Doctor of Philosophy in Zoology in the Graduate College the University of Illinois.

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METHODOLOGY

hty caves in the mid-west region were investigated to learn of the ation of bat populations in winter and summer. I investigated 52 n winter, 51 in summer, and 23 in both summer and winter. These epresent a random group of caves, since as many different ones were d in any particular area as time allowed. This was done to observe es of cave environments existing in this area. Estimates were made numbers of bats of all species in each cave. This was done by direct g in the case of small numbers. If a cave contained a large colony nt of about 1,000 was counted and the remaining were estimated by he counted group as a basis.

Temperatures in the caves were taken with a centigrade, mercury-bulb ermometer. Relative humidities were taken with a sling hygrometer. emperatures of the microenvironment, bat clusters, and rectal temper-ures of bats were taken with a thermistor enclosed in a rounded-end glass obe. This instrument was loaned by Dr. C. Ladd Prosser, University of linois. The detailed studies of habits throughout the year were conducted 14 caves as follows: ILLINOIS: *La Salle County:* Blackball Mine; *Hardin ounty:* Cave Spring Cave; INDIANA: *Crawford County:* Wyandotte Cave; reene *County:* Ray's Cave; *Monroe County:* Coon's Cave; Grotto Cave; ENTUCKY: *Carter County:* Bat Cave; *Edmonson County:* Coach Cave; mes Cave; Bat Cave; Long's Cave; Dixon Cave; Colossal Cave; Wilson ve. A number of caves in Missouri and Tennessee were investigated, t very little time was spent in these areas.

In these caves 9,863 *Myotis sodalis* were banded in winter hibernation, 321 in summer, and 373 in the fall as they were returning to hibernation. me banding was done during five consecutive winters and three summers, d recoveries were made each year. These recovery data are analyzed for asonal movement, non-seasonal movement, and returns to same caves in nter and summer. The bands used were United States Fish and Wildlife 1 bird bands and #1B lipped bat bands.

Important parts of five caves were mapped for the purpose of plotting sitions of bats throughout the year. The mapping was done with a Brun-n Compass and tape measure or by means of pacing. Weight changes re studied by weighing bats in the field throughout the year. In Coach ve, Edmonson County, Kentucky, guano was collected with a plastic eet over a guano pile to study seasonal activity and feeding.

Geographic variation of *Myotis sodalis* was studied by examining 1,235 ecimens contained in the above listed collections. All specimens are skins d skulls unless otherwise indicated in the list of specimens examined. xternal measurements are those taken by the collectors. Seven cranial easurements were taken with an inside micrometer and ocular micrometer ounted in a binocular microscope in the following manner.

Greatest length: Distance from the anteriormost border of the premaxilla, exclusive of incisors, to the posterior limit of the braincase.

Condylobasilar length: Distance from the anteriormost border of the premaxilla, exclusive of incisors, to the posterior projection of the occipital.

Mastoidal breadth: Breadth of skull taken between the most lateral projections of the mastoids, just dorsal to the auditory bullae.

Width of braincase: Breadth of skull taken between the most lateral limits of the braincase.

Interorbital breadth: Taken as the least diameter of the interorbital constriction of the frontals.

asal breadth: Breadth of the rostrum taken between the vertical flat surfaces just anterior to the infraorbital foramen.
andibular length: The greatest length of the mandible, exclusive of incisors.

he mean, standard deviation, and standard error were calculated for measurements at each locality. Color was analyzed by establishing s of colors based on the mixture of brown and gray. Seven color s were set up as follows: 1) dark gray; 2) medium gray; 3) light 4) dark brown; 5) medium brown; 6) light brown; and 7) reddish . Males and females were at first analyzed separately, until it be- evident that no sexual dimorphism existed. For this reason all sta- are calculated from the combined sexes.

TAXONOMY

yotis sodalis was described in 1928 by Miller and Allen in their re- of North American *Myotis*. Since then many additional specimens been collected to fill in the limits of the range of *M. sodalis*, yet these ens have never been analyzed in regard to geographic variation and le race formation. With the greater number of specimens now avail- study of such variation is possible.

Myotis sodalis Miller and Allen

sodalis Miller and Allen, 1928, Bull. U. S. Nat. Mus., No. 144: p. 130.

lotype: Museum of Comparative Zoology, Harvard, 10980; adult ; skin and skull; collected 7 March 1904; by J. O. Sibert; from lotte Cave, Crawford County, Indiana.
tribution: Mid-west and eastern United States from the western edge rk region in Oklahoma to central Vermont, to southern Wisconsin, far south as northern Florida. Distribution is associated with cavernous limestone areas and areas just north of cave regions.
nter and summer ranges are plotted separately in figures 1 and 2. r distribution is not well known, but seems to coincide closely with nter distribution, except that there are records north of cave areas in laces, such as northern Indiana and southern Michigan.
cription: Myotis sodalis is a medium-sized, dark-colored *Myotis*. nall, but not as small as *M. californicus* or *M. subulatus*. Hairs on ort and inconspicuous. Color dark gray to dark brown to light but not glossy. Color of base of hairs dark black for over two- of its length, followed by a narrow, grayish band, not sharply de- from black band of base. Tips of hair may be either dark gray to

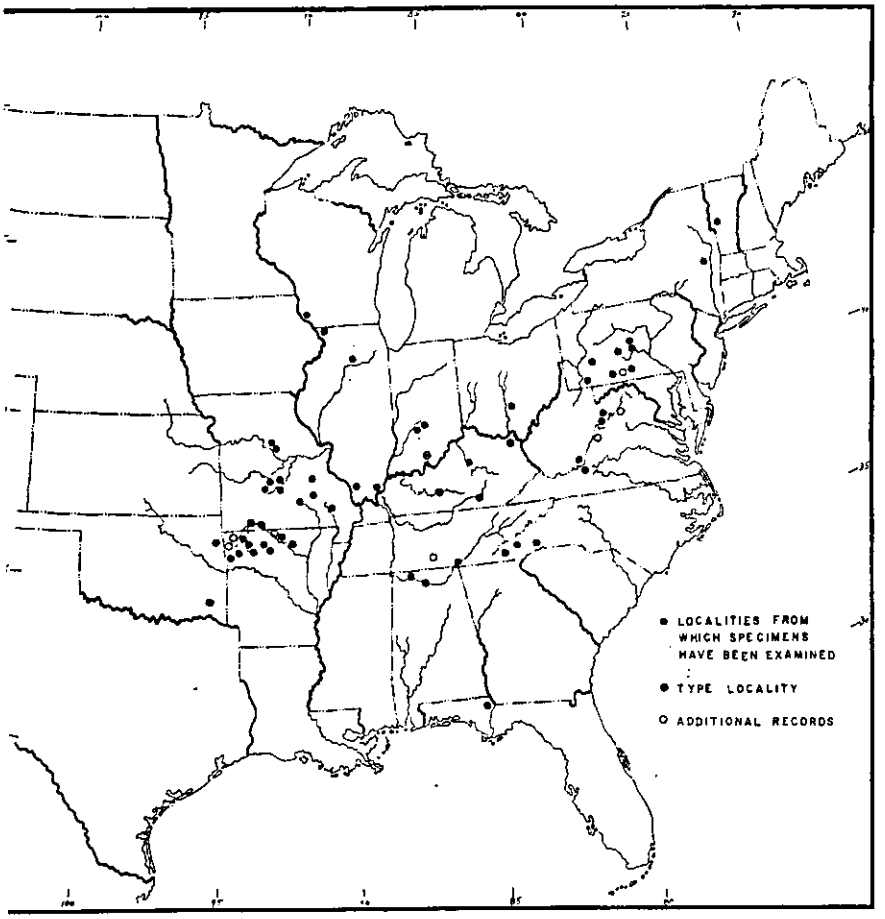


FIGURE 1. The distribution of winter colonies of *Myotis sodalis*.

lack or dark brown to light brown. When tips are brown, never glossy burnished. Fur when viewed in yellow light sometimes gives an illusion f being tinted dark purple. Tri-coloration of fur weakly evident, since arious bands not sharply delimited and dark gray tip may be same color s middle gray band.

Calcar strongly keeled (figure 3). On dry skin, keel evident as bump posterior edge of interfemoral membrane. On fresh specimen, cartiginous keel clearly seen by holding membrane before strong light. Skull ather delicate with rather narrow braincase (6.40–7.20 mm) and narrow nterorbital region (3.29–4.27 mm). Teeth essentially indistinguishable om other similar-sized *Myotis*, with exception that cingulum of premolars ather heavy and prominent.

Measurements: See tables 1 and 2.

omparisons: Myotis sodalis is most easily confused with *Myotis luci-*
s. It is distinguished from *lucifugus* by its dark, non-glossy fur, which
cifugus is a burnished, glossy brown. The dark band of the base of the
in *lucifugus* is much darker, and more sharply delimited from the color
e tip. *M. lucifugus* has a larger foot, with long conspicuous hairs. In
ucifugus the calcar is not keeled as in *sodalis* (figure 3). The skull of
gus is more robust, with a wider braincase (6.96–7.60 mm) and greater
orbital breadth (3.62–4.25 mm).

'yotis grisescens is larger than *M. sodalis;* the hairs are an even gray
from base to tip; the skull is larger, but proportions about the same
dalis; the sagittal crest much more pronounced than *sodalis;* and the
not keeled.

yotis austroriparius is similar in size to *sodalis,* but the fur is much

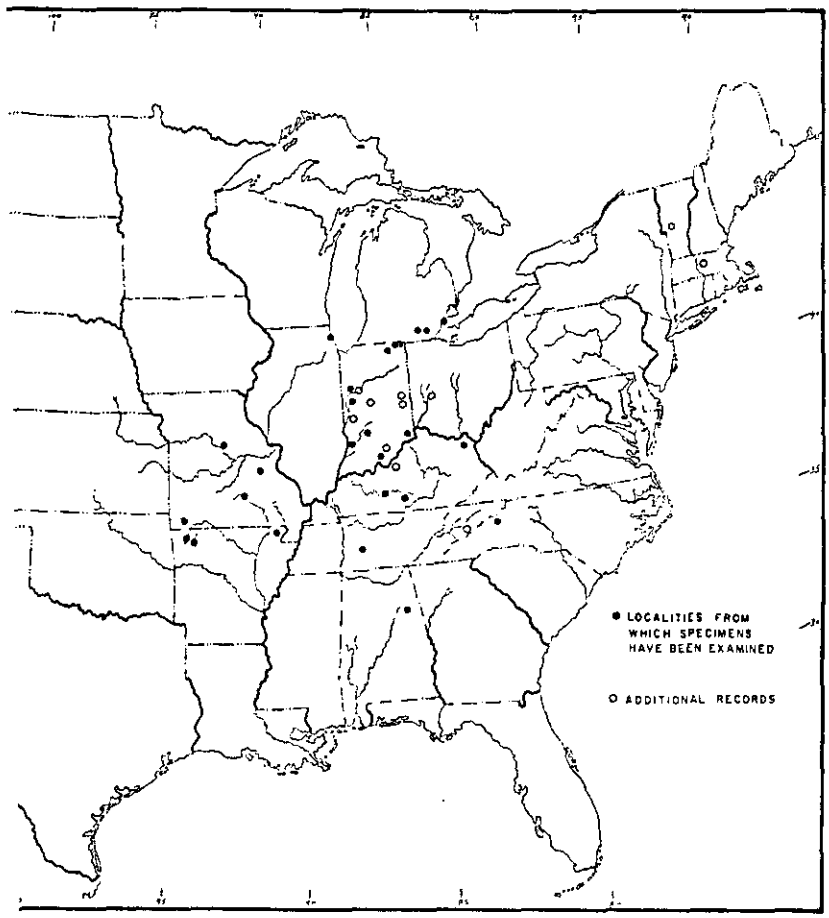


FIGURE 2. Summer records of *Myotis sodalis.*

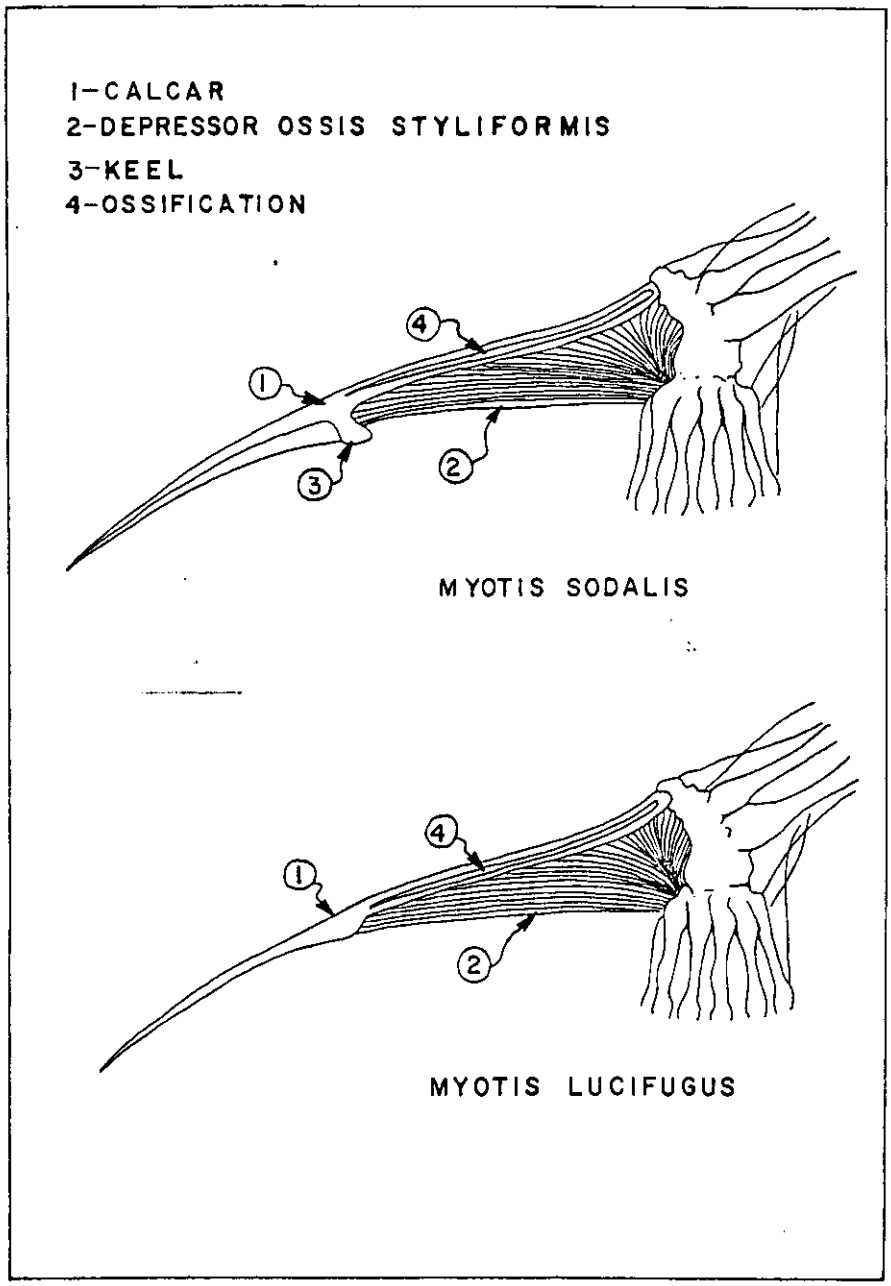


FIGURE 3. Right hind foot of *Myotis sodalis* and *Myotis lucifugus* with the skin removed to show the calcar and associated structures.

er, the color on the dorsum is orange-brown to buff-brown; the under- are much whiter than *sodalis;* and the calcar is not keeled.

