

POPULATION TRENDS OF WINTERING BATS IN VERMONT

STEPHEN C. TROMBULAK¹, PHILIP E. HIGUERA^{1,2}, AND MARK DESMEULES³

ABSTRACT - We report the results of all readily available inventories of wintering bats in Vermont. Surveys at 23 hibernacula were compiled from the literature and unpublished data of numerous biologists and cavers. The earliest Vermont records date back to 1934. Only five hibernacula were systematically surveyed for more than 45 years. Despite data limitations, several trends have emerged. Since the 1930s, wintering populations of *Myotis sodalis* have dramatically declined; wintering populations of *M. lucifugus* have increased; and wintering populations of all other Vermont species (*M. leibii*, *M. septentrionalis*, *Eptesicus fuscus*, and *Pipistrellus subflavus*) have remained small.

INTRODUCTION

Numerous studies have shown that populations of several species of North American bats have declined in recent decades (Hill and Smith 1984, Humphrey 1978, Pierson 1998, Tuttle 1979). Currently, six species are listed as endangered by the U.S. Fish and Wildlife Service. In Vermont, these species include the federally endangered Indiana bat (*Myotis sodalis* Miller and Allen) and the Vermont state threatened small-footed bat (*M. leibii* Audubon and Bachman). Many species of bats whose populations were considered secure have shown recent population declines (Pierson 1998). For other species, current information is insufficient to assess trends in their population sizes.

Factors contributing to bat population declines (generally reviewed in Hill and Smith [1984] and Altringham [1996]) include pesticide poisoning (Geluso et al. 1976, Reidinger 1976, Tuttle 1979), chemical pollution (Tuttle 1979), siltation of waterways (Tuttle 1979), flooding (Hall 1962), deforestation (Tuttle 1979), disturbance by biologists and caving enthusiasts (Humphrey 1978, Speakman et al. 1991), and human interference (Fenton 1970, Tuttle 1979). The foremost factor leading to population declines is the wanton destruction of roost sites, particularly hibernacula (Humphrey 1978, Sheffield et al. 1992). Thus, North American bat conservation efforts have focused largely on protection of hibernacula from vandalism and physical alterations.

Eighteen of the 45 bat species present in North America rely substantially on caves or abandoned mines for roosting sites. Thirteen use

¹ Department of Biology, Middlebury College, Middlebury, VT 05753. trombulak@middlebury.edu; ² Present address: College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195; ³ The Vermont Nature Conservancy, 27 State Street, Montpelier, VT 05602; Present address: Box 266 Route 194, Alna, ME 04535.

caves and mines year-round for both reproduction and winter roosts, while the remaining five use them exclusively for hibernation (Barbour and Davis 1969). Bats choose suitable hibernacula based on temperature, humidity, air circulation, and morphology of the cave or mine (Hitchcock 1949, Raesly and Gates 1987, Twente 1955). The range of acceptable conditions is typically narrow. Thus, desirable caves and mines are relatively rare but essential to the survival of a population. Because of their dependence on caves and mines for hibernation, inventories of bats at hibernacula provide a useful index to population trends over time. These indices can aid in the status assessment of bat species within a defined geographic area.

In addition to *M. sodalis* and *M. leibii*, four other bat species hibernate in Vermont: *M. lucifugus* Le Conte (little brown bat), *M. septentrionalis* Trouessart (northern long-eared bat, = *M. keenii septentrionalis*), *Eptesicus fuscus* Palisot de Beauvois (big brown bat), and *Pipistrellus subflavus* F. Cuvier (eastern pipistrelle). Unpublished research on cave bats in Vermont dates back to 1913; however, the earliest documented inventories did not begin until 1934 (Fichtel 1992). We report the results of all available inventories of wintering bats in Vermont. This information may facilitate a better understanding of trends in wintering bat populations in Vermont and assist in efforts to promote their conservation.