'gotis velifer is distinguished from *sodalis* in having a much lighter ı color; no keel on the calcar; and a skull which is larger, with maxil- :eeth that are broader.

elationships: The morphological similarity of *M. sodalis* to *M. luci-* might indicate close relationship. However, the habits of *sodalis* are different from those of *lucifugus* (see life history discussion). *M. is* is a typical cave bat as is *M. velifer, M. grisescens,* and *M. austro- us.* It is possible that *sodalis* represents one species of a group which ;ave rise to *velifer* and *grisescens,* if habits are to be taken as indicat- lationships. Conversely, *sodalis* may have been derived from a group ling *M. lucifugus.* The centers of population of *sodalis* are in the cave of Kentucky and Missouri. This species may well have split off from k of *M. lucifugus* in the southern portion of the range in association large caves. The range of *lucifugus* includes nearly all the range of s at the present time, but the major centers of population of *lucifugus* northern United States.

olt: Adults apparently molt once each year during early summer. a few specimens have been collected in summer, and they do not rep- a good time series. The period of molting is probably rather short, ; the middle of June. Male specimens from Shannon County, Mis- on 30 May show no sign of molting. Male and female specimens from 11 June to 16 June in Edmonson County, Kentucky, and Mad- 'ounty, Arkansas, show definite indications of molting in process. This lent by the lack of distinct banding of the fur. The new hair pushing . the old dropping out gives the skin a dark grayish appearance, with ndication of distinct color bands to the fur. One specimen collected ' as 2 July in Edmonson County, Kentucky, shows signs of molting. :er, other specimens collected at this time show no such evidence of Some variation must occur in molting time, since some specimens ed in mid-June show no evidence of molt. In a series of five males ed 13 June 1959, in Long's Cave, Edmonson County, Kentucky, three] sign of molting and two did not.

ographic Variation: Color of coat can be divided into two groups as :: 1) those which are gray to black; and 2) those that have brownish the fur. A gray color lacking traces of brown is more typical. The n of gray-brown specimens is plotted for various localities in figure e smallest fraction of brown is in central Kentucky and the largest tages of brown specimens are on the periphery of the range in south- Missouri, eastern West Virginia, and Vermont. The population in rn Illinois has a low fraction of brown. Some areas have too few ens to give any meaning to this fraction, such as southern Illinois, n North Carolina, and southeast Missouri. The one specimen from

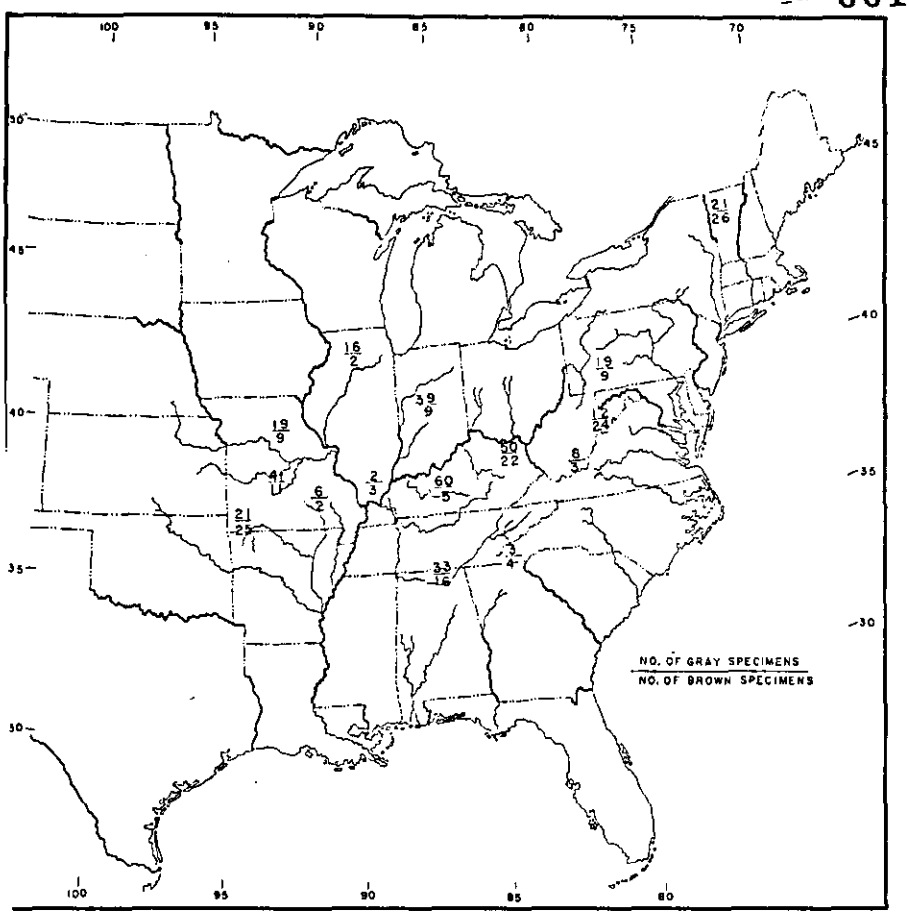


FIGURE 4. Geographic variation of color in *Myotis sodalis*.

orthern Florida is not included in figure 4. It is reddish brown and this olor was noticed in a few other specimens from other localities.

The Vermont specimens seem to have a more distinct banding to the ur, with the black bases being set off more sharply from the color band at he tip of the hair. The hairs on the feet appear to be a little longer on 'ermont specimens. These differences do not seem strong enough to war- ant a subspecific designation for this population.

The grayish and brownish color is typical for *M. sodalis*. A number of harp variants have been noted in the examination of specimens. These olor variants show various degrees of whiteness in the fur as follows: 1) ne small white spot on mid-dorsum: Pulaski County, Missouri (UI) (spot 5 × 20 mm); Pulaski County, Missouri (UI) (spot 10 × 10 mm); Pendleton County, West Virginia (WGF) (spot very small); 2) white hairs dispersed

Locality			Length	Condylo-basilar	Mastoidal breadth	Width of brain-case	Inter-orbital breadth	Nasal breadth	Mandibular breadth
Southeastern Kentucky	(10)	Number	14	14	14	14		14	14
		Mean ± S.E.	14.52 ± .05	13.77 ± .05	7.38 ± .08	6.92 ± .03		4.36 ± .04	10.82 ± .05
		Range	14.25–14.85	13.45–14.05	7.08–7.65	6.73–7.14		4.00–4.55	10.45–11.20
Eastern Kentucky Southern Ohio	(11)	Number	71	69	71	72	72	72	70
		Mean ± S.E.	14.37 ± .03	13.68 ± .03	7.38 ± .02	6.85 ± .02	3.73 ± .01	4.36 ± .02	10.63 ± .03
		Range	13.85–14.90	13.00–14.25	7.05–7.77	6.43–7.20	3.29–4.08	3.98–4.87	10.15–11.05
Southeast Tennessee Northern Alabama	(12)	Number	44	43	42	44	45	45	46
		Mean ± S.E.	14.42 ± .01	13.70 ± .04	7.37 ± .03	6.81 ± .02	3.71 ± .02	4.36 ± .03	10.71 ± .04
		Range	13.85–15.05	13.20–14.20	7.00–7.65	6.45–7.12	3.50–4.13	4.05–4.73	10.25–11.20
Western North Carolina	(13)	Number	7	7	7	7	7	7	7
		Mean ± S.E.	14.61 ± .12	13.74 ± .10	7.28 ± .06	6.79 ± .06	3.74 ± .07	4.41 ± .08	10.77 ± .09
		Range	14.25–15.00	13.35–14.10	7.15–7.55	6.55–7.02	3.62–3.82	4.10–4.72	10.50–11.10
Southeast West Virginia Western Virginia	(14)	Number	10	10	10	10	10	10	10
		Mean ± S.E.	14.35 ± .08	13.62 ± .10	7.34 ± .04	6.83 ± .04	3.73 ± .04	4.39 ± .03	10.53 ± .07
		Range	13.70–14.55	12.95–14.05	7.07–7.52	6.62–6.97	3.55–3.91	4.26–4.59	10.05–10.80
Eastern West Virginia	(15)	Number	36	36	36	36	36	36	35
		Mean ± S.E.	14.52 ± .03	13.78 ± .05	7.40 ± .02	6.86 ± .02	3.71 ± .03	4.38 ± .03	10.72 ± .04
		Range	13.90–15.05	13.00–14.30	7.15–7.67	6.59–7.24	3.55–3.94	4.03–4.80	10.25–11.15
Southwestern Pennsylvania	(16)	Number	4	4	4	5	5	5	5
		Mean ± S.E.	14.25 ± .25	13.55 ± .15	7.32 ± .06	6.79 ± .08	3.78 ± .03	4.31 ± .07	10.40 ± .06
		Range	14.15–14.35	13.30–13.70	7.21–7.37	6.66–6.90	3.72–3.89	4.12–4.45	10.20–10.55
Central Pennsylvania	(17)	Number	15	13	12	14	14	14	14
		Mean ± S.E.	14.44 ± .11	13.82 ± .10	7.40 ± .04	6.89 ± .04	3.73 ± .03	4.37 ± .04	10.64 ± .09
		Range	13.60–15.20	13.20–14.35	7.18–7.61	6.60–7.15	3.53–3.96	4.20–4.66	10.20–11.30
New York Vermont	(18)	Number	38	38	36	37	39	38	37
		Mean ± S.E.	14.48 ± .03	13.76 ± .04	7.39 ± .02	6.87 ± .02	3.68 ± .02	4.29 ± .02	10.67 ± .02
		Range	14.10–15.00	13.30–14.35	7.17–7.67	6.62–7.19	3.43–3.96	4.07–4.63	10.30–11.30

roughout fur: Edmonson County, Kentucky (KU) (UI), three specimens; arter County, Kentucky (UI), three specimens; Pendleton County, West irginia (AMNH); Camden County, Missouri (UM); 3) fur white, but ings and membranes normally pigmented: Newton County, Arkansas JAZ); Iron County, Missouri (UM); Carter County, Kentucky (JSH). letzger (1956) reported collecting an *M. sodalis* in Carter County, Kenicky, which was white except for the wing membranes and ears.

The means, ranges, and standard errors are given for four external easurements and seven skull measurements in tables 1 and 2 for 18 ouped localities, which cover the entire range of the species. There is ttle variation in these measurements over the range of *M. sodalis*. At e extremes of the range are populations in Vermont and those in the zark area of Missouri and Arkansas. No significant variation is seen beeen these two populations. Those from the southern Ozarks (1) have a ean length of body 2.7 mm larger than the Vermont series, but the standd errors are 1.3 and 2.1, indicating that these differences are not signifint. The means for the other three external measurements are all less an 1 mm different in the two extreme populations. Likewise, there are o significant differences in means of external measurements between any the other 16 localities.

Measurements of the skull are much more reliable than external measements, because they can be made more accurately, and usually one pern does the measuring. The lack of variation is even more striking with e more refined measurements of the skull. Again, in comparing populations at the extremes of the range, the means for six of the skull measureents are very similar for the Vermont population (18) and the southern zark population (1) (table 2). One measurement, nasal breadth, is sigficantly smaller at the 1 percent level for Vermont specimens ($4.29 \pm .02$) an for Ozark populations ($4.41 \pm .03$).

The life history studies indicate that movements of individual groups of . *sodalis* may be restricted to certain areas within the total range. Many cords of movement were obtained between central Kentucky, Indiana, stern Kentucky, and southern Ohio. No records were obtained for movent between Kentucky and Missouri. It is postulated that river routes e used in navigation and that this tends to break the species up into popucions which remain isolated, because their routes of movement do not erlap. For this reason variation should be consistent with these isolated pulations. All localities involved in the movement records for Kentucky d Indiana (7–10 of tables 1 and 2) were combined to obtain means for measurements and were compared with the means obtained for all the zark populations (1–4 of tables 1 and 2). The differences between means these grouped localities are less than for the individual localities menned above. This is probably due to the increase in sample size. If the ablishment of populational ranges has acted as an isolating mechanism,

nabia, 3 (OAM); *Adair County:* (1) Adair Cave, 5 mi. S Little Kansas, 2 (OAM); NNSYLVANIA: *Westmoreland County:* (16) Hillside, 2 (CM); *Mifflin County:* (17) kin Cave, 1 mi. NE Siglerville, 2 (AMNH), 1 skel. (AMNH), 7 (CU), 1 (MVZ);) Maitland Cave, Lewistown, 2 (KU); *Franklin County:* (17) Kittatinny Tunnel, dbury, 1 (UF), 1 (RPM); (17) Blue Mt. Tunnel, 1 (RPM); (17) Tuscarora Tunnel, RPM); *Fayette County:* (16) Dulany Cave, 7½ mi. SE Uniontown, 3 (CM); *tre County:* (17) Penn's Cave, Center Hall, 10 (CU), 3 (RPM); (17) Woodward ve, Woodward, 6 (USNM), 1 (RPM); *Huntingdon County:* (17) Historic Indian ve, 1 (RPM); *Bedford County:* (17) Hipple Cave, 5 (RPM); TENNESSEE: *Marion unty:* (12) Nickajack Cave, 3 mi. S Jasper, 1 (UF), 2 (WGF), 25 (MVZ), 3 (KU), RPM); VERMONT: Rutland County: (18) Brandon, 3 (MVZ), 2 (USNM); (18) kwacket Bat Cave, North Chittenden (Chittenden) (Proctor), 4 (AMNH), 9 (MCZ), (USNM), 16 (MVZ); VIRGINIA: *Giles County:* (14) Tony's Cave, 2 mi. N Newport, CM); WEST VIRGINIA: *Monroe County:* (14) Greenville Saltpetre Cave, Greenville, (UI); *Pendleton County:* (15) Trout Cave, 16 (WGF); (15) Smoke Hole, 20 MNH); WISCONSIN: *Grant County:* (6) Atkinson's Diggings, 2¼ mi. W Beetown, UI).

Summer: Total number 56 from the following localities:

ALABAMA: *Calhoun County:* Weaver's Cave, Anniston, 1 ale. (MCZ); ARKANSAS: *don County:* Bat Cave, 5 mi. NW War Eagle, 1 (KU); *Madison County:* Denney ve, 5 mi. E Alabam, 2 (KU); *Clay County:* Greenway, 2 (CNHM); ILLINOIS: *Cook unty:* F.M.N.H. Bldg., Chicago, 1 (CNHM); INDIANA: *Crawford County:* Wyante Cave, 3 ale. (USNM); *Greene County:* Ray's Cave, 2 (REM); *Parke County:* rkey Run State Park, 1 (WGF), 1 (REM), 1 (NW), 2 (CNHM); *Steuben County:* mi. E Orland, 2 (REM); *Warren County:* 7 mi. E and 1½ mi. N Pine Village, REM); *La Grange County:* 2 mi. W and ¾ mi. N Mongo, 1 (REM); *Montgomery unty:* Shades State Part, 1 mummy (NW); *Ripley County:* Friendship, 2 (NW); *sciusko County:* Shock Lake, No. Webster, 1 (JMM); *Knox County:* Wheatland, le. (USNM); Bicknell, 1 ale. (USNM); KENTUCKY: *Edmonson County:* Coach ve, Park City, 1 (UI); Long's Cave, Mammoth Cave National Park, 6 (UI); Dixon ve, Mammoth Cave National Park, 7 (UI), 2 (UK); *Adair County:* Jones Cave, lumbia, 1 (NW); *Carter County:* Bat Cave, Carter Caves State Park, 1 (UI); CHIGAN: *Washenaw County:* 6 mi. WNW Chelsea, 1 (UMMZ); Ann Arbor, 1 MMZ); *Wayne County:* Grosse Isle, 1 (USNM); MISSOURI: *Boone County:* Columbia, 1 (UM); *Shannon County:* Bat Cave, 2 (UI); *Franklin County:* Mushroom ve, Meramec State Park, 2 (UM); *Barry County:* Cassville, 2 (UMMZ); NORTH OLINA: *Mitchell County:* Roan Mt., Littlerock Creek, 1 ale. (USNM); TENNESSEE: *kman County:* 1 (AMNH).

Additional Records: Winter: ARKANSAS: *Baxter County:* Twigly Cave, 1 mi. E dway (Sealander and Young, 1955); *Benton County:* Logan Cave, 8 mi. E Siloam ings (*ibid.*); Cave Springs Cave, at Cave Springs (*ibid.*); OHIO: *Highland County:* le and Moulthrop, 1942); PENNSYLVANIA: *Westmoreland County:* Bear Cave ohr, 1932b); *Bedford County:* New Paris Caves (*ibid.*); *Fulton County:* Sideling l Tunnel (*ibid.*); TENNESSEE: *Bedford County:* Ward Cave (Kellogg, 1939); VIRIA: *Montgomery County:* Nellie's Hole (Handley and Patton, 1947); *Shenandoah unty:* Madden's Cave (*ibid.*); *Bath County:* Withero's Cave (*ibid.*).

Summer: INDIANA: *Tippecanoe County:* Lafayette (Kirkpatrick and Conaway, 8) (Mumford and Cope, 1958); *Marion County:* Indianapolis (present study); *Clay unty:* Brazil (Mumford and Cope, 1958); *Washington County:* (*ibid.*); *Wayne unty:* Centerville (*ibid.*); *Montgomery County:* (*ibid.*); *Randolph County:* Winster (present study); KENTUCKY: *Bullitt County:* Shepherdsville (present study);

of *M. sodalis* and *M. lucifugus* is shown in figure 6. These two species differ enough in regard to these three measurements to show clearly that the skulls from the bone deposit are those of *M. sodalis*.

Flooding of the cave obviously destroyed this *sodalis* colony. The vertical distance of the passage above the base level of the river was measured with a level sight and rod. A cross-sectional diagram of the cave indicating the relationship of the cave with recent flood levels of the river is shown in figure 7. In order to flood the passage the river must rise to 49 feet. In 1937 the Green River flooded to about 58 feet in this area (Records of Mammoth Cave National Park). The river represents the water table in this limestone area. Any rising of the river causes the water table all through the surrounding limestone to rise.

The volume of a sample of the bone deposit was measured and the number of individuals in that volume determined by picking out the humeri (whole or distal ends). From only 18 cubic inches of deposit, 380 humeri

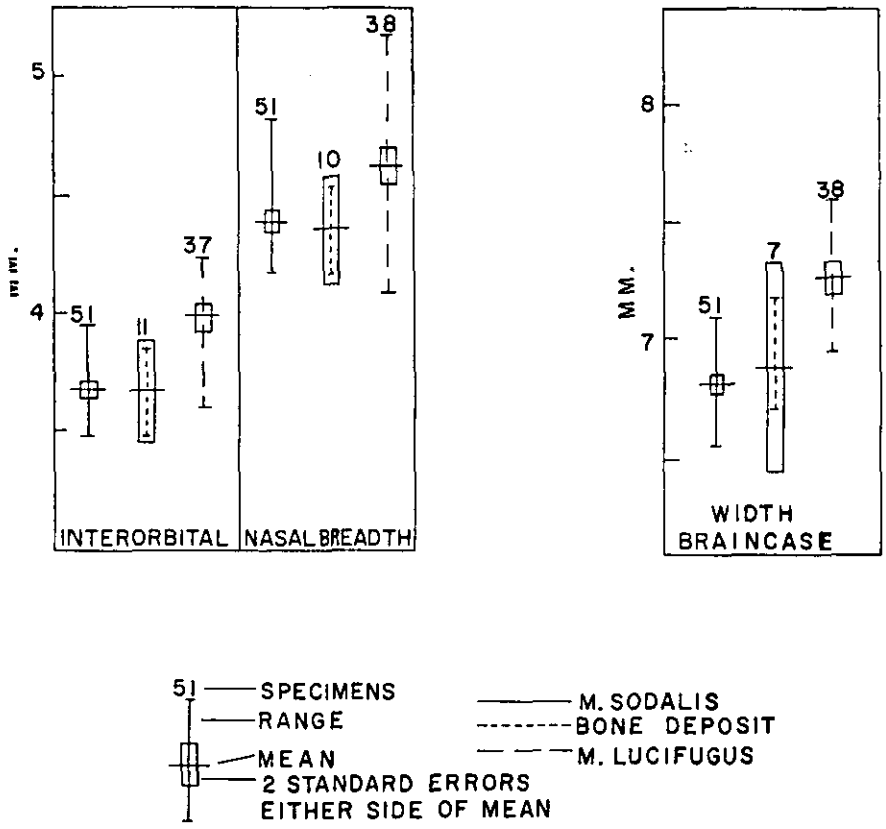
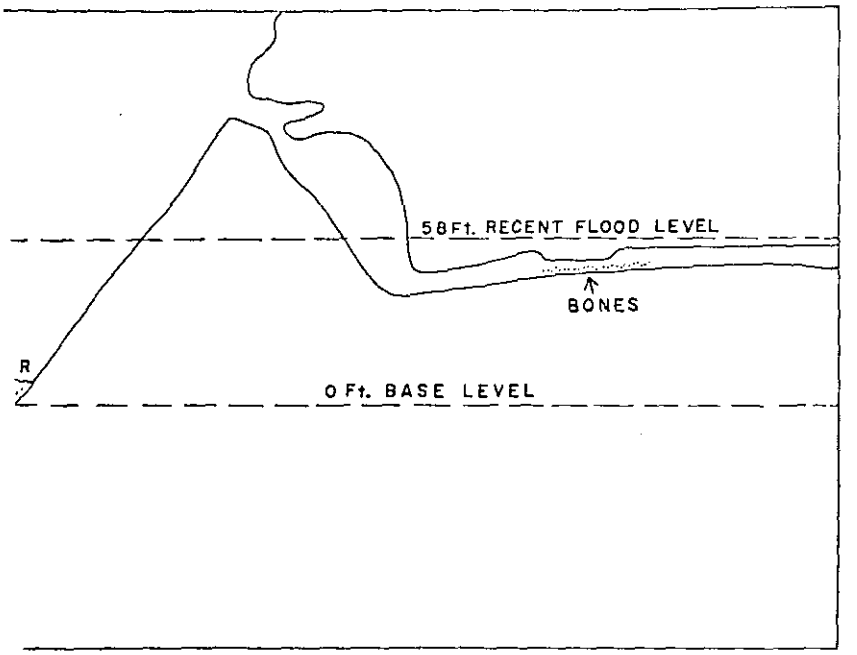


FIGURE 6. Comparisons of three skull measurements of bone deposit in Bat Cave, Edmonson County, Kentucky, with recent *Myotis sodalis* and *Myotis lucifugus*.



GURE 7. Cross-sectional diagram of Bat Cave, Edmonson County, Kentucky, g bat bone deposit in relation to recent flood level of Green River.

ecovered, representing about 200 individuals. A minimal estimate of tal deposit is 15 cubic feet, being composed of an estimated 300,000 dual bats. This *sodalis* colony was considerably larger than the largesent colony in the area (100,000). It may indicate a past, greater ance of the species.

Eastern Kentucky Populations

ere are several areas in a limited portion of eastern Kentucky where caves are abundant. One such area is in Jessamine and Garrard s. Although this area was not surveyed during this study, two speciwere examined from a cave in Jessamine County. Another "cave s" occurs in southeastern Kentucky along the Cumberland River in i and Wayne counties. Study of this area, in summer only, prono *M. sodalis*, but a series of winter specimens were examined from rland Cave, Pulaski County (UMMZ).

number of medium-sized caves occur in northeastern Kentucky in County. One, Bat Cave, has a large wintering population of about) *M. sodalis*. This is one of the four large winter colonies known. opulation has been large for many years and is well known. Welter lberger (1939) reported that 100,000 *sodalis* hibernated there in 1937.

South-Central Indiana Populations

A tongue of cavernous limestone extends from the Ohio River in southern Indiana, north about 80 miles to Owen, Monroe, and Brown counties. The largest caves are in the south, with Wyandotte the largest. *Myotis sodalis* occurs in Wyandotte and to the north near the northern limits of the limestone in central Indiana. The winter population in Wyandotte Cave is similar in size to Long's, Colossal, and Dixon caves in central Kentucky, with 2,000 to 3,000 individuals.

About sixty miles north of Wyandotte there are several caves with hibernating colonies of *M. sodalis*. These are all close to the White River, a tributary of the Wabash. There appear to be no populations of *sodalis* in the area between Wyandotte Cave and this northern area. Ray's Cave, Greene County, is much smaller than any of the previously mentioned caves. The colony of *sodalis* apparently fluctuates greatly in this cave. In the winter of 1958–1959 only about 100 were in the cave, but the next winter about 500 were seen. These small populations of *sodalis* fluctuate considerably from year to year. Coon's Cave, Monroe County, only a few miles from Ray's Cave, has a very small colony. Nine were seen here in 1957–1958 and none in 1958–1959. Grotto Cave, one-half mile from Coon's Cave, was visited only once and it contained about 200 *sodalis*. This is also a rather small cave, when compared to the caves of southern Indiana and Kentucky.

Ozark Populations

The Ozark region of southern Missouri, northern Arkansas, and northwestern Oklahoma contains hundreds of caves. Several wintering colonies of *sodalis* are found along the Casconade River in Phelps and Pulaski counties, Missouri. Tunnel Cave, Pulaski County, contained a medium-sized colony in 1954, when Wayne H. Davis banded 1,300 *sodalis* here. When I visited the cave in 1958 only 200 *sodalis* could be found. It seems that this population has decreased markedly in only four years. The reason for this is apparently human disturbance by the increasing number of so-called cave explorers. As a result, the bats have left except for a small remnant. Declines of bat populations due to human disturbance have been noted in the northeastern United States by Mohr (1953). Small colonies of *sodalis* are found in Onyx and Piquet caves, Pulaski County (table 3).

Bat Cave, Shannon County, Missouri, along the Current River in southern Missouri, was visited once in April 1959. The population was then about 100,000. Nothing is known of the past population here since it was only discovered in 1958 by Richard Myers. He has told me that when he visited the cave in 1958 the population was about 50,000.

Fifty miles northeast of Bat Cave, Shannon County, there is a large

ny in an abandoned mine tunnel, Pilot Knob Mine, Iron County. I
: not visited the mine, but Myers gave me information concerning this
: and showed me photographs of the huge clusters of *sodalis*. This
e, because of its danger, has little human disturbance. The mine is one
he four places where large colonies of *sodalis* are found. It has been
lable to bats for about 50 years.

Sealander and Young (1955) found *sodalis* hibernating in 11 caves in
hern Arkansas. The populations were all small, the largest cluster ob-
:d contained only 34 bats. Thus it appears that large populations of
lis do not exist in northern Arkansas.

The Ozark cave region extends into eastern Oklahoma. In a study of
aves in the area, Glass and Ward (1959) found two *sodalis* in Adair
:, Adair County, and three individuals in Bower's Trail Cave, Push-
ha County, in the Ouachita biotic district.

Northern Illinois–Southern Wisconsin Populations

Lyotis sodalis has evidently dispersed northward by way of the Mis-
ppi and Illinois rivers. The species has been found in two mine tunnels
to the Mississippi River. One is in the northwest corner of Illinois
d Mine, Galena, Jo Daviess County). Smith and Parmalee (1954)
d three individuals in the mine in 1953. Davis and Lidicker (1955)
d a single individual in southern Wisconsin in a mine tunnel beside the
issippi River (Atkinson's Diggings, Grant County).

small colony hibernates in a large, abandoned cement mine in La Salle
ty, Illinois, close to the Illinois River (Blackball Mine, La Salle
ty). The mine includes about 40 acres underground, but the small
y of *sodalis* was always found in the same precise spot. This made it
ble to learn something of fluctuations in numbers. The mine was
d many times each winter and exact counts were made of the *sodalis*.
maximum number each winter has decreased gradually from 1953 to
In 1953 Davis banded 600 *sodalis* in this mine. In 1956 the maxi-
number was 337 and in 1960 only 120 *sodalis* were found. This mine
ween visited by many persons, including vandals and professional col-
's (Sanborn, 1951). This disturbance has resulted in a decline of the
ation in this mine. The colony has apparently been established from
.tion out of either the Ozark population or the Kentucky-Indiana
ation. The dispersal route has evidently been the Mississippi and
is rivers.

Southern Illinois Populations

small number of *sodalis* hibernate in caves in extreme southern
is. In 1953 W. H. Davis found 83 in Cave Spring Cave, Hardin
ty. In 1957 I found none in two visits and only two individuals in

1958. The colony in this cave fluctuates considerably from year to year. One specimen was examined from Guthrie Cave, Cobden County.

Like the northern Illinois population, this group must have been derived from either the Ozark area to the west or the Kentucky-Indiana area to the east. Many caves were searched in western Kentucky, but no *sodalis* were found.

Other Areas

Winter colonies of *M. sodalis* occur along the Tennessee River in northern Alabama and southeastern Tennessee. Mohr (1932a) reported 1,500 in Nickajack Cave, Marion County, Tennessee, and five in Saltpetre Cave, Lauderdale County, Alabama. Wayne H. Davis banded 389 in Hughes Cave, Morgan County, Alabama, in 1955. There are many caves in this area, and it seems that medium-sized and small winter populations occur here. From this area a few have apparently dispersed over the Appalachian Divide into northern Florida. Jennings and Layne (1957) found one individual in a cave in Jackson County.

From Alabama the range of *M. sodalis* extends northward with its eastern edge closely approximating the limestone region and the Appalachian Divide. The species has dispersed over the Divide in a few places where it is present just west of the Divide. The pattern of dispersal is easily seen. The species is found in western North Carolina along the Little Tennessee River, a short tributary of the Tennessee River. The one locality for the species east of the Divide in North Carolina is just 50 miles from the head waters of the Little Tennessee River. This same type of relationship exists for a few localities east of the Divide in Virginia, West Virginia, and Pennsylvania. The species has dispersed to a considerable distance from the Mississippi River drainage in the northeast as far as Vermont.

Little is known of population size in the east and north. Wayne H. Davis banded *sodalis* in 11 caves in West Virginia. The greatest number banded in one cave was 514. Mohr (1932b, 1942) reported populations in 12 caves and tunnels in Pennsylvania. The largest colony was 2,000 in Penn's Cave, Centre County, and the rest were 500 or less.

Griffin (1940) reported maximum numbers of *sodalis* seen in several caves in the northeast. However, it is possible that some of these were misidentified *M. lucifugus* (Griffin, in litt.). I have examined specimens of *sodalis* collected by Griffin from only two localities. One is Haile's Cave, Albany County, New York. He reported seeing only eight in this cave. The other is a cave in Crittenden, or North Crittenden, Rutland County, Vermont. Griffin reported that he banded 241 in this cave. Apparently no large populations are present in the eastern and northeastern parts of the range. The cave area of Missouri and Kentucky is the center of abundance of the species.

Sex Ratios

A number of workers have reported a disproportionate sex ratio among
: that are found hibernating in caves of eastern United States and Can-
(Griffin, 1940; Mohr, 1945; Hitchcock, 1949; and Davis, 1959). These
orts indicate that male bats comprise from 60 percent to 80 percent of
rnating populations of *Myotis keenii, Myotis lucifugus, Myotis subu-
s, Eptesicus fuscus,* and *Pipistrellus subflavus.* These works have shown
iderable variation in the sex ratios from one cave to another and from
area to another. It has been noted that sex ratios become more nearly
l in the southern parts of the United States (Davis, 1959). There has
much discussion about the probable reasons for the presence of more
es in caves in winter. Davis (1959) presents evidence from banding re-
ries to indicate that female *Pipistrellus subflavus* may have a higher
tality rate than males. His evidence is based on the fact that banded
es are recovered in greater numbers than banded females from year to
in any one cave. Other explanations are that females may winter elsе-
re or may tend to move from one hibernating cave to another more than
es.

ex ratios of *Myotis sodalis* in winter hibernating colonies were calcu-
l for 15 caves in six states (table 4). In most instances the sex ratio
M. sodalis was about even. The only ones that even approached the
roportionate ratio reported for other bats are those for the colonies in
kball Mine, La Salle County, Illinois, and three caves in West Vir-
. In Blackball Mine males comprised 60, 65, 61, 61, and 59 percent
e population during different years. In three caves in West Virginia
s comprised 63, 72, and 76 percent of the populations in one year. On
occasions female *M. sodalis* were found in greater abundance. In
h Cave, Kentucky, during the winter of 1958–1959, males were cal-
ed to comprise 39 percent of the population and in the winter of 1960–
, 43 percent. Again, in Long's Cave, Kentucky, males comprised 32
nt of the population. However, samples taken at other times in these
contained about equal numbers of both sexes.

he few caves which had a greater proportion of male *M. sodalis* were
small populations—39 to 600 individuals. However, other small pop-
ons were found to have an even sex ratio. The percentage of about 60
ales at Blackball Mine, Illinois, seems to be a reality, since it was
ured during five consecutive years. The four caves with a higher per-
ge of males still did not approach the high values for other species.
explanation might be that female *M. sodalis* do not have a higher mor-
rate than males, except in some areas of its range. These four caves
the edges of the range in northern Illinois and eastern West Virginia,
may be a factor in determining these sex ratios. An analysis of band
eries and bearing on survival in *M. sodalis* will be published at a later

TABLE 4. SEX RATIOS OF *Myotis sodalis* FROM WINTER COLONIES IN KENTUCKY, INDIANA, ILLINOIS, MISSOURI, WEST VIRGINIA, AND ALABAMA

Cave	Percent Male	Total bats counted	Year	Population
	Kentucky			
Coach, Edmonson Co.	55	1,110	'56–'57	100,000
Coach, Edmonson Co.	49	146	'57–'58	100,000
Coach, Edmonson Co.	50	168	'57–'58	100,000
Coach, Edmonson Co.	39	770	'58–'59	100,000
Coach, Edmonson Co.	43	1,158	'60–'61	100,000
Bat, Carter Co.	51	1,294	'56–'57	100,000
Colossal, Edmonson Co.	51	181	'57–'58	1,000
Colossal, Edmonson Co.	41	450	'58–'59	2,250
Long's, Edmonson Co.	46	672	'58–'59	2,000
Long's, Edmonson Co.	32	175	'58–'59	1,500
	Indiana			
Ray's, Greene Co.	46	85	'58–'59	100
Ray's, Greene Co.	50	500	'59–'60	500
	Illinois			
Blackball, La Salle Co.	60	572	'53–'54	572
Blackball, La Salle Co.	65	113	'56–'57	113
Blackball, La Salle Co.	61	90	'57–'58	90
Blackball, La Salle Co.	61	109	'58–'59	120
Blackball, La Salle Co.	59	118	'59–'60	118
Cave Spring, Hardin Co.	40	82	'53–'54	82
	Missouri			
Tunnel, Pulaski Co.	58	579	'53–'54	1,200
Tunnel, Pulaski Co.	52	1,386	'54–'55	1,386
Maxey, Pulaski Co.	47	1,973	'54–'55	2,000
	West Virginia			
Trout, Pendleton Co.	54	460	'51–'52	600
Trout, Pendleton Co.	48	665	'52–'53	665
Minor Rexroad, Pendleton Co.	51	514	'52–'53	600
Martha's, Pocahontas Co.	76	151	'52–'53	151
Blowing, Tucker Co.	63	119	'52–'53	119
McFerrin, Greenbrier Co.	72	39	'52–'53	39
	Alabama			
Hughes, Morgan Co.	44	392	'54–'55	392

Incidental work with *Myotis grisescens* reveals that the sex ratio is also equal in this species in hibernating caves. During the winter of 1959–1960, in James Cave, Edmonson County, Kentucky, 1,444 were banded from a hibernating colony of over 100,000. The proportion of the sexes was exactly 50 percent each. In the winter of 1960–1961, the sex ratio of *grisescens* in this colony again was exactly even in a sample of 1,502.