METHODS

A thorough search of the literature, state agency records, and unpublished data of biologists and cavers who have studied bats in Vermont was performed to obtain information on wintering population sizes. Banding and census data from October to April (1934-1999) were gathered from the following sources: (1) Harold Hitchcock's personal field notebooks from Middlebury College's Starr Library Archives (Middlebury, Vermont); (2) Donald Griffin's personal Vermont field notebooks from Middlebury College's Starr Library Archives; (3) Griffin (1940a); (4) Griffin (1945); (5) Davis and Hitchcock (1965); (6) Records from the Nongame and Natural Heritage Program, Vermont Fish and Wildlife Department, 103 South Main Street, Waterbury, Vermont 05471-0501; (7) Fichtel (1992); (8) Data from Marc DesMeules not available from Source 6; (9) Data from Alan Hicks (New York State Department of Environmental Conservation) not available from Source 6; and (10) Data from William Kilpatrick (Department of Biology, University of Vermont) not available from Source 6. The Vermont Nongame and Natural Heritage Program (Source 6) is a repository for field notes from bat researchers in Vermont, particularly Chris Fichtel (Vermont Nongame and Natural Heritage Program and the Vermont Nature Conservancy), William Kilpatrick, Kevin O'Classen (Vermont Cavers Association), Steve Parren (Vermont Nongame and Natural Heritage Program), and Stephen Trombulak.

Data from 23 caves and mines in Vermont were compiled. Five were censused at irregular intervals from the 1930s to the present: Dorset (also known as Mt. Aeolus) Cave (in the township of Dorset), Nickwacket Cave (Chittenden), Plymouth Caves (Plymouth), Ely Copper Mine (Vershire), and Quarry Cave (Danby). Wyman's Cave (Sunderland) was only censused once (1936-37). Seventeen were only censused during the late 1980s and 1990s: Greeley Talc Mine (Stockbridge), Brandon Silver Mine (Brandon), Morris Cave (Mt. Tabor), Argonaut Mine (Ludlow), Hammondsville Mine (Reading), Camp Brook (Bethel), Pike Hill Mines (Corinth), Clifton Adit (Chester), Rousseau Talc Mine (Cambridge), Kents Cave (Arlington), Milton Cave (Milton), Bristol Cave (Bristol), 1867 Cave (Sudbury), Porcupine Caves (Danby), Skinner Hollow Cave (Manchester), Fox Gold Mine (Tyson), and Barrel Cave (Bristol). It is likely that more caves and mines in Vermont serve as hibernacula. However, credible census data were found only for the 23 hibernacula listed in this paper.

Census data were collected using four different methods: (A) number of bats counted while banding, (B) number of bats counted when not banding, (C) population size estimated by mark-and-recapture, and (D) the maximum number of bats "taken" at any one time. The latter method was used only by Griffin (1940a), who did not specify what he meant by "taken," so we list this method separate from the others.

RESULTS

Dorset Cave. This cave is currently owned by the Vermont Nature Conservancy and a "bat-friendly" gate was installed in 1985. Populations have been inventoried at Dorset Cave irregularly since 1934-35 (Table 1). In all years in which surveys were conducted (with the exception of 1960-61 and 1961-62), the maximum number of bats in the winter ranged from 202 to 3,000 bats. Total numbers show no obvious trend over time; year-to-year variation in population size during the 1930s to 1960s is roughly the same as during the 1980s and 1990s. The extremely high number of bats documented during the 1960-61 and 1961-62 surveys could be due to either the total area surveyed or the estimation method used (see Discussion), and therefore may not be comparable to counts made in other years.

The population size of *Myotis sodalis* has declined dramatically at Dorset Cave since the 1930s. During the 1930s and 1940s, wintering population sizes of *M. sodalis* ranged between 182 and 232 individuals. Sometime between the early 1940s and early 1960s, however, they virtually disappeared from this hibernaculum. Since the 1980s, these bats have been present in very low numbers. In contrast, the number of *M. lucifugus* has increased during this period. During the early to mid-1930s, their numbers were less than 200. From 1938 to 1959, they numbered between 200 and 700. Since 1960, their numbers have fluctuated, but regularly exceed 1000. *M. leibii* was largely absent during the

Table 1. Census estimates of bats at Dorset (Mt. Aeolus) Cave, Bennington Co., Vermont. *M. lei.* = *Myotis leibii*; *M. luc.* = *M. lucifugus*; *M. sep.* = *M. septentrionalis*; *M. sod.* = *M. sodalis*; *M. spp.* = unidentified *Myotis*; *E. f.* = *Eptesicus fuscus*; *P. s.* = *Pipistrellus subflavus*. Total = total number of bats present (censused) regardless of whether they were identified to genus or species. Source and method codes follow those described in the Methods section of the text.