COMPARISON OF SPECIES

The several species of bats found in the caves studied show differences in regard to the number of caves utilized and population sizes. These data indicate various degrees of aggregation of different species. *Pipistrellus*

avus was found in 40 (79 percent) of the 51 caves studied in winter, *tis lucifugus* in 27 (53 percent) of the caves, *Myotis sodalis* in 19 (37 ent), and *Myotis grisescens* in three (6 percent) of the caves. These 51 s can be considered as a random group of caves, since as many different were explored as time allowed. Other species were encountered, but above four are the common bats in caves during the winter in this

A correlation exists between the number of caves used by a species t, maximum numbers in caves, clustering habits, and size of geographic e. The pipistrelle is the most randomly distributed, but its numbers in e are far less than the other species (table 5). It does not form clus-

TABLE 5. COMPARISONS OF FOUR SPECIES OF BATS AS TO CAVES FOUND IN, POPULATION NUMBERS, TYPE OF CLUSTER, AND GEOGRAPHIC RANGE

Species	Number of caves in which species is found (51 studied)	Maximum number	Type of cluster	Geographic range
rellus subflavus	40	500	None	Large
s lucifugus	27	8,000	Semi-dense	Large
s sodalis	19	100,000	Dense	Small
s grisescens	3	100,000	Dense	Small

t any time. Its range is large, occupying all of eastern United States Canada and continuing into Central America. *Myotis lucifugus* has a andom distribution, using fewer caves than the pipistrelle. A cave contain several thousand individuals. This bat forms semi-dense clus- but not packed, tight clusters. Its range is also large, occupying most ed areas of North America. *Myotis sodalis* and *Myotis grisescens* a decidedly clumped type of distribution, being found in fewer caves the other two species. However, they may accumulate in large num- up to about a 100,000 maximum. Both species form tight and com- clusters. Their ranges are relatively small, being restricted to eastern id-west United States.

ese data show various degrees of aggregation in the distribution of nt wintering species. The basic behavior responsible for the type of ution is the specific type of clustering habit for each species. The bat have the habit of forming large, dense clusters have a restricted umped type of distribution. The bats that form semi-dense clusters a more dispersed or random distribution, and those that have an anti- ing habit are most widely and randomly distributed. The details of clustering habits are discussed in the section dealing with hibernation

DISCUSSION OF WINTER POPULATIONS

e distribution of winter populations of *Myotis sodalis* coincides closely e areas of the mid-west region in the area drained by the Mississippi

River and its tributaries. Only a small part of the range is just east of the Appalachian Divide. The major populations are centered in areas of cave "nuclei," where there are many caves in a small area. Small populations may occur in any area where rather small caves occur. The vast majority of hibernating caves are close to major rivers. Dispersal probably has been accomplished by following riverways.

Hibernating populations occur in three sizes. The highest level is a population of about 100,000. Four such colonies are known: two in Kentucky and two in Missouri. The next level is a population of 1,000 to 3,000. The lowest level is less distinct, consisting of populations of 500 to only a few individuals.

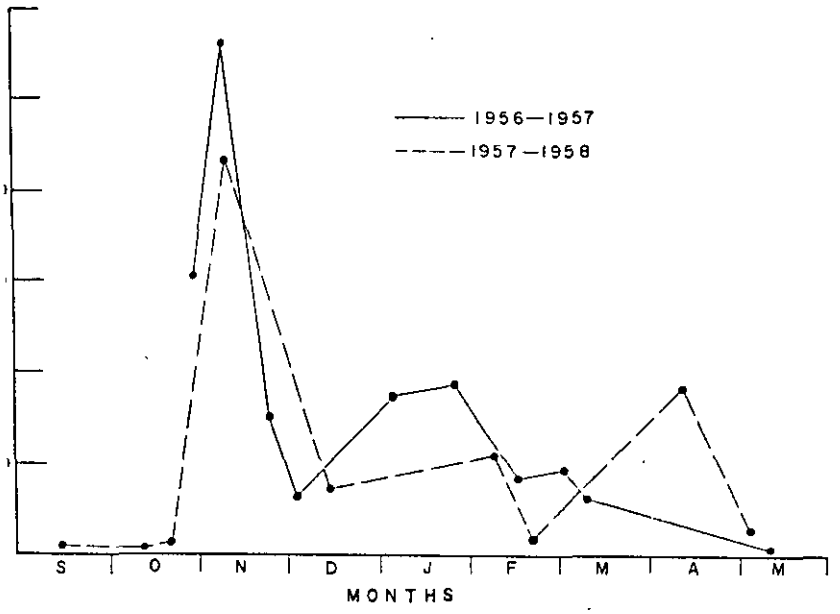
The four large cave populations contain 97% of the total estimated number of *sodalis* in the 19 caves that were found to contain this species. It appears that the species will accumulate to a level of about 100,000 individuals in one cave which serves as a "headquarters." Other caves in the immediate vicinity may then be used if the population is too large for the one cave.

The habit of aggregation has been carried to an extreme degree in this species. Whether we can evaluate the adaptive significance of aggregation or not, such value surely exists for this species. It may be that the selection for this habit of aggregation has carried the species to a high level of specialization, where only a slight change in selective pressures could cause this habit to be a great danger to the species. The species now aggregates so intensively in winter that a few caves contain a high percentage of the total individuals of the species. One such population was destroyed by a sudden flooding in Bat Cave, in Mammoth Cave National Park. This deposit of bones so obviously represents a catastrophic death that its import for the species cannot be minimized. The habit of intense aggregation makes local catastrophe of great importance to the species. Local catastrophies mean little for a randomly distributed species, but become very important when a large portion of a species is aggregated in only a few small places. Thus, any selective pressure against aggregation could cause, very rapidly, a near or complete extinction of the species.

THE HIBERNATING PERIOD

Bats in temperate regions must either hibernate or migrate to warmer areas during the winter. *Myotis sodalis* is a species which hibernates by accumulating in caves. This period of hibernation lasts from fall until spring, when the bats leave the caves for a summer habitat. The actual length of hibernation is difficult to determine when speaking of individuals, but the period of hibernation for the population as a whole can be determined rather accurately. The period of hibernation of *M. sodalis* was

ed most critically at Blackball Mine, La Salle County, Illinois, and
n, Long's, Coach, and Colossal caves, Edmonson County, Kentucky.
he small *sodalis* colony in Blackball Mine, Illinois, consisting of 100
0 individuals, was always found in one particular area and in exact
in this area. In figure 8 the numbers of *sodalis* observed on various
throughout two winters are plotted. The earliest date for entrance
hibernation was 14 September 1957. This was one individual only.
najor build-up of the colony occurs during October and the first part
vember. Some variation of two to three weeks was observed in regard
: time of entrance of the main colony over a four-year period. This



URE 8. Numbers of *Myotis sodalis* seen at Blackball Mine, La Salle County,
, during two winters.

entered later in 1957 than in 1958 and 1959. The colony seems to
been in hibernation earlier in 1956 than in the three subsequent years.
peak in numbers of *sodalis* was encountered in mid-November during
o years when observations were made in November (figure 8). The
f the colony then declined to about one-third maximum in mid-De-
r. This was not merely a moving to another area of the mine, since
ntire mine was searched on several occasions. As previously men-
, the *sodalis* were always found in a precise area. The habit of going
ict spots was noted in all caves where repeated observations were
This fluctuation apparently represents a movement out of the mine
November. There seems to be an increase in numbers again in mid-

winter, followed by a sharp decline in late February. A sharp increase was seen once in early April (1958). Hibernation ends about the first week of May in this mine. Twelve *sodalis* were still hibernating on 2 May 1958 and none on 11 May 1957.

The fluctuations of numbers of *sodalis* indicate movements throughout the winter, which must involve an actual leaving and entering of the mine. Other points to which the species may be moving are not known. Similar movement of *Eptesicus fuscus* in and out of a cave during the winter in Indiana was reported by Mumford (1958). Krzanowski (1959) reports that bats come and go all winter in a cave at Pulawy, Poland, resulting in considerable variation of numbers and individuals throughout the winter.

Central Kentucky is a populational center for *sodalis* in winter. As previously mentioned, the species was seen in seven caves with populations of 00,000 in Coach Cave, 2,000 to 3,000 in Long's, Dixon, and Colossal caves, and 10 to 500 in James, Bat, and Wilson caves. The *sodalis* hibernate in a definite area in each cave. This area is close to the entrance in a zone where the temperature drops to 4° to 5° C in mid-winter. Farther within the cave there is an area of constant temperature, being about 12° to 14° C all year. In this area are located guano piles. At these piles *sodalis* are found in small clusters in winter in an active and non-hibernating condition. These are the same guano piles where *sodalis* may be found in summer, although they are not found in the hibernating areas in the summer. The guano piles are in an area of activity, whether it is winter or summer activity. The relationship of hibernating areas to active areas is shown for three caves in figures 9 to 12. The winter hibernation can be said to begin when bats are found torpid in the hibernating areas. On 1 September 1959, no *sodalis* were hibernating in Dixon, Long's, and Colossal caves. In Coach Cave, about 50 were in the hibernating area marked A in figure 9. There were clusters of active *sodalis* numbering several hundred at the guano piles in Dixon, Long's, and Coach caves. The sex ratios at the piles were 45 percent females : 55 percent male (Dixon Cave) and 67 percent female : 33 percent male (Coach Cave). These bats were carrying on normal feeding activities at night, as during the summer months. However, the sex ratio at these piles in mid-summer is 95 to 100 percent males. Thus by September 1, the females were returning to the hibernation caves, but were not yet in hibernation. The fact that there were a few in hibernation in Coach Cave on this date indicates that the period of hibernation may have been just beginning.

One month later, on October 3, hibernation had truly begun, but only a small fraction of the bats had entered hibernation. About 1,000 were in the hibernation area of Dixon Cave. These were clustered near the back part of the hibernating area. The normal mid-winter population is about 3,000. In Coach Cave about 2,500 were in hibernation in the areas marked A, C, and D, and in areas close to the guano pile F (figure 9). Most, about

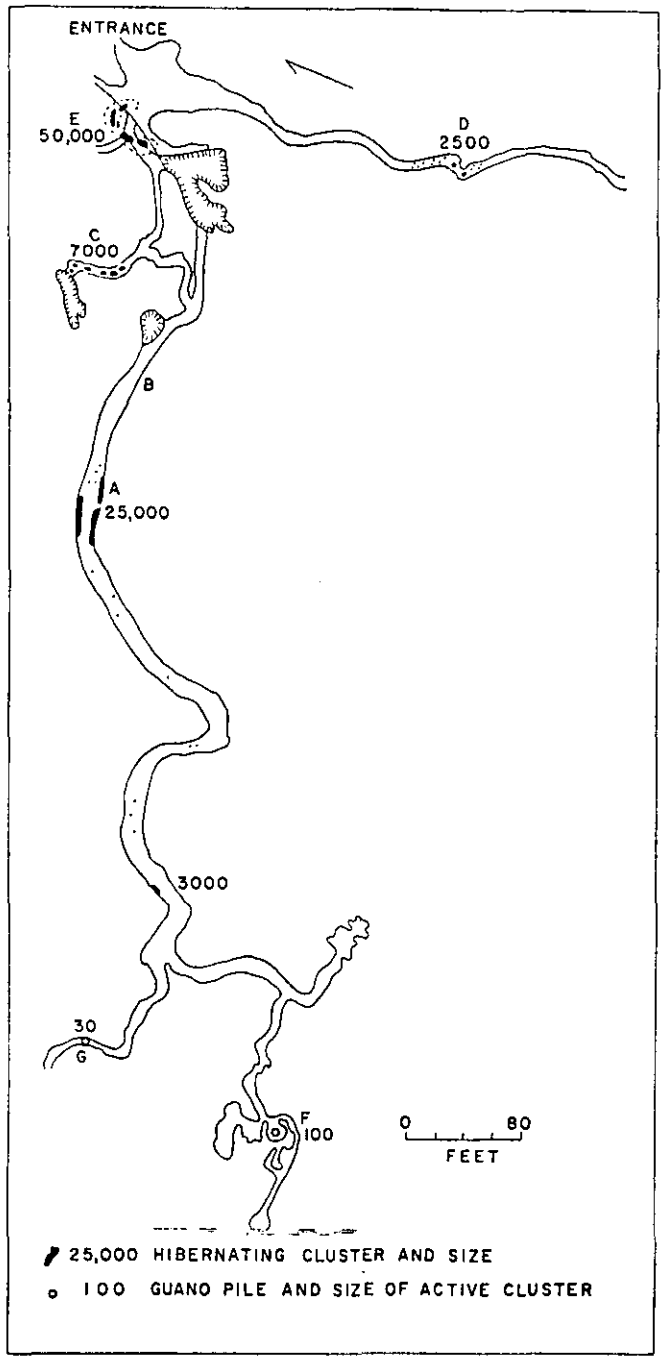


FIGURE 9. Position of hibernating and active clusters of *Myotis sodalis* in Couch , Edmonson County, Kentucky, on 1 January 1959.

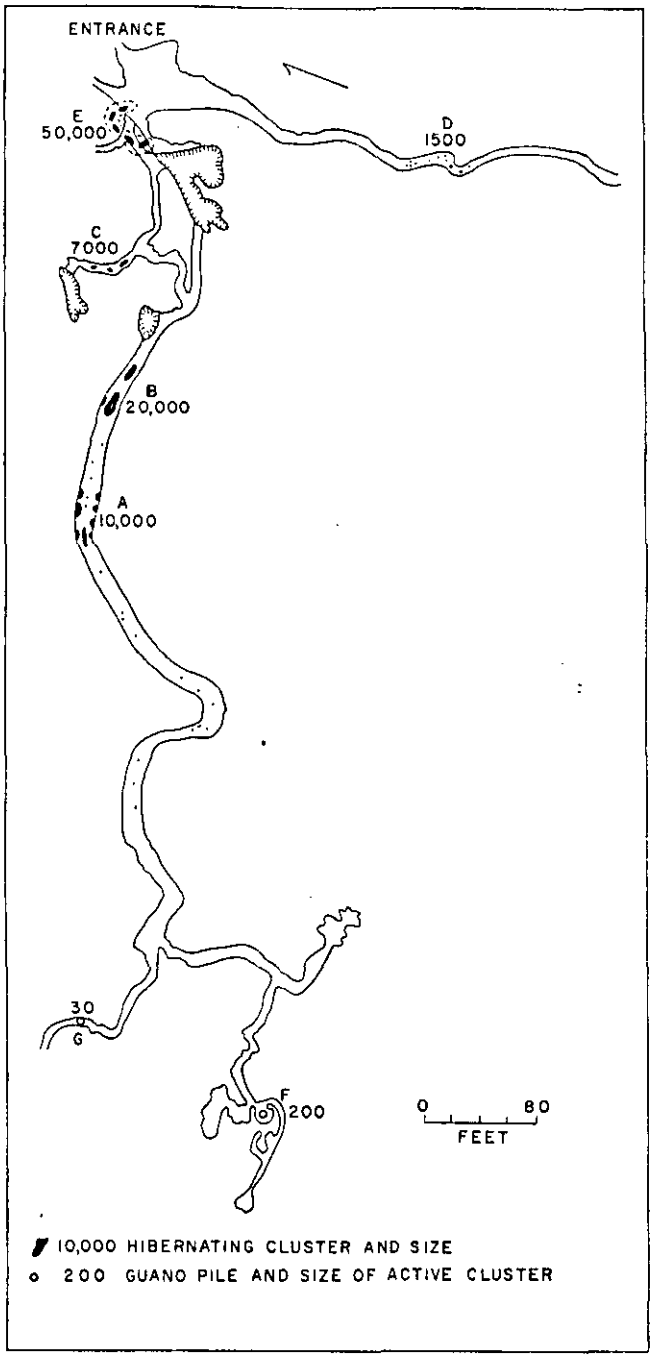
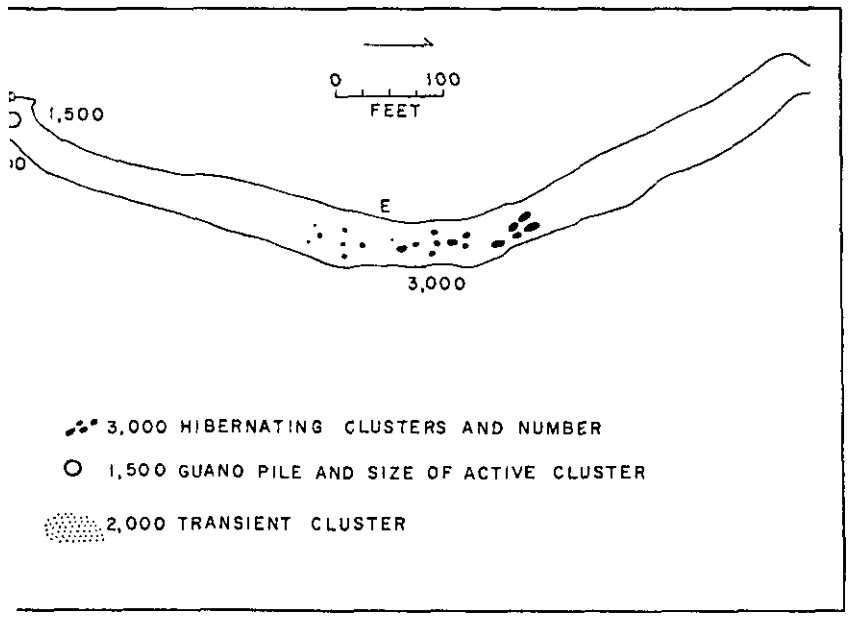


FIGURE 10. Position of hibernating and active clusters of *Myotis sodalis* in Coach ave, Edmonson County, Kentucky, on 27 March 1959.

), were in area A in the exact spot where the large clusters form in early
er. The maximum winter population in this cave is about 100,000. sex ratio of the hibernating clusters was 26 percent female : 74 percent . Many more bats were at the guano piles than in September. In n Cave a total of about 1,500 male and female *sodalis* were clustered nd the guano-pile area. These were feeding at night and carrying on ng activities. Another group of non-hibernating bats was present at spot marked A in figure 14. About 3,000 *sodalis* were clustered here. cluster was still present on October 9, but was never seen at any other of the year. These individuals are interpreted as being transient bats



gure 11. Hibernating, active, and transient clusters of *Myotis sodalis* in Dixon Edmonson County, Kentucky, on 9 October 1959.

were in the process of moving to other caves. Such a group was observed in any other cave.

n October 9, the hibernating clusters in Dixon Cave were at a maxi- level of 3,000 in the usual areas indicated in figure 11. In Coach about 10,000 were hibernating in areas A, C, and D. This was an se of about 7,500 in six days. These areas contain about 50,000 in inter, or one-half of the cave population, the other one-half being er levels marked E. At this rate all the *sodalis* should have been in Cave in about five more weeks. This would place the end of the ce period about mid-November.

rge numbers of bats were still at the guano piles on October 9, feed-

ing and carrying on mating activities. The transient area in Dixon Cave still contained about 2,000 bats. In Long's Cave on October 9 only a few *sodalis* were in hibernation and only a few were at the guano pile. These data show variation from cave to cave in regard to the return to hibernation. Bats return sooner to Dixon Cave and extra bats are present in the transient area. Bats return a little later to Coach Cave and still later to Long's Cave.

Dixon Cave may be an orientation point for *sodalis* returning to the area. This cave is on the banks of the Green River, whereas the other caves are several miles back from the river. The fact that bats banded in Dixon Cave during this returning period moved to Coach Cave later in

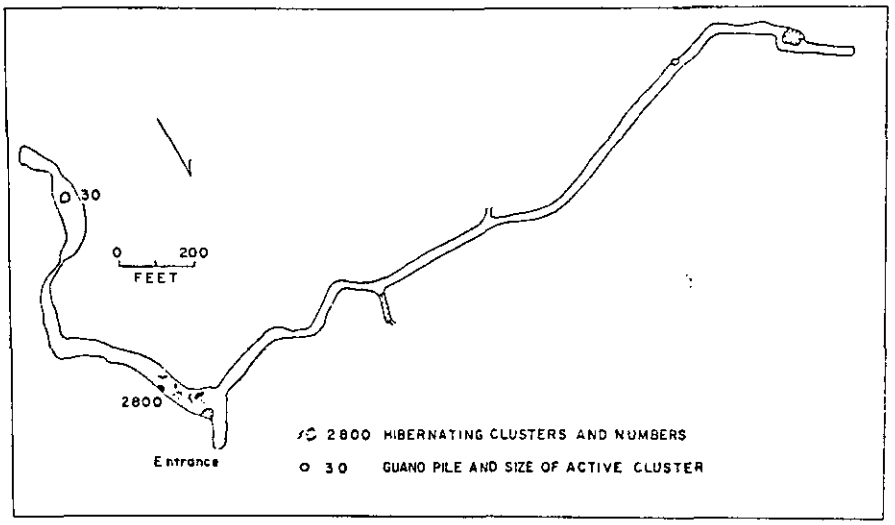


FIGURE 12. Hibernating and active clusters of *Myotis sodalis* in Long's Cave, Edmonson County, Kentucky, on 2 March 1958.

winter supports this contention. A male *sodalis* banded in Dixon Cave on September 1 was recovered two days later in Coach Cave. A male *sodalis* banded in Dixon Cave on October 9 was recovered in Coach Cave on December 18. Movement from Coach Cave to other caves was not noted for bats banded in the returning period. The importance of the river in navigation is indicated by these observations.

By late November the hibernating colonies are at a maximum in these caves. Bats were not observed feeding, a few were at guano piles, and no mating activities were noted during the last week of November.

The large hibernating colonies in these caves remain fairly constant during the winter. However, there are movements of clusters which occur at certain spots at definite times. There may be unnoticeable fluctuations of small numbers throughout the winter. In the case of the small popula-

) in Blackball Mine, Illinois, a slight movement is very noticeable. as it seems that a large scale turnover of *sodalis* colonies does not occur winter, but small numbers may move in or out of a cave throughout winter.

The hibernating colonies start diminishing in early April. A few bats e observed flying out of Dixon Cave at night as early as April 1 (1958). reased feeding must start as early as mid-March as indicated by in- ased guano deposition in Coach Cave (table 6). By April 18 (1958 1959) the colonies in Coach, Dixon, and Long's Caves were one-half wo-thirds of maximum. On May 3 (1959) in the upper levels of Coach e about 6,500 or 13 percent of the 50,000 were still in hibernation; in on Cave about 500, or 17 percent of the mid-winter colony, were still rnating. No *sodalis* are in hibernation during the first week of June. s reasonable to place the end of hibernation at mid-May. There is a five- to six-week period during which the bats are in stages of leav-

TABLE 6. GUANO DEPOSITED AT THE GUANO PILE IN COACH CAVE, EDMONSON COUNTY, KENTUCKY, DURING 1959

Period	Days	Grams/Day
1 January to 29 January	28	0.2
29 January to 7 March	37	0.2
7 March to 27 March	20	4.6
27 March to 3 May	37	7.4
3 May to 16 June	44	5.5
16 June to 10 July	24	13.4
10 July to 2 September	54	15.1
2 September to 3 October	31	45.6

he cave. This is about the same amount of time involved in the period ntrance in the fall.

he length of hibernation as determined from earliest entrance to st departure is about 210 days. The total hibernation period as taken earliest entrance to latest departure is about 252 days. The average th may be taken as the time when about one-half of the population entered in the fall and one-half has left in the spring. This would be about October 15 to April 20, or 187 days.

here are several aspects of behavior during hibernation that are of est, such as: 1) the habit of returning to exact spots at certain times e winter; 2) clustering habits; 3) activity; and 4) the process of leav- ibernation.

s previously mentioned, *sodalis* hibernate in exact places in a cave. zone of the cave in which they hibernate may be of considerable size, xact spots are used in the zone. This is well seen in Colossal Cave, onson County, Kentucky. The *sodalis* may be found along a one-half length of the main passage, but the clusters occur at precise spots,

hich do not vary by more than two to three feet from year to year. Black all Mine, Illinois, is a vast underground quarry, yet almost all the *sodalis* ere clustered in one corner of one blind passageway. They were sometimes found in other spots nearby, but always these places were exact.

In Coach Cave, Kentucky, clusters formed in the same spots each inter. These places are indicated in figures 9 and 10. Exactness is seen ot only in the spot occupied, but in the size of the cluster formed at any rticular spot. Large clusters always form each year in exactly the same aces. This is particularly striking in caves with large populations. The

FIGURE 13. A hibernating cluster of *Myotis sodalis* in Bat Cave, Carter County, ntucky.

rge clusters marked A in Coach Cave (figure 9) always were present in rly and mid-winter in the proportions indicated. These were on the les of the passage on overhanging ledges. During January they begin to eak up and reform on the ceiling at spots marked B and A in figure 10. his was observed during two successive winters. Thus not only are the ot and the size of the cluster the same, but the time of the winter when e clusters form is about the same from year to year. Characteristic sters in November were seen in two caves. One such cluster was obrved only during the second week in November at the same spot on two ccessive years in Blackball Mine. In Dixon Cave, Kentucky, a similar

ter was seen on two successive years during the last week of November pot E on the side wall (figure 11). The number of bats in this cluster between 500 and 1,000. The cave was visited during every month of year, and this was the only time of the year when the cluster was ent.

Clusters do not necessarily contain the same individuals every year. If cluster is banded the bats tend to disperse themselves immediately ughout many other clusters. The exact sizes of clusters at certain s must be determined by some physical factor at the spot in conjunc- with the habit of forming dense clusters.

One of the most characteristic habits of the species is the type of cluster ch is formed. A typical cluster of *M. sodalis*, as shown in figure 13, s directly on flat surfaces, such as ceilings or overhanging ledges on walls. A tight, compact cluster is formed by the bats pushing snugly nst each other, and affixing their claws into an irregularity of the rock.

TABLE 7. *Myotis sodalis* AT GUANO PILE IN DIXON CAVE, EDMONSON COUNTY, KENTUCKY, THROUGHOUT THE WINTER HIBERNATION PERIOD.
(D—Daytime N—Night)

1958				1959	
April (N)	1,500	4 April (D)	300	1 January (D)	6
April (D)	25	18 April (D)	150	26 January (D)	200
April (N)	1,500	19 April (N)	150	8 March (N)	15
November (D)	30	26 November (D)	40	28 March (D)	6
		28 November (D)	20	17 April (N)	500
		29 November (D)	20	18 April (D)	500
February (D)	200	29 December (D)	60	18 April (N)	500
April (N)	50			1 May (N)	300
April (N)	800			2 May (D)	300
April (D)	5				

tight cluster is apparently formed by the bats placing their feet beside feet of an adjoining bat. The feet have many hairs which could be ory in nature. This grouping behavior may cause a radiating cluster rm. The bats at the edge would be nearly in a horizontal position, their feet affixed near the center of the cluster and their bodies partly orted by adjacent bats. The cluster is always one tier in depth, the not hanging on one another. The hibernating cluster grows in an ir- lar manner, forming no definite shape. The wings are always folded ly against the body.

nformation concerning activity in winter was obtained by observing ity at guano piles. All through the winter, small groups of *sodalis* e found clustered in an active condition over the guano piles in Dixon, 's, and Coach caves. The numbers seen during mid-hibernation (De- er–February) are variable, but do not exceed 200 in Dixon Cave e 7). In Coach Cave as many as 500 may be present over guano piles id-winter. These bats, which have evidently awakened from hiberna-

ion, are always very active. How long an individual may remain active nd how often an individual may become active is not known. It appears hat periods of activity are a normal part of hibernation.

Other species of bats have been noted to awaken periodically during the inter (Hahn, 1908; Folk, 1940; Rysgaard, 1941; and Twente, 1955). How-ver, the details of this phenomenon have remained largely unknown. *Iyotis sodalis* has the unique habit of going to these specific places over uano piles when they come out of the hibernation-torpidity. Evidence is nat one individual may awaken more than once during the winter. A nale *sodalis* was caught at the guano pile in Dixon Cave on 28 February 958, and was caught again at the pile on 1 April 1958.

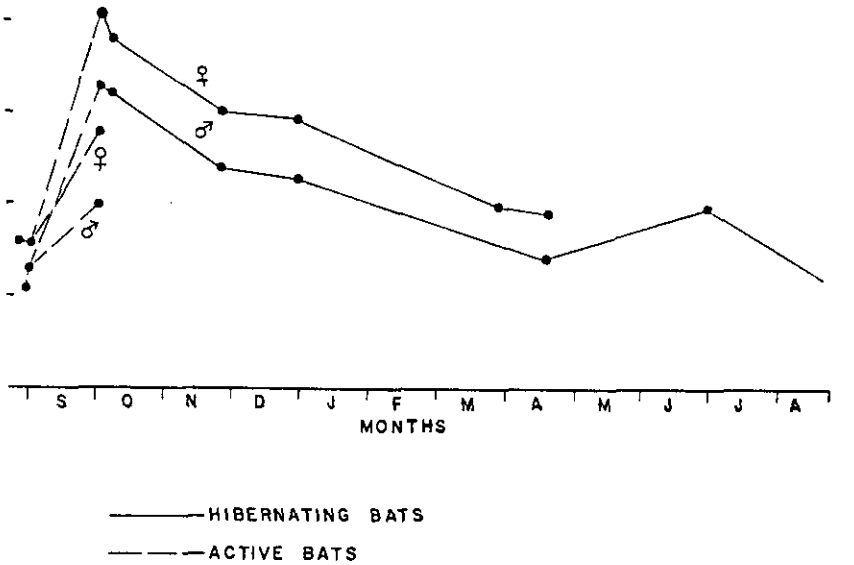
Guano was collected with a plastic sheet over the pile in Coach Cave 'om 1 January 1959 to 3 October 1959. The guano was collected, dried, nd weighed at the intervals indicated in table 6. During mid-winter, 'om January 1 to March 1, guano was deposited by the active bats at the ile at the rate of 0.2 grams per day. The increase in guano deposition in Iarch is an indication of increased activity with the onset of the period f leaving hibernation. The guano deposited in mid-winter is full of chitin. his fecal discharge in winter is small, but its source must be explained. . comes either from food material eaten just before entering hibernation, ' from food eaten during periods of activity in mid-winter. It seems un-kely that fecal material would remain in the intestinal tract for periods f time up to four months, even if the bat is in a torpid condition. Bats hich were kept in artificial hibernation in a temperature control room at ' C discharged some fecal material every day or two. This material was a ack, mucous material, since the bats had not eaten recently. This may ot be a normal situation, but does attest to the activity of the digestive 'stem, even when the body temperature is low.

The small amount of fecal discharge of *M. sodalis* in Coach Cave, entucky, in winter indicates the possibility that a few *sodalis* engage in nited feeding in mid-winter. Bats were observed flying during warm eriods in January at Mammoth Cave National Park. The only species ollected was the red bat, but other species could also be flying.