| Date | <i>M. lei.</i> | <i>M. luc.</i> | <i>M. sep.</i> | <i>M. sod.</i> | <i>M. spp.</i> | <i>E. f.</i> | <i>P. s.</i> | Total | Source | Method |
|-------------|----------------|----------------|----------------|----------------|----------------|--------------|--------------|---------|--------|--------|
| 11 Nov 1934 | | 19 | 1 | 182 | | | | 202 | 1 | A |
| 29 Nov 1935 | | 174 | 1 | 200 | | | 12 | 387 | 1 | A |
| 3 Apr 1936 | | 99 | 3 | 111 | | | | 213 | 1 | A |
| 27 Nov 1936 | | 61 | 2 | 237 | | | 8 | 308 | 1 | A |
| 4 Apr 1937 | | 51 | 1 | 2 | | | | 54 | 1 | A |
| 5 Dec 1937 | | 136 | 8 | 195 | | | 2 | 341 | 1 | A |
| 27 Feb 1938 | | 17 | 3 | 30 | | | 3 | 53 | 1 | A |
| 12 Nov 1938 | | 656 | | 28 | | | | 684 | 2 | A |
| pre-1940 | | 693 | 8 | 232 | | | 12 | 945 | 3 | D |
| 24 Nov 1940 | | 566 | | 6 | | | | 572 | 2 | A |
| pre-1945 | | | | | | | | 500 | 4 | C |
| 27 Mar 1948 | | 234 | 4 | 2 | | | 3 | 243 | 1 | A |
| 12 Dec 1948 | | 414 | 6 | 2 | | | 3 | 425 | 1 | A |
| 25 Feb 1951 | | 202 | 6 | 3 | | | 3 | 214 | 1 | A |
| 15 Mar 1953 | | 304 | 1 | 7 | | | 1 | 313 | 1 | A |
| 29 Nov 1958 | | | | | | | | 1,200 | 2 | B |
| 14 Nov 1959 | | 310 | | | | | | 310 | 1 | A |
| 23 Apr 1960 | | 353 | 1 | | | | | 354 | 1 | A |
| 30 Apr 1960 | | 2,000 | | | | | | 2,000 | 5 | C |
| 9 Oct 1960 | | 270 | | | | | | 270 | 5 | C |
| 11 Dec 1960 | | 30 | | | | | | 30 | 1 | A |
| 4 Apr 1961 | | 356 | | | | | | 356 | 1 | A |
| 6 Apr 1961 | | | | | | | | 475 | 1 | A |
| 16 Apr 1961 | | 800 | 21 | 1 | | | 1 | 823 | 1 | A |
| 23 Apr 1961 | | 1,600 | | | | | | 1,600 | 5 | C |
| 26 Apr 1961 | | | | | | | | 300 | 1 | A |
| 30 Apr 1961 | | 3,000 | | | | | | 3,000 | 5 | C |
| 1960-61 | | | | | | | | 333,693 | 5 | C |
| 13 Oct 1961 | | | | | | | | 814 | 1 | A |
| 19 Nov 1961 | | 415 | | | | | 8 | 423 | 1 | A |
| 3 Apr 1962 | | 53 | | | | | | 53 | 5 | A |
| 8 Apr 1962 | | 48 | | | | | | 48 | 5 | A |
| 13 Apr 1962 | | 84 | | | | | | 84 | 5 | A |
| 15 Apr 1962 | | 186 | | | | | 2 | 188 | 1 | A |
| 16 Apr 1962 | | 83 | 2 | | | | | 85 | 1 | A |
| 20 Apr 1962 | | 1,300 | | | | | | 1,300 | 5 | C |
| 22 Apr 1962 | | | | | | | | 1,500 | 1 | B |
| 28 Apr 1962 | | 1,500 | | | | | | 1,500 | 5 | C |
| 1961-62 | | | | | | | | 286,217 | 5 | C |
| 13 Oct 1962 | | | | | 814 | | | 814 | 1 | A |
| 22 Oct 1962 | | 271 | | | | | | 271 | 5 | A |
| 4 Nov 1962 | | 189 | | | | | | 189 | 5 | A |
| 6 Apr 1963 | | 451 | 10 | | | | | 461 | 1 | A |
| 21 Apr 1963 | | 750 | | | | | | 750 | 5 | C |
| 5 Dec 1964 | | | | | 436 | | | 436 | 1 | A |
| 28 Mar 1965 | | | | | 149 | | | 149 | 1 | A |
| 24 Oct 1965 | | 1,329 | 10 | | | | | 1,339 | 1 | A |
| 23 Oct 1966 | | 315 | | | | | | 315 | 1 | A |
| 3 Apr 1981 | 1 | 320 | 22 | 2 | | 2 | 1 | 348 | 9 | B |
| 2 Nov 1983 | | 993 | 110 | | | | 1 | 1,104 | 8 | B |
| 26 Feb 1986 | | 986 | 29 | | | | 2 | 1,017 | 8 | B |
| 13 Feb 1987 | | 815 | 3 | 3 | | | 1 | 822 | 8 | B |
| 24 Feb 1988 | | 1,265 | 2 | 3 | | | | 1,270 | 8 | B |
| 29 Oct 1988 | | 1,800 | 12 | | | | 2 | 1,814 | 10 | B |
| 30 Nov 1988 | | 1,106 | | | | | | 1,106 | 8 | B |
| ? Jan 1989 | | 556 | 15 | 7 | | | | 578 | 8 | B |
| 30 Jan 1990 | 2 | 1,160 | | 8 | | | | 1,170 | 8 | B |
| 6 Mar 1992 | | 290 | | 3 | | | | 293 | 8 | B |
| 29 Jan 1993 | | 289 | 15 | 3 | | | 2 | 309 | 8 | B |
| 5 Feb 1994 | | 371 | 18 | | | | | 389 | 8 | B |
| 29 Jan 1998 | | 1,025 | 1 | 1 | 13 | | | 1,040 | 6 | B |