Groups of 50 to 100 bats of each sex were weighed throughout the year. 'eight relationships of males and females throughout the year are shown figure 14. In the fall, as *sodalis* are returning to the hibernation area, uring late August and September, their weight is at the lowest point of the ar. At this time dissection reveals no stored fat in the animal. Weight, the form of fat, is rapidly gained in September. Hibernation begins hen the bat has reached a maximum weight. This is higher for females an males. Bats taken from hibernation on October 3 weigh much more an those taken in an active state at guano piles (figure 14). Weight is st rather rapidly during the early part of hibernation. From October 3 November 27 the rate was 0.16 grams every 10 days for both males and

dles. During mid-winter weight loss is decidedly less. From November
o January 1 the rate was only 0.03 grams per 10 days, about one-fifth
ate during early winter. Weight loss during the latter part of winter
eater than mid-winter, but less than early winter. From January 1 to
l 18 the rate of loss was 0.09 grams per 10 days for females and 0.08
is for males.

'hese differences in weight loss throughout the winter are due to tem-
ture changes and activity. The *sodalis* occupy the same area of the
all through the winter. When they enter hibernation the temperature
is area is 9° to 10° C. The temperature drops gradually, but in late



GURE 14. Weight changes of *Myotis sodalis* throughout the year. Each dot repre-
the average weight of 50 or more bats taken in a cave in Edmonson County,
cky.

nber it is still 6° to 7° C. By January 1 the temperature is down to
inimum of 4° to 5° C, which is characteristic of the hibernating area
yotis sodalis in all the caves studied. Thus the temperature during the
winter is higher than in mid-winter. This results in greater weight
Also, early winter is a time of entering hibernation. Bats which enter
are disturbed by bats coming later. Weight loss in mid-winter is re-
to a low rate by the low temperature and reduced activity. In late
ry activity increases, as noted by the moving of clusters. The tem-
are in the hibernating areas begins to rise during March, and with in-
d activity causes a rise in the rate of weight-loss.

oth sexes of *sodalis* apparently enter hibernation in the fall at the
rate. In the spring, however, the females leave at a faster rate than

he males. The sex ratios of hibernating clusters in Coach Cave from November through March are even. The sex ratio in late April becomes unbalanced with more males than females, and by May 3 nearly all hibernating bats are males. The sex ratio of active bats at guano piles in Dixon and Coach caves from November through March are even. In late April the sex ratio of active bats becomes unbalanced, with more females than males. This indicates that there is greater activity among females at this time and that they are leaving hibernation at a faster rate than males. Sex ratios for hibernating clusters and active *sodalis* are given for Coach Cave in table 8 and for active clusters in Dixon Cave in table 9.

Discussion of Hibernation

Hibernation begins in the fall for an individual *Myotis sodalis* after much fat has been accumulated. This is an individual activity, and consequently much variation occurs. This individual variation accounts for an extended period for entrance into hibernation, lasting about six weeks from mid-September to early November. Some fluctuation occurs from year to year in the time when the major population in a cave is in hibernation.

Limited activity in some bats, possibly all, occurs throughout the winter. Evidence supports the view that some bats actually enter and leave a cave in winter. Great variations are noted among small populations, which seem to have peaks in November and again in mid-winter. Such behavior is difficult to observe with large populations because only a few individuals are involved at any one time. Some *sodalis* possibly engage in feeding during the winter. When a bat awakens from hibernation it leaves the hibernating area, which is fairly close to entrances, and goes to a deeper, warmer part of the cave where there are guano piles. The zone of hibernation is

Table 8. Sex Ratios of *Myotis sodalis* in Coach Cave, Edmonson County, Kentucky, from Hibernating Clusters and Guano Pile Clusters Throughout the Winter

Date	Hibernating		Guano pile active	
	Male	Female	Male	Female
1957				
3 February	.55	.45	Not taken	
20 April	.69	.31	Not taken	
30 November	.49	.51	Not taken	
1 March	.50	.50	Not taken	
1958				
4 April	.40	.60	.24	.76
19 April	.64	.36	.36	.64
1959				
7 March	.39	.61	.41	.59
18 April	.63	.37	.07	.93

E 9. SEX RATIOS OF *Myotis sodalis* AT GUANO PILE DURING WINTER IN DIXON CAVE, EDMONSON COUNTY, KENTUCKY

Guano pile active		Date	Guano pile active	
Male	Female		Male	Female
		1958		
.53	.47	29 November	.53	.47
		29 December	.60	.40
		1959		
.41	.59			
.36	.64	26 January	.57	.43
.47	.53	18 April	.08	.92

e the temperature in mid-winter goes down to 4° to 6° C. By mid-ch many bats are in need of feeding, and numbers of active bats in-se greatly. A large population of 100,000 leaves hibernation gradually mid-March to the first of May.

The females leave at a faster rate than the males. Either the females up fat more rapidly and thus lose weight faster, or the departure of emales is associated with reproduction. It has been shown that the sexes weight at the same rate. Hence this early departure of females must ssociated with the onset of ovulation and pregnancy.

Myotis sodalis, upon entering hibernation, occupy the same spots year year, even though the temperature is similar throughout much of the in early fall. The bats have the habit of returning to the same place e cave, which is the place where the temperature in mid-winter reaches roper hibernating temperature of this species. The habit of returning e same spot assures the bat of being in the proper temperature zone in winter. This is possible in these large limestone caves, because tem-ture changes are gradual and relatively constant from year to year. averns with many large entrances temperature changes may not be ual *or similar from year to year and bats must find the proper temper-* zone by trial and error (Twente, 1955).

SELECTION OF THE HIBERNATION SITE

he habit of hibernation in bats has arisen in response to the need of g through several months when little food is available. Fat reserves accumulated in a short period in the fall. The bats spend winter ths in a state of torpidity in which the temperature of the body ap-ches that of the environment. The fat reserve is expended during these ths. The temperature of hibernation must be low enough that metab-does not proceed at too fast a rate, but not so low that the bat will e. The success of hibernation depends upon metabolic rates and the equent speed of the using of the fat reserve. Rates of metabolism vary

rom species to species according to many factors, such as size, sex, temperture, age, and activity. Metabolic rates have been studied carefully in only few mammals—man and laboratory animals such as rats, mice, and rabits. In a study of metabolic rates of *M. lucifugus*, Hock (1951) found that xygen consumption varies nearly directly with body temperature. This neans that the warmer the temperature of the hibernating habitat, the igher will be the metabolic rate of a bat. No studies have been done on he metabolic rates of different species and the correlation with the differnt habitats selected by different species.

The present study analyzes the habitat selection of *Myotis sodalis* and ther species found in the same caves. Each species has definite environental requirements for hibernation. This was clearly seen by Twente 1955) in a study of bats in several caves in Kansas. He concluded that he bats he studied found their proper cave habitat by a trial and error nethod. His studies were made in caverns where temperature fluctuated reatly, and where the bats would have to rely on a trial and error method o find the proper habitat.

Factors which must be taken into account when analyzing the hiberating habitat of a bat include: size of cave entrances; size and nature of ooms and passageways; temperature; moisture; nature of ceilings and alls; air movements; clustering characteristics; previous occupancy; and ther species. A combination of these factors and possibly others are inolved in the proper habitat for hibernation of a species. This proper comination must permit a species to maintain a minimum metabolic rate durng the winter.

Habitat Selection of *Myotis sodalis*

Myotis sodalis accumulates in large numbers in a few caves to hibernate. hese caves are the same ones from year to year. This species was found the same seven caves and no others in Edmonson County, Kentucky, uring five consecutive winters. This species is precise in choosing the cave or hibernation. This varies from the case of *Myotis velifer*, which seems ot to return necessarily to the same caves each winter in Kansas (Twente, 955). *Myotis sodalis* is typically found in large caves. The cave area of dmonson County, Kentucky, contains some of the world's largest caves. he sizes of these caves can be roughly divided into three gradations: 1) ery large, with many miles of passageways (Mammoth, Salt's, and Crystal aves); 2) medium-sized, with large passageways, but not extending for reat distances (Dixon, Colossal, Coach, James, Long's, Bat, and Wilson aves); and 3) small caves with low, narrow passageways, many hundreds f which are found in Edmonson County. The seven caves that contain olonies of *sodalis* are included in two, the medium-sized caves. The very arge caves are apparently too dry for this species. The small caves are not uitable for this species. It is only the medium-sized caves, which have

· large passageways, but still are very moist, which *M. sodalis* uses for
nation and summer activities.

he relative humidity of the caves inhabited by *M. sodalis* is very high.
ost passageways it is 85 percent or more throughout the year. Where
: is abundant, such as in dripping pits, the humidity is near 100 per-

The only case where differences in humidity may be important is
M. lucifugus, which commonly hibernates in places where water is
dant and the humidity is near the saturation point.

emperature is the most important factor involved in the selection of
ibernation site. The large limestone caverns of the mid-west have
ite temperature characteristics. Any particular cave is divided into
zones of temperature. One is a certain area close to the entrances
: the temperature fluctuates considerably throughout the year but does
luctuate daily. The second zone, farther within, is the deep cave en-
ment where temperature remains nearly constant throughout the year.
the first zone which is utilized by bats for hibernation, with the ex-
on of *Pipistrellus subflavus*, which hibernates in the deep parts of a

s was pointed out in the discussion of habits of hibernation, *M. sodalis*
rectly to specific spots upon entering hibernation. These spots are
· and occur in the area of the cave where the temperature reaches a
num of 4° to 6° C in mid-winter. These minimum temperatures were
l in all areas where *sodalis* hibernates. However, when the *sodalis*
hibernation in the fall the temperature in the areas close to entrances
to 10° C. The bats go directly to the area which will reach 4° to 6°
mid-winter. This relationship is illustrated in figure 15. The tem-
ure fluctuation of this area close to entrances is that of gradual change,
cooling in winter and warming in summer. This means that the tem-
ure at any particular spot in the cave at any time of the year will be
t the same from one year to the next.

he *sodalis* must select the spot to hibernate not on the basis of temper-
at the time of entrance, but with the anticipation of the temperature
d-winter, two or three months later. This is accomplished by merely
ning to the same spots each year, and by forming dense clusters at
spots. The method by which the bats are able to find the same spots
year has not been determined. It is possible that they know the con-
ation of the cave through previous echo-location in the cave. Scent
also be important in orientation in caves. Once a cluster has begun
rm, other bats would be attracted to them by sounds of the bats at
luster. Since the temperature change is the same each year in these
, the habit of going to the same spots each year makes it possible for
ats to get into the proper temperature zone before that ideal minimum
erature is reached. This is important in conserving energy, since
wise they would have to use a trial and error method.

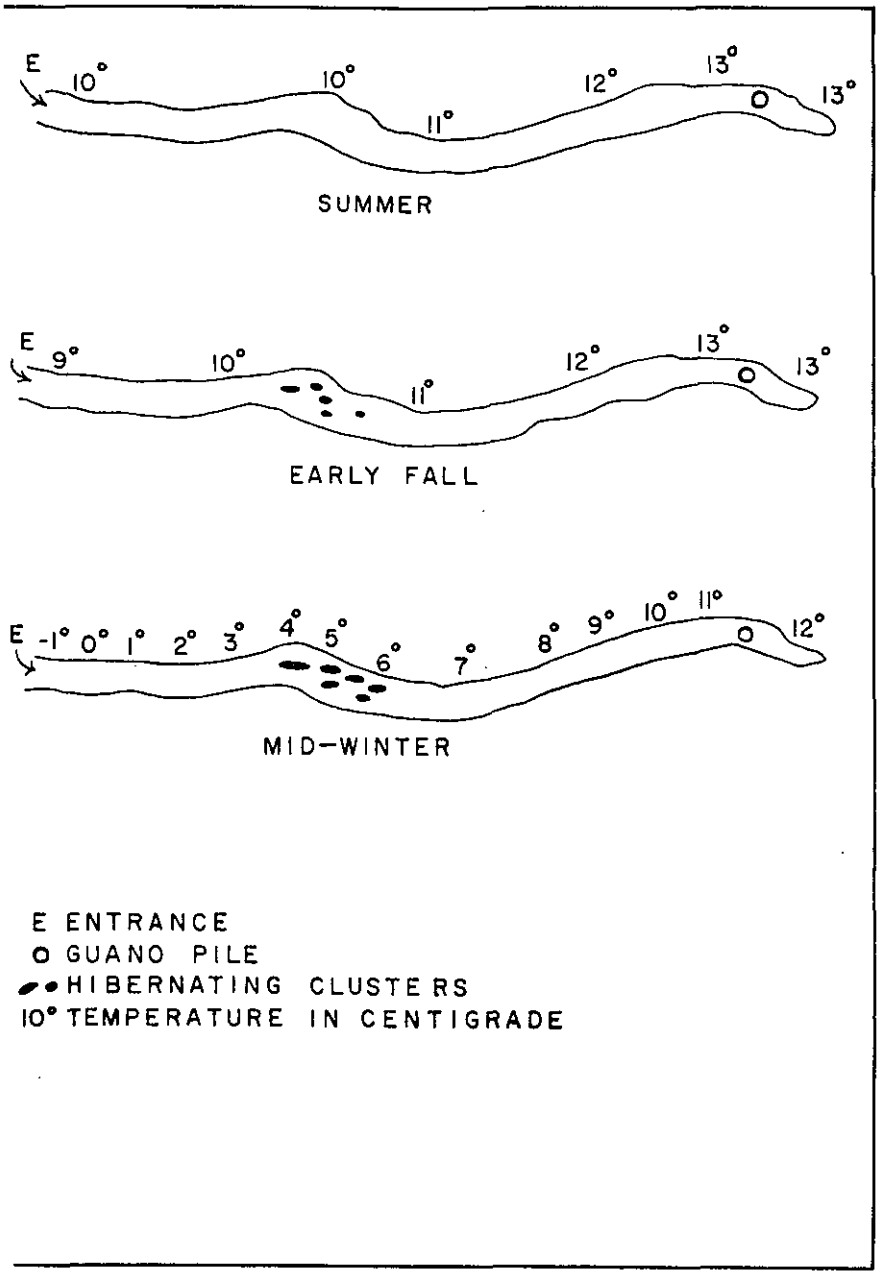


FIGURE 15. A diagrammatic representation of temperature changes and position of hibernating clusters of *Myotis sodalis* in a cave.

Myotis sodalis cluster on the flat surfaces of ceilings or overhanging
es. The ceiling need be only slightly rough for the bats to hang on by
claws. In some cases, however, the ceiling may be too smooth. In
cases, any available rough surface in the immediate vicinity may be
. In Long's Cave, Edmonson County, Kentucky, the ceiling is too
oth for the bats to hold by the claws. The *sodalis* here hang on rough
s along ceiling cracks.

One of the most interesting features of the behavior of bats is the clus-
g habit. An important problem is that of evaluating the adaptive
e of the specific clustering habit. Many species of *Myotis* form dense
ers in the hibernating season. Twente (1955) studied the possible
e of clustering of *Myotis velifer* in caves in Kansas. His studies were
e in caves where temperatures varied considerably. He postulated that
cluster protects bats from the fluctuating periods of warmer temper-
es. He assumed that the bats at the edges of the clusters had been
less time than bats in the center of clusters. He also assumed that a
which had been in hibernation longer was less irritable, and therefore
difficult to awaken. He found that the body temperature of bats in
enters of clusters was slightly lower than those on the edges of clusters.
conclusion as to the function of the hibernating cluster is to prevent the
from warming temperatures of circulating air.

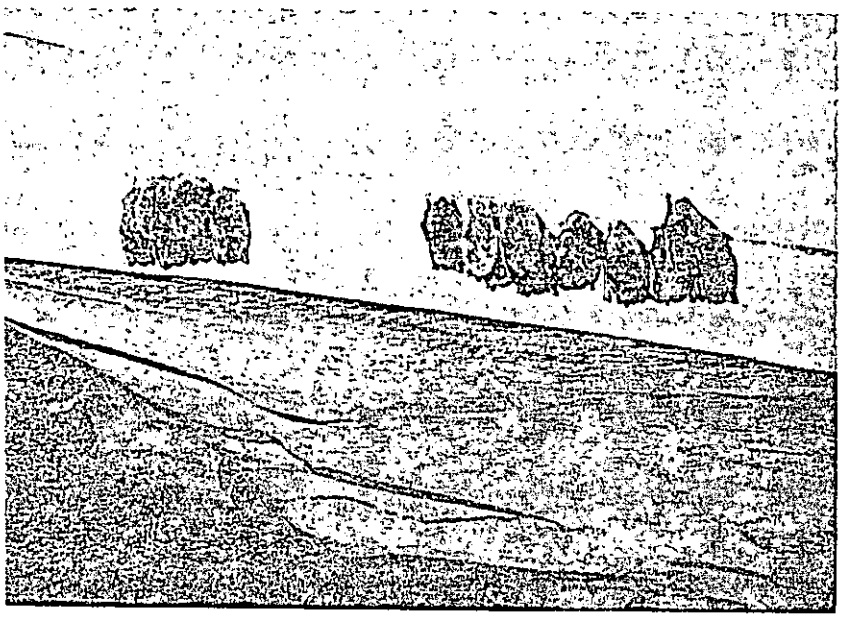
The situation of *Myotis sodalis* is considerably different. The caves in
sodalis hibernates do not exhibit much temperature fluctuation. The
nating cluster of *sodalis* is very tight and compact (figure 13). The
ers do not necessarily form as Twente described for *M. velifer*. There
guarantee that bats in the centers of clusters have been there longer
those at the edges. It was observed that *sodalis* can enter the cluster
acking in between other bats. Also clusters may form rapidly, so that
atire cluster may have been in hibernation about the same time. This
stantiated by banding information. When bats are banded in a cave
released, it is noted that within an hour banded individuals are found
in hibernating clusters, deep inside and not necessarily on the edges.
ectal temperatures of *sodalis* were taken with a thermistor instrument
e nearest 0.5° C, as was the micro-environmental temperature. The
mperature is 1° warmer than the cave-wall temperature. This was
also by Twente (1955). The body temperatures of *sodalis* are gener-
he same as the temperature of the wall, not the temperature of the air.
is true of *sodalis* from the edges of clusters as well as from the centers
sters. Studies of body temperatures were not made of clusters of
than 200 individuals. In a measurement of 30 individuals hanging
st a wall of 4° C, the following temperatures were recorded: 18 indi-
ls at 4°; seven at 4.5°; four at 5°; and one at 6° C.

The difference of these results from those of Twente for *M. velifer* may
be due to the fact that in caves where *sodalis* hibernate there are no

Habitat Selection of Other Species

Eptesicus fuscus is fairly common in the same caves as *sodalis*. This ies typically hibernates in colder areas, from -2° to 5° C. This has also noted by Hitchcock (1949) and Rysgaard (1941). *Eptesicus* normally gs on sidewalls or jams into cracks or holes. They do not form tight ers and usually hang singly.

Myotis lucifugus has a much wider tolerance of temperature than *M. lis*. It has been seen hibernating in areas of -1° up to 13° C. The of hibernation seems to be controlled more by moisture than temper- e. It is typically found where the humidity is near 100 percent. This



IGURE 16. Hibernating clusters of *Myotis lucifugus* in Bat Cave, Carter County, ucky.

lly is in dome-pits in the caves of central Kentucky, where water is lly abundant. In Blackball Mine, Illinois, *M. lucifugus* are concen- d over pools of water. This species forms semi-dense clusters. This er is different from *sodalis* in that the bats hang along cracks where claws can be hooked over flat projections. The clusters are typically ed in an overlapping fashion, with a belly-to-back relationship (figure

he bat which most closely approaches the ecological requirements of *odalis* is *M. grisescens*. Its habits of aggregation are similar to those *odalis*. Little has been published concerning this species in winter nation. A large wintering colony is found in James Cave, Edmonson

County, Kentucky. This is only one-half mile from the large wintering population of *M. sodalis* in Coach Cave. This is the only wintering colony known of *grisescens* in Kentucky or Tennessee. This species also forms dense clusters like *sodalis*. When they become active, *grisescens* go to specific guano piles as do *sodalis*. The type of cluster is slightly different from *sodalis*. It is best described as an interwoven cluster, which may be several tiers in thickness, instead of one as in *sodalis*. The *grisescens* do not fold the arms tightly beside the body, but rather stick them out at a sharp angle, and this makes the cluster truly interwoven by the arms of the bats. Temperature relationships of the clusters have not been studied. However, observations indicate a much different situation than for *sodalis*. It appears that an entire cluster may warm up at the same rate, and apparently much faster than *sodalis*.

The temperature of the large rooms in James Cave where *M. grisescens* hibernate is 10° to 11° in mid-winter. The size of this *grisescens* colony numbers between 100,000 and 150,000 individuals. This population was not discovered until March 1959. During the first two winters of study, no *grisescens* were seen in Coach Cave. During the winter of 1958–1959 about 10,000 *grisescens* suddenly appeared in Coach Cave. The puzzle about where they came from was solved when the large colony in James Cave was discovered later the same winter. The next winter, 1959–1960, the number in Coach Cave increased to about 50,000. Obviously the gray bats are rapidly taking over Coach Cave as a hibernating site. The individuals and clusters have for the most part remained separate from the *sodalis* clusters in Coach Cave. Clusters of *grisescens* are in a zone of temperature from 7° to 10° C. However, there is some overlap of the hibernating areas of *M. grisescens* and *M. sodalis* in Coach Cave. In this overlap zone, the *grisescens* tend to hang directly on clusters of *sodalis*. This could be a disturbing influence on the *sodalis*. It may be that the 4° to 6° C temperature where *sodalis* hibernates is too cold for *grisescens* and active competition for hibernating space may not occur.

The other species commonly found in these caves is *Pipistrellus subflavus*. This is the smallest bat of the area and occupies the warmer, deeper parts of the cave where the temperature is 12° to 13° C. This preference for a hibernating site makes a large area available to this species in these large caves. This availability of space may explain why *Pipistrellus* does not form clusters.

SUMMER DISTRIBUTION AND ACTIVITY

One of the most perplexing problems in the life history of *M. sodalis* is its distribution and habits in summer. Miller and Allen (1928) suggested that the large winter colonies are composed of individuals from widespread summer groups. Some references to the species in summer have been pub-

d. Black (1936) reported taking one specimen in Denney Cave, Madi- County, Arkansas, on 11 June 1933 and another on 7 July 1934, and one Bat Cave, Benton County, Arkansas, on 6 July 1934. Mohr (1933) rted finding a cluster of 69 male *sodalis* in Dixon Cave, Edmonson ıty, Kentucky, on 28 June 1932. Summer records for the species in ana have been summarized by Mumford and Cope (1958). These rec- include a few specimens which have been shot while feeding at a num- of localities in Indiana. They report that a small group of adults with ıg were seen under a bridge at Turkey Run State Park, Parke County. r summer records for Indiana include two caves: Ray's cave, Greene ıty; and Wyandotte Cave, Crawford County.

The localities of summer specimens that have been examined are plotted gure 2. In general, this distribution agrees closely with the winter dis- ıtion. Winter areas which have no summer records are northern da, eastern Tennessee, North Carolina, Virginia, West Virginia, Penn- ınia, New York, and New England. The summer records from northern ois, northern Indiana, and southern Michigan are slightly north of the er range. It seems that the summer range coincides fairly closely with vinter range.

Most of the summer specimens are males. Females have been taken in central Kentucky, and in Indiana, from Tippecanoe, Parke, Wash- ın, Kosciusko, Knox, Ripley, and La Grange counties. This area in- es a large portion of Indiana.

ince most summer specimens are from caves, field work was con- ıated in cave areas in the mid-west in an attempt to learn of the habits *dalis* in the summer months. During June, July, and August, in 1957, , and 1959, fifty-two caves were investigated of which 34 are in Ken- y, eight in Tennessee, four in Illinois, three in Missouri, and two in ına. These include 12 of the 19 caves in which this species was studied inter. Most of the detailed study was done in central Kentucky. *tis sodalis* were found in seven caves as follows: INDIANA: Ray's Cave, ne County; MISSOURI: Bat Cave, Shannon County; KENTUCKY: Bat , Carter County; Coach Cave, Edmonson County; Long's Cave, Ed- son County; Dixon Cave, Edmonson County; and Colossal Cave, Ed- son County. These seven caves are ones which also have hibernating ies in winter. *Myotis sodalis* were not found in any cave in summer h did not contain a winter colony. Five caves that have winter colonies ot contain summer colonies as follows: ILLINOIS: Blackball Mine, La County; KENTUCKY: Wilson Cave, Edmonson County; James Cave, onson County; and Bat Cave, Edmonson County.

Two adult females were found in Ray's Cave, Greene County, Indiana, 3 July 1959. This cave apparently does not contain a regular summer ıy, but only an occasional *sodalis* enters the cave in summer. Mumford Cope (1958) collected two immature males from this cave on 5 August

57. A colony of about 300 male *sodalis* were seen over a guano pile in
it Cave, Shannon County, Missouri, on May 30, 1959. This cave contains
e of the large winter colonies of about 100,000 individuals. On 11 August
58, three male *sodalis* were collected in Bat Cave, Carter County, Ken-
ky. There appears to be no major summer colony in this cave, which
es contain one of the larger winter colonies.

Concentrated field work was done in the caves of Edmonson County,
ntucky, during the summers of 1957, 1958, and 1959. *Myotis sodalis*
re found quite abundantly in Coach, Long's, Dixon, and Colossal caves,
previously mentioned. They were nearly always found clustered over
guano piles in these caves. There is no guano pile in Colossal Cave,
t during the summer the *sodalis* cluster in an active condition deep in the
ve, at the kind of location where guano piles are found in other caves.
ne bats in summer are in the deeper and warmer parts of the cave, whereas
hibernating clusters are close to entrances, where it is much colder, even
the summer. The species and numbers of bats found at these piles are
ite variable throughout the summer. Composition of these summer clus-
's is given for Dixon Cave in table 10.

The principal bats at the piles in summer are male *M. sodalis*. In five
ys of observation during the summer of 1958 in Dixon Cave, 900 bats
re estimated to be at the pile. Of these, 218 were caught. Male *M.*
dalis comprised 87 percent of those caught; female *M. sodalis*, 4 percent;
ale *M. lucifugus*, 7 percent; female *M. lucifugus*, 2 percent; and male *M.*
'sescens, 4 percent. In 1959 observations were made in Dixon Cave on
different days in June, July, and August. The total number of bats esti-
ated in these visits was 2,192. Of these, 1,212 were caught and the com-
sition was as follows: male *M. sodalis*, 81.9 percent; female *M. sodalis*,
percent; male *M. lucifugus*, 1 percent; female *M. lucifugus*, 0.1 percent;
ale *M. grisescens*, 9 percent; and female *M. grisescens*, 0.1 percent. This
ve does not have a permanent colony of bats in summer. They apparently come by groups to the cave and stay for one or two days. A typical
servation is as follows. On June 26 (1959) no bats were in the cave
ring the day. During the night bats started entering the cave about 9:00
M and continued to enter for several hours. In the morning, a cluster of
out 200 bats was over the guano pile. These were active at 8:00 AM,
t by 10:00 AM the cluster had become inactive. The individuals were
pid, with the body temperature lowered close to the environment
4° C). This torpidity persisted for several hours, but by late afternoon
bats were again active. It was expected that these bats would then
ve the cave at night, but only a few did leave. The remaining stayed
the pile and did not leave the cave during the night. This cycle of
tivity was repeated on the following day, except that the next night the
tire cluster left the cave at dark. The following night another group came
o the cave. This was a different group, because 91 were caught and

l in the first group on June 28, and none was recovered when 200 were from the second group on June 30. During the 18 visits to Dixon during the summer of 1959, 993 males and 91 females were banded. se only three were taken again in subsequent visits in the same sum- These data show that groups of bats, which are mostly male *M.* , visit certain caves for short periods of time during the summer and ove on and are replaced by other groups.

10. Composition of Active Clusters of Bats in Dixon Cave, Edmonson County, Kentucky, During June, July, and August

	No. estimated at guano pile	Number caught	*Myotis sodalis*		*Myotis lucifugus*		*Myotis grisescens*	
			Male	Female	Male	Female	Male	Female
ne	50	0						
ly	120	60	51	3	6	0	0	0
ly	200	0						
ly	300	158	136	4	8	1	9	0
ly	230	0						
	900	218	187	7	14	1	9	0
ne	130	0						
ne	150	0						
ne	114	114	41	0	1	0	72	0
ne	26	26	12	0	0	0	14	0
ne	0	0						
ne	8	0						
ne	15	15	12	0	0	0	3	0
ne	0	0						
ne	0	0						
ne	200	0						
ne	130	91	84	0	1	0	4	1
ne	250	200	192	3	0	0	5	0
ly	300	208	197	6	0	0	5	0
ly	130	53	49	1	2	1	0	0
y	270	221	206	10	0	0	3	0
y	9	9	2	0	7	0	0	0
ly	160	124	116	6	2	0	0	0
gust	300	151	80	65	3	0	3	0
	2,192	1,212	993	91	16	1	109	1

se data can be used to determine the approximate number of *M.* which visited this one cave during the summer. The total number estimated at the guano pile in 18 visits was 2,192. Of these, 82 , or 1,797, would be male *sodalis* and 8 percent, or 175, female . This is an average of 100 males per day and 10 females per day sited Dixon Cave. For an entire summer from May 15 to September days, the total number would be 12,400 male and 1,240 female *M.* that entered the cave. Four caves in the area are known to have the ituation as Dixon Cave.

From this it is apparent that male *M. sodalis* are abundant in central entucky in summer. The numbers of males estimated to be entering the .ves are great enough to explain the presence of nearly all those known to bernate in the area in winter. Actual band recoveries are indicative of is, as is pointed out below.

MOVEMENTS AND SEASONAL BEHAVIOR

Many thousands of bats have been banded in North America since 32. With all this banding activity it seems that much should be known seasonal and non-seasonal movements of bats, and movement ranges ould be well worked out. Such is not the case. Little has been reported specific movements and recoveries of banded bats. Most reports are isolated recoveries, largely associated with homing experiments, which .ve not revealed much of natural movement patterns. Not enough re-veries of any one species have been made to define adequately movement nges between seasons, or within one season. The best results with any e species is the work done with movements of *Myotis lucifugus* in the rtheast United States by Griffin (1940, 1945). There are no published cords of movements of banded *M. sodalis* or recoveries from one season another.

Myotis sodalis were banded in Illinois, Indiana, and Kentucky, during nter and summer months, in an attempt to make recoveries of banded indi-duals, and to understand seasonal and non-seasonal movements. Banding s done in five areas: northern Illinois, southern Illinois, south-central diana, eastern Kentucky, and central Kentucky. In the five winters tween late 1956 and early 1961, the following *sodalis* were banded in caves d mine tunnels of the above areas respectively: 236 males and 174 females nded in Blackball Mine, La Salle County, Illinois; two males banded in ve Spring Cave, Hardin County, Illinois; 186 males and 190 females m Ray's Cave, Greene County, and Wyandotte Cave, Crawford County, diana; 663 males and 618 females from Bat Cave, Carter County, Ken-cky; 3,743 males and 4,052 females from Dixon, Colossal, Coach, Long's, d Bat caves, Edmonson County, Kentucky. This is a total of 4,830 males d 5,034 females banded during hibernation.

Additional *sodalis* banded by other workers in winter during recent ars include several thousand by James B. Cope and Russell Mumford (in .) in south-central Indiana; about 20,000 in Missouri by Richard Myers litt.); 392 in northern Alabama by Wayne H. Davis (in litt.); and 47 in West Virginia by Davis.

Winter to Summer Recoveries

None of the 1,693 *M. sodalis* banded in winter in northern Illinois, south-Illinois, and eastern Kentucky was recovered in summer. Of the 376

l in south-central Indiana only one was recovered in summer. This female banded in Ray's Cave, Greene County, on 18 December 1958, ecovered in the same cave on 29 July 1959. Of the 7,795 *sodalis* l in central Kentucky in winter, 16 were recovered in summer. This tal recovery rate of only 0.21 percent. Eleven of these 16 were re- d in the same cave in summer as the one where they were banded in . Five of these were from a group of 183 males banded in Colossal Edmonson County, Kentucky, in January 1959, and recovered in al Cave in July 1959. This is a recovery rate of 2.73 percent for this Four males from a group of 359 banded in Long's Cave, Edmonson y, Kentucky, in January 1959 were recovered in Long's Cave in June One female from 475 banded in Long's Cave in January 1959 was red in Long's Cave on 2 September 1959.

the 4,399 males banded in Coach Cave, Edmonson County, Ken- in winter, four were seen in summer. One is a male banded in April nd recovered in the same cave in July 1958. The other three were red some distance from Coach Cave. One, which was banded in Cave in March 1959, was recovered in a farm building near Shep- ille, Bullitt County, Kentucky, in October 1960, some 60 miles NNW ie point of banding. Another male banded in February 1957 was re- l in a building in Indianapolis, Marion County, Indiana, on 26 Sep- 1958, some 180 miles north of Coach Cave. The third male was l in Coach Cave in March 1959 and recovered in Winchester, Ran- County, Indiana, in July 1960, some 225 miles NNW of the winter

the 2,336 females banded in Coach Cave in winter, two were re- l in summer. One was banded on 20 April 1957, during hibernation, overed in a building in Indianapolis, Marion County, Indiana, on 27 960, some 180 miles north. The other female was banded on 7 March nd recovered near Urbana, Champaign County, Ohio, on 2 May ome 240 miles NE.