entire time for which we have records, with only one individual observed in 1980-81 and two in 1989-90. Both *M. septentrionalis* and *Pipistrellus subflavus* have been present in low numbers throughout the entire period (< 30 bats), with the sole exception of 110 *M. septentrionalis* counted in 1983-84. *Eptesicus fuscus* has been documented at this cave only once (1980-81).

Plymouth Caves. These caves are currently owned by the Vermont Nature Conservancy and were both gated in 1990. Patterns at Plymouth Caves (a pair of two closely adjoining caves) are similar to those at Dorset Cave, with the exception that the total number of bats increased between 1966 and 1984 (Table 2). Prior to 1966, the maximum number of bats never exceeded 118. After 1985, the number of bats fell below 200 only once. *M. sodalis* was common during the 1930s; however, it declined after 1940 and has not been seen since 1945-46. Populations of *M. lucifugus* increased from less than 75 individuals during the 1930s-40s to greater than 200 during the 1990s. *M. leibii* was recorded in only three years (1935-36, 1985-86, and 1990-91). *M. septentrionalis* and *P. subflavus* have been present in low numbers throughout the entire period (< 30 bats), and only a single *E. fuscus* has ever been recorded there (1987-88).

Nickwacket Cave. This cave is currently privately owned and ungated, and until recently it has experienced considerable recreational use. Counts of all bat species at Nickwacket Cave, except *P. subflavus*, have declined over time. Bat populations decreased from 385 bats in 1940-41 to consistently less than 60 in the 1990s (Table 3). During the 1930s and 1940s, Nickwacket Cave was second only to Dorset Cave in terms of numbers of bats; today it is a minor hibernaculum in Vermont. As at Dorset Cave and the Plymouth Caves, the population size of *M. sodalis* has exhibited the greatest change. During the 1930s it was the most numerous species during the winter, with recorded population sizes as great as 268. The population declined in the earlier 1940s, and disappeared between 1948 and 1955. *M. lucifugus* also declined over this time, decreasing from consistently more than 100 individuals during the 1930s to fewer than 30 during the 1990s. *M. leibii* has generally been absent, with only a few individuals documented prior to 1989-90. *M. septentrionalis* and *P. subflavus* have generally been present in low numbers throughout the entire period (< 11 bats), with the exception of 21 *P. subflavus* counted in 1998-99. *E. fuscus* has not been recorded there.

Ely Copper Mine. This mine is privately owned and is ungated, but access to the mine is strictly regulated by the owner, and disturbance to the bats during the winter is practically nonexistent. Operations at the mine were halted during the late 1950s. Bats were inventoried at the Ely Copper Mine in 1937 and from 1983 to 1998 (Table 4). *M. sodalis* was present in low numbers (13 bats) in 1936-37, but has not been observed there since. *M. lucifugus* increased from 132 in 1936-37 to greater than 300 in the 1990s. (The high roof of some of the mine chambers makes

identification of *Myotis* species difficult, potentially affecting the number of *Myotis* spp. recorded there in some years.) *P. subflavus* has consistently been present in low numbers (< 7 bats). The Ely Copper Mine has consistently housed relatively large populations of *M. leibii* (up to 14), *M. septentrionalis* (up to 70), and *E. fuscus* (up to 163).

Quarry Cave. This cave is privately owned and ungated; however, we believe that it is rarely visited. Quarry Cave was first inventoried in 1949-50, with infrequent visits ending in 1992-93 (Table 4). Over this period, the total number of bats increased (100 to greater than 300 bats), due exclusively to a shift in the number of *M. lucifugus* using this cave. *M. sodalis* has never been recorded here. All other species, including *M. leibii*, have only been recorded in low numbers (< 7 bats).

Greeley Talc Mine. This mine is in the Green Mountain National Forest, and was gated by the US Forest Service in 1993. Operations at

Table 2. Census estimates of bats at Plymouth Caves, Windsor Co., Vermont. Species abbreviations are as in Table 1. Source and method codes follow those described in the Methods section of the text.

| Date | <i>M. lei.</i> | <i>M. luc.</i> | <i>M. sep.</i> | <i>M. sod.</i> | <i>M. spp.</i> | <i>E. f.</i> | <i>P. s.</i> | Total | Source | Method |
|-------------|----------------|----------------|----------------|----------------|----------------|--------------|--------------|-------|--------|--------|
| 10 Nov 1934 | | 14 | 2 | 73 | | | 2 | 91 | 1 | A |
| 3 Apr 1935 | | | 1 | 1 | | | | 2 | 1 | A |
| 2 Nov 1935 | | 24 | 2 | 17 | | | 1 | 44 | 1 | A |
| 1 Dec 1935 | | 5 | 6 | 44 | | | | 55 | 1 | A |
| 5 Apr 1936 | 2 | 20 | | 15 | | | 1 | 38 | 1 | A |
| 26 Nov 1936 | | 18 | 24 | 61 | | | 2 | 105 | 1 | A |
| 8 Apr 1937 | | 6 | 6 | 7 | | | 1 | 20 | 1 | A |
| 12 Oct 1937 | | 31 | 7 | 20 | | | 3 | 61 | 1 | A |
| 4 Dec 1937 | | 2 | | 3 | | | | 5 | 1 | A |
| pre-1940 | 2 | 31 | 21 | 73 | | | 2 | 129 | 3 | D |
| 23 Apr 1940 | | 18 | 6 | 35 | | | 4 | 63 | 2 | A |
| 15 Nov 1940 | | 28 | 7 | 81 | | | 2 | 118 | 2 | A |
| 7 Dec 1941 | | 27 | 20 | 3 | | | | 50 | 2 | A |
| 2 Dec 1944 | | 74 | 18 | | | | | 92 | 1 | A |
| pre-1945 | | | | | | | | 75 | 4 | C |
| 18 Jan 1946 | | 61 | 14 | 2 | | | | 77 | 1 | A |
| 12 Dec 1948 | | 92 | 4 | | | | 1 | 97 | 1 | A |
| 16 Apr 1949 | | | | | | | | 28 | 1 | A |
| 1 Oct 1949 | | | | | | | | 10 | 1 | A |
| 4 Feb 1951 | | | | | | | | 44 | 1 | A |
| 20 Nov 1955 | | 81 | 19 | | | | | 100 | 2 | A |
| 25 Nov 1955 | | 19 | 11 | | | | | 30 | 2 | A |
| 27 Dec 1955 | | 16 | 16 | | | | | 32 | 2 | A |
| 18 Jan 1957 | | | | | | | | 32 | 1 | A |
| 29 Nov 1958 | | 34 | 7 | | | | | 41 | 2 | A |
| 30 Dec 1960 | | | | | | | | 30 | 1 | A |
| 5 Mar 1961 | | | | | | | | 11 | 1 | A |
| 16 Oct 1961 | | | | | | | | 7 | 1 | A |
| 19 Oct 1962 | | | | | 24 | | | 24 | 1 | A |
| 1 Nov 1963 | | | | | | | | 20 | 1 | A |
| 8 Jan 1965 | | | | | | | | 12 | 1 | A |
| 10 Dec 1965 | | | | | | | | 26 | 1 | A |
| 10 Nov 1966 | | 37 | 8 | | | | | 45 | 1 | A |
| 9 Apr 1985 | | 145 | 3 | | | | | 148 | 8 | B |
| 5 Mar 1986 | 3 | 180 | 17 | | | | | 200 | 8 | B |
| 23 Feb 1988 | | 3 | 26 | | | 1 | 6 | 36 | 8 | B |
| 24 Jan 1991 | 16 | 194 | 7 | | 7 | | | 224 | 8 | B |
| 20 Mar 1992 | | 264 | 11 | | | | 3 | 278 | 8 | B |
| 17 Mar 1994 | | 212 | 10 | | | | 5 | 227 | 8 | B |
| 27 Jan 1998 | | 276 | | | | 1 | 23 | 300 | 6 | B |