Summer to Winter Recoveries

er *M. sodalis* were banded in summer, and most of them were males. the summer months of June, July, and August of 1957, 1958, and n south-central Indiana, eastern and central Kentucky, 1,279 male female *sodalis* were banded. All but seven of these were banded in Colossal, and Coach caves, Edmonson County, Kentucky.

the summer of 1958, eighteen female and 261 male *sodalis* were in Edmonson County, Kentucky. Seven of the males were recovered er in caves of this same county. This is a recovery rate of 2.51 . Two of these were banded in Dixon Cave in summer and recovered same cave in winter. Three were banded in Dixon Cave in summer overed in Coach Cave in winter, five miles away. One was banded

ıort distances of a few miles between caves in Edmonson County, Ken-ıcky. Likewise, two movements are of a few miles between caves in reene and Monroe counties, in Indiana. The remaining 13 records involve nger distances between colonies in central Kentucky, southern Indiana, ›rthern Illinois, and eastern Kentucky.

These movements between winter colonies involve essentially the same ea as that of the seasonal movements previously described. There may be nsiderable movement from one winter to the next. The longest distance of a bat that moved 320 miles from northern Illinois to central Kentucky, on one winter to the next. Fifteen of the 20 records are for females. This dicates that females tend to change their cave of hibernation more than ales. This difference is significant at the .01 level. A greater number of cords will be necessary to say with certainty that female *sodalis* change eir hibernating site more often than males.

A large number of *M. sodalis* have been banded in recent years in e Ozark area of Missouri by Richard Myers. We have obtained no cords of *M. sodalis* movement between the Ozark area and the area in-lved in the previously described movements in Illinois, Indiana, and Ken-cky.

Discussion of Movement

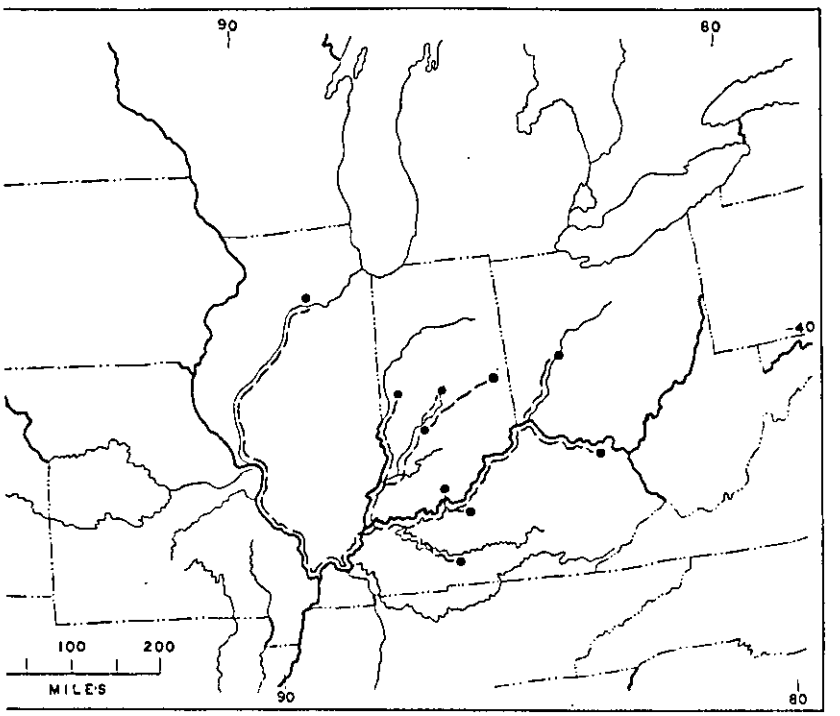
Male *Myotis sodalis* are abundant in summer in the same areas where ey are abundant in winter. The males travel around in small groups and n be found over guano piles in the large caves in which they hibernate in nter. The exact pattern of movement is not well understood. Any one oup apparently visits a cave only once or twice during the entire summer. ese groups probably include almost all the same individuals that win-ed in the cave. They must be moving to other places, but no records are ailable to indicate where these other places are.

The movement area in summer may be rather large. The records for ovement from the winter caves in Edmonson County, Kentucky, to a sum-r area in southern and central Indiana, and central Ohio, are noted above. vo juveniles that were banded in central Indiana in summer traveled to ntral Kentucky to hibernate, one being recovered during the first winter its life. This individual had found its way to a hibernating cave of its n species 170 miles from where it was born. When this bat was recovered was in the same cluster with another *sodalis* which had been banded three ars previously in a cave in Indiana, 65 miles from where the juvenile was nd. It appears that the juvenile was traveling with adult bats from In-na.

What do bats orient on in traveling the 170 to 320 miles as *M. sodalis* ve been found to do? It is postulated here that the major rivers are navi-tion routes for *sodalis*. The caves used by this species are all fairly close rivers. One of these, Dixon Cave, in central Kentucky on the very banks

Green River, apparently serves as an orientation point for bats com-
the area in the fall and for large groups moving in the spring. In late
several thousand *M. sodalis* may enter this cave at night and then
on in a few hours. In fall, this cave contains more bats earlier than
other cave of the area. These bats then move to other hibernating
situated several miles back from the river.

irly definite movement areas may exist for certain populations of *M.*
's. Movement records are numerous between Indiana, Illinois, and



URE 19. Possible routes of travel by riverways involved in the movements of *sodalis* shown in figures 17 and 18.

cky, but no records exist between Kentucky and Missouri. The bats become familiar with certain areas by traveling with other bats. Once riverways are learned, the bats can travel easily over some large Possible routes used by *M. sodalis* in the movements described are ated in figure 19.

is has bearing on so-called "homing" abilities of bats. It has been strated by several workers, as summarized by Cockrum (1956), that s may return from distances of over 200 miles when removed from oosts. *Eptesicus fuscus* have returned from over 300 miles (Smith and

oodpaster, 1958). These experiments do not take into account the possible atural movement and familiar territory of the bats under observation. he ability of an animal to find its way back to its roost from within its nown territory does not demonstrate a remarkable homing ability, but nerely shows that the animal has the habit of returning to a particular area t a certain time of the year. The natural range of populations of bats must e discovered first, before homing experiments will reveal much about ori-ntation in bats.

REPRODUCTION

Details of the reproductive cycles of those species of bats which spend ie winter in hibernation have been studied carefully by several workers nce about 1930. Reviews of literature are presented by Hartman, 1933; 'imsatt, 1942; Wimsatt and Kallen, 1957; and Wimsatt and Trapido, 1952. *'yotis sodalis* has been studied only by Guthrie (1933). Apparently the ittern of reproduction is similar for all those species which hibernate. This udy adds nothing to the knowledge of reproductive cycles of these bats, it some significant observations were made concerning the time, place, and reumstances of mating in *M. sodalis*. An important problem still exists as the location of the nursery colonies of females and their young, and thus so the care and development of the young. Some information on these 'oblems was obtained from the examination of museum specimens.

Bats that spend the winter in hibernation mate in the fall as they enter bernation, and the sperm are stored in the uterus until spring, when the male ovulates upon leaving hibernation (Guthrie, 1933; Wimsatt, 1942, 944). However, little is known of the circumstances of mating, since evi-nce for mating comes largely from the recovery of sperm in the female.

Actual observations of mating are few and have never involved large mbers of bats. Wimsatt (1945) describes in detail the mating of *M. luci-gus* and *M. subulatus* in caves throughout the winter. He saw only a few irs and usually mating occurred only after the bats were aroused by the 'esence of the observers. *Myotis sodalis* were observed closely throughout e year. A fairly good idea of the circumstances of mating was obtained. 'ating occurs only during a definite period in the fall, deep in the hibernat-g caves near the guano piles, late at night. Observations were made at ixon Cave, Edmonson County, Kentucky, during the fall of 1959. On 'ptember 1, no mating activity was observed at the guano pile at which 0 to 400 bats were roosted. Hibernation had not yet begun. On October hibernation had begun for some individuals. There were, however, about 500 *M. sodalis* at the guano pile both day and night. No mating activity as observed during the day. At night activity increased with some flying t to feed, some returning after feeding, and mating activity was taking ace. The number of bats at the pile increased as the night progressed.

y pairs were seen mating and males were observed scurrying around
ng for mates.

male actively seeks out a female by crawling along the ceiling of the
He cautiously approaches her from behind, crawls over her, then
s the female just in back of her head with his teeth, and holds her se-
y. The female immediately tries to escape, and sometimes manages to
way. The male gets his hind quarters underneath the interfemoral
brane, and at the same time bends his tail and membrane back onto the
g, and out of the way. The penis is inserted by strong pushing of the
quarters. The female is constantly trying to escape, but the male
tains a firm hold with the teeth, and spreads his wings around the fe-
to restrain her. Once the penis is introduced, the female seems to quiet
and the male loosens his grip, but brings the forearms forward and
them against the back of the head of the female, and actually bends
eck down a little. The mating lasts for several minutes, but actual
g means little, since the bats were considerably disturbed by the pres-
of the observers.

his mating behavior is essentially the same as that described for *Myotis*
gus by Wimsatt (1945). On October 9, the hibernating colonies were
nereasing, and there were still many active bats at the guano pile en-
in mating activities. The next date of observation was November 27.
ating was observed then, or at any other time throughout the winter,
though many bats would be at the guano piles in an active condition.
limited mating was observed in late April as the bats were leaving
nation. This involved only a few pairs, not the mass mating as in the
Myotis sodalis thus seems to have a more definite period of mating
does *M. lucifugus*. Whereas *lucifugus* may mate throughout the
, *sodalis* mates only in the fall and again to a lesser degree in spring.
important problem is whether or not a cave population in winter is
breeding population. In these mating groups in Dixon Cave, 16
d bats were recovered. All of these were ones which had been banded
on Cave, either in winter or summer. However, bats banded in Dixon
in September, before the mating season, were recovered in Coach Cave,
miles away in winter. One was recovered the day after banding.
g the fall mating season in Dixon Cave, a large number of bats are
ated in what can be called the transient area. It may be that these
e bats which are moving on to other caves and keep themselves sepa-
om the colony of Dixon Cave. Some movement from one winter cave
ther does take place as was pointed out before. It seems that the in-
als in a hibernating colony are for the most part a breeding colony,
th some interchange possible between colonies in certain areas. It is
own where the young that are born to the females of any particular
ay go to mate and hibernate. The movements of the only two juve-
ver banded have already been discussed. Both these two juveniles

ere banded from the same small cluster in Indiana, but were found hibernating in different caves in central Kentucky. It seems more realistic to ink of a breeding population as those bats which are found within a natral populational movement area. One such area apparently involves Kenucky, Indiana, Illinois, and southern Ohio. There seems to be little or no ovement to other areas, where populations of *M. sodalis* occur.

The place and circumstances of the birth and rearing of the young of *M. odalis* are unknown. Only one pregnant female has ever been seen or taken REM. 1839). This bat was shot by Larry Calvert near Mongo, La Grange ounty, Indiana, on 18 June 1959. This female contained one embryo 39 illimeters in length. Juveniles have been collected a number of times. uvenile records for Indiana are summarized by Mumford and Cope (1958). he youngest is a male collected 24 July 1952, under a bridge at Turkey un State Park, Parke County, Indiana. This individual was 71 mm long d had its adult teeth. On July 27, 1957, a group of immature *M. sodalis* ere caught at this same bridge (Mumford and Cope, 1958). One specimen llected was 87 mm long. The others were banded and their movements ve been discussed previously. Mumford and Cope reported that three mmature *sodalis* were shot while feeding near a wooded area in Steuben ounty, Indiana, 27 July 1957. Mumford collected two immature *sodalis* Ray's Cave, Greene County, Indiana, on 5 August 1957. These were estially adult-size, except that the wing epiphyses were still open.

Other juvenile specimens were found in the examination of specimens: o mummies from Greenway, Clay County, Arkansas, on 10 July 1898 NHM); one taken at Grosse Isle, Wayne County, Michigan (USNM), th no data; three males taken in Penn's Cave, Centre County, Pennsylnia, on 2 November 1924 (CU); one male from Aitkin Cave, Mifflin unty, Pennsylvania, on 17 November 1940 (CU); one female taken in tle's Cave, Albany County, New York, on 2 March 1941 (MCZ); and one nale taken in Nickwacket Cave, Crittenden, Rutland County, Vermont, 22 February 1935 (MCZ).

For a species as abundant as *M. sodalis* there are few records of breeding nales and juveniles. It seems that the young are born in late June and on the wing by mid-July. In the southern parts of the range, the wing physes are closed by the beginning of hibernation in the fall. In the thern portion of the range, from Pennsylvania to Vermont, the epiphymay still be open when the bats enter hibernation. They thus can be tinguished throughout the winter as young of the year.

SUMMARY

1. *Myotis sodalis* is restricted in winter to the major cavernous limestone as of the mid-west and eastern United States. Localities occur in groups reas where there are many large caves in a small area.

Most localities are close to major rivers. These rivers apparently are ·tant in navigation and may be avenues of dispersal. The eastern di- ›etween the Atlantic Coastal drainage and the Mississippi drainage has as somewhat of a barrier to dispersal.

The summer range is less well known, but appears to be about the as the winter range, except for a slight extension to the north beyond ıve areas.

Characters of the skin and skull show no indication of race formation › the species. Measurements vary little over the entire range of *M.* *s.*

The winter distribution of cave populations is decidedly one that is gated. Four caves are known in Kentucky and Missouri which have · colonies of about 100,000 individuals. Other caves have only 1,000)0 or less. One such large population was destroyed by flooding in re- ime in central Kentucky. This species is extremely specialized in re- o the habit of aggregation.

The period of hibernation is about 190 days on the average. *Myotis* ‹ form characteristic dense clusters on ceilings in the same spots each . These spots are in the zone of the cave where the temperature s 4° to 6° C in mid-winter. Considerable activity occurs throughout nter, as well as some limited feeding.

The cluster takes advantage of a rather narrow zone of temperature eave and protects the bats from excessive disturbance during hiber-

)ther species form different types of clusters and are adapted to dif- temperature zones. This has allowed several species to occupy a cave er.

Male *M. sodalis* wander around in small groups during the summer. nay be found hanging over guano piles in the same caves in which bernated. These guano piles are in the deeper, warmer parts of the The *sodalis* fly out to feed at night from these roosting places. Other , such as *Myotis lucifugus* and *Pipistrellus subflavus*, may be found › caves in summer, but they are nearly always in a torpid condition. o not exhibit daily activity, but remain in a cold, torpid condition for days. *Myotis sodalis* has been able to adapt to cold caves, live in uring the summer, and still carry on normal activity. This is a basic ce between a true cave-inhabiting bat in temperate regions and one ıses caves only for hibernation. *Myotis grisescens* and *M. austrori-* are also true cave bats in this area.

The same individual *M. sodalis* may be present in the same area and summer, or may move as much as 230 miles between seasons. › band recoveries indicate that certain movement areas exist for cer- ılations. One such populational range includes Kentucky, Indiana, and southern Ohio. No movement apparently takes place between

his area and the Ozark area of Missouri and Arkansas. The postulated outes of navigation are the major rivers.

11. A *sodalis* may hibernate in one cave one winter and in another the ext or subsequent winters, but the tendency is to return to the same cave ach winter. The area of movement between hibernating caves is the same s that involved in seasonal movement.

12. Females tend to change their cave of hibernation more than males as ndicated from actual movement records.

13. The sex ratio of *M. sodalis* is equal in the winter colonies.

14. In comparing the habits of several species of *Myotis* found in eastern nd mid-western United States, it can be seen that *M. sodalis, M. grisescens, I. velifer,* and *M. austroriparius* have similar habits in regard to cave adaptations and aggregation. *Myotis lucifugus, M. keenii,* and *M. subulatus* use aves only to hibernate in. If they enter caves in summer, they go to a torid condition as in hibernation. *Myotis sodalis* and *M. lucifugus* resemble ch other more closely in morphology, but *sodalis* may well be more closely lated to *M. grisescens, M. velifer,* and *M. austroriparius.*

15. *Myotis sodalis* has apparently evolved through adaptations for utiliation of the larger caves of Missouri and Kentucky. This species has beme a true cave-adapted *Myotis.* The major cave areas of Kentucky and lissouri are centers of abundance at the present time.

16. The establishment of populational ranges restricts gene flow within ie species. This apparently has not been in effect long enough to allow ice differentiation to occur.

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