the mine were halted in the late 1920s. Although first identified as a hibernaculum in 1992, Greeley Talc Mine has consistently contained large numbers of *M. lucifugus*, and is currently the second largest hibernaculum in Vermont (Table 4). It also consistently houses large numbers of *M. septentrionalis* (up to 56 bats). *E. fuscus* was recorded there for the first time in 1998-99. (A few *E. fuscus* were observed in a nearby mine shaft in years prior to 1998-99, but never before in the talc mine itself; S. Trombulak, pers. obs.). Prior to 1998-99, few *M. leibii* and *P. subflavus* were observed at this site, but both species increased dramatically that year. *M. sodalis* has never been recorded.

All other Vermont hibernacula. No other hibernacula have been inventoried long enough to yield meaningful trends (Table 4). As a whole, these hibernacula exhibited similar trends during the 1990s: where individuals were identified to species, a majority of the bats were *M. lucifugus*, with only a few *M. leibii*, *M. septentrionalis*, *E. fuscus*, and *P. subflavus* recorded. *M. sodalis* was not recorded in any of these surveys, although one *M. sodalis* reportedly was collected at Skinner Hollow Cave in 1950 (Fichtel 1992).

DISCUSSION

Four aspects of the available data limit our ability to assess trends in wintering bat populations in Vermont. First, records only extend back to 1934. This was a time of large-scale reforestation throughout Vermont following the height of forest clearing in the 1880s (Klyza and Trombulak 1999). Thus, the earliest records cannot serve as a baseline for wintering bat populations as they were influenced in unknown ways by historical changes in the landscape.

Table 3. Census estimates of bats at Nickwacket Cave, Rutland Co., Vermont. Species abbreviations are as in Table 1. Source and method codes follow those described in the Methods section of the text.

| Date | <i>M. lei.</i> | <i>M. luc.</i> | <i>M. sep.</i> | <i>M. sod.</i> | <i>M. spp.</i> | <i>E. f.</i> | <i>P. s.</i> | Total | Source | Method |
|-------------|----------------|----------------|----------------|----------------|----------------|--------------|--------------|-------|--------|--------|
| 10 Nov 1934 | | 9 | | 121 | | | | 130 | 1 | A |
| 22 Feb 1935 | | 104 | | 246 | | | | 350 | 1 | A |
| 3 Apr 1935 | | 119 | | 149 | | 1 | | 269 | 1 | A |
| 30 Nov 1935 | | 38 | | 268 | | 3 | | 309 | 1 | A |
| 4 Apr 1936 | | 103 | | 192 | | | | 295 | 1 | A |
| 26 Nov 1936 | | 24 | | 188 | | 5 | | 217 | 1 | A |
| 7 Apr 1937 | 1 | 129 | | 105 | | 3 | | 238 | 1 | A |
| 12 Oct 1937 | | 8 | | 14 | | 3 | | 26 | 1 | A |
| 4 Dec 1937 | | 22 | 1 | 89 | | 1 | | 113 | 1 | A |
| 10 Apr 1938 | | 76 | | 157 | | 1 | | 234 | 1 | A |
| pre-1940 | | 136 | 2 | 241 | 1 | 5 | | 385 | 3 | D |
| 3 Mar 1940 | | 59 | | 3 | | | | 62 | 1 | A |
| 8 Dec 1940 | | 59 | | 12 | | 1 | | 385 | 2 | A |
| 1 Mar 1942 | | 29 | | 6 | | 3 | | 38 | 2 | A |
| pre-1945 | | | | | | | | 300 | 4 | C |
| 22 Jan 1946 | 2 | 30 | 2 | 4 | | 2 | | 40 | 1 | A |
| 14 Nov 1948 | | 12 | | 2 | | 1 | | 14 | 1 | A |
| 29 Dec 1955 | 3 | 21 | 11 | | | 7 | | 42 | 2 | A |
| 1 Dec 1989 | | 20 | 6 | | | | | 26 | 8 | B |
| 1 Feb 1992 | | 28 | 7 | | | 10 | | 45 | 7 | B |
| 10 Dec 1992 | | 29 | | | | 4 | | 33 | 6 | B |
| 11 Feb 1999 | | 27 | 3 | | 3 | 21 | | 54 | 6 | B |

Table 4. Census estimates of bats at all other known hibernacula in Vermont. Species abbreviations are as in Table 1. Source and method codes follow those described in the Methods section of the text.

| Hibernaculum Date | <i>M. lei.</i> | <i>M. luc.</i> | <i>M. sep.</i> | <i>M. sod.</i> | <i>M. spp.</i> | <i>E. f.</i> | <i>P. s.</i> | Total | Source | Method | |
|----------------------|----------------|----------------|----------------|----------------|----------------|--------------|--------------|-------|--------|--------|---|
| Ely Copper Mine | | | | | | | | | | | |
| 9 Apr 1937 | 7 | 132 | 66 | 13 | | 28 | 3 | 249 | 2 | A | |
| 8 Nov 1983 | | 445 | 7 | | | 24 | | 476 | 8 | B | |
| 8 Apr 1992 | 8 | 487 | 22 | | | 44 | | 561 | 7 | B | |
| 5 Jan 1993 | 4 | 380 | 4 | | 243 | 163 | 3 | 797 | 6 | B | |
| 17 Jan 1994 | 9 | 340 | 70 | | 173 | 96 | 6 | 694 | 6 | B | |
| 3 Feb 1998 | 14 | 454 | 66 | | | 103 | 2 | 639 | 6 | B | |
| Quarry Cave | | | | | | | | | | | |
| 4 Feb 1950 | | 98 | | | | 1 | 1 | 100 | 1 | A | |
| 14 Jan 1955 | | 175 | | | | 1 | 1 | 177 | 1 | A | |
| 16 Apr 1966 | | 157 | 2 | | | | | 159 | 1 | A | |
| 14 Dec 1991 | 1 | 326 | 2 | | | 6 | 6 | 341 | 7 | B | |
| Greeley Talc Mine | | | | | | | | | | | |
| 30 Jan 1992 | 7 | 834 | 31 | | 3 | | 2 | 877 | 7 | B | |
| 16 Dec 1992 | | 585 | 6 | | | 382 | 2 | 975 | 6 | B | |
| 29 Dec 1993 | | 240 | 56 | | | 681 | 4 | 981 | 6 | B | |
| 26 Jan 1999 | 25 | 251 | 12 | | | 394 | 1 | 86 | 769 | 7 | B |
| Brandon Silver Mine | | | | | | | | | | | |
| 10 Dec 1992 | 2 | 49 | 4 | | | 2 | 6 | 63 | 6 | B | |
| 30 Dec 1993 | | 58 | 17 | | | 2 | 5 | 82 | 8 | B | |
| 11 Feb 1999 | 4 | 100 | | | 20 | 9 | 2 | 135 | 6 | B | |
| Wyman's Cave | | | | | | | | | | | |
| 8 Apr 1937 | | 14 | 4 | | | | 5 | 23 | 2 | A | |
| Morris Cave | | | | | | | | | | | |
| Feb 1989 | ? | | | | | | | 120 | 7 | B | |
| ? Jan 1992 | | | | | | | | 101 | 7 | B | |
| Argonaut Mine | | | | | | | | | | | |
| 26 Mar 1992 | | 51 | 5 | | 28 | | 2 | 86 | 7 | B | |
| Hammondsville Mine | | | | | | | | | | | |
| 26 Mar 1992 | | 11 | | | | 74 | | 85 | 7 | B | |
| Camp Brook | | | | | | | | | | | |
| 1 Feb 1992 | | 40 | 12 | | | | | 52 | 7 | B | |
| Pike Hill Mines | | | | | | | | | | | |
| 14 Feb 1992 | | 20 | | | 5 | 13 | | 38 | 7 | B | |
| Clifton Adit | | | | | | | | | | | |
| 5 Feb 1992 | | 22 | | | | 7 | | 29 | 7 | B | |
| Rousseau Talc Mine | | | | | | | | | | | |
| 2 Feb 1992 | | 27 | | | | | | 27 | 7 | B | |
| Kents Cave | | | | | | | | | | | |
| 1 Apr 1991 | | 9 | 1 | | | 1 | 1 | 12 | 7 | B | |
| Milton Cave | | | | | | | | | | | |
| 22 Feb 1992 | | | | | | 5 | | 5 | 7 | B | |
| Bristol Cave | | | | | | | | | | | |
| 2 Feb 1991 | | 3 | 1 | | | | | 4 | 7 | B | |
| 1867 Cave | | | | | | | | | | | |
| 9 Feb 1999 | 17 | 6 | | | | | 2 | 25 | 6 | B | |
| Porcupine Caves | | | | | | | | | | | |
| 19 Feb 1997 | | | | | | | | 32 | 6 | B | |
| Skinner Hollow Cave | | | | | | | | | | | |
| ? Dec 1998 | | | | | | | | 100 | 6 | C | |
| Fox Gold Mine | | | | | | | | | | | |
| 15 Nov 1998 | | | | | | | | 300 | 6 | C | |
| Barrel Cave | | | | | | | | | | | |
| ? Feb 1997 | | | | | | | | 30 | 6 | C | |

Second, surveys conducted since the early 1930s were not made at regular intervals, resulting in long periods for which no information on wintering population sizes is available. Thus, the time at which a change in a population occurred often can only be identified to within a couple of decades.

Third, survey techniques have varied greatly. For example, during the 1930s-1960s, Griffin, Hitchcock, and Davis banded large numbers of bats, whereas during the 1980s-present, surveys in Vermont did not involve banding. Comparison of census values collected by different techniques is difficult; counts of banded bats are more likely to undersample a hibernaculum than total counts, leading to an inherent tendency for population estimates to increase based on changes in census method that was employed.

Fourth, intrayear variation in population estimates can be quite large. For example, Hitchcock and Davis banded bats in Dorset Cave 10 times during 1961-62, and based on banding records, reported populations ranged from 48 to 814 bats (Table 1). Regardless of whether this variation reflects real changes in population size or of sampling error, it underscores the problem of calculating population size based solely on a single count.

Despite these limitations, several patterns have emerged from the data. First, during the 1930s, *M. sodalis* was the most abundant wintering bat species in Vermont, yet it declined by an order of magnitude at all four hibernacula where it was recorded (Dorset Cave, Plymouth Caves, Nickwacket Cave, and Ely Copper Mine). This species disappeared entirely from three of these hibernacula and presently exists (albeit in low numbers) only at Dorset Cave.

Reasons attributed to declines reported throughout their range (eventually resulting in its listing as an endangered species) include human disturbance at hibernacula and degradation of forestland used as summer habitat (USFWS 1999). Whether these factors explain the decline in Vermont cannot be known. The decline observed from the 1930s to the present may reflect large-scale deforestation during the 1800s, which at its peak involved the clearing of over 60% of the state (Klyza and Trombulak 1999), a pattern that occurred throughout the northeastern U.S. (Williams 1989) within the summering range of bats likely to hibernate in Vermont (Davis and Hitchcock 1965; Griffin 1940b, 1945). Although forest cover increased throughout this region during the 1900s (Litvaitis 1993), current forest management practices do not promote the return of standing dead trees favored by *M. sodalis* as maternity sites (Callahan et al. 1997). It is also possible that the decline is simply a random fluctuation in a population at the northern edge of its geographic range.

The second pattern is the increase in number of *M. lucifugus* at many hibernacula since the 1930s. This increase is not easily explained by methodological differences. In the 1930s, low numbers of *M. lucifugus* were reported at the same time as high numbers of *M. sodalis*, showing that the technique used by Griffin, Hitchcock, and Davis was capable of

indicating large numbers. Their field notes do not suggest that they intended to preferentially capture *M. sodalis* over *M. lucifugus*; thus, the data probably indicate an actual increase in numbers present.

The increase could be due to random fluctuations or to a positive response to environmental factors either during the summer or winter. It cannot be shown whether the construction of “bat-friendly” gates at three of the hibernacula have led to an increase in bat populations. Populations have increased only at hibernacula that have been gated or have restricted access (Dorset Cave, Plymouth Caves, Ely Copper Mine, and Quarry Cave) and have declined at the one ungated hibernaculum with open access (Nickwacket Cave). However, the increase in *M. lucifugus* at both Dorset and Plymouth Caves predate the construction of their gates. Perhaps the increase in *M. lucifugus* reflects an increase in suitable summer habitat, affecting reproduction and/or survival.

The other bat species known to hibernate in Vermont—*M. leibii*, *M. septentrionalis*, *E. fuscus*, and *P. subflavus*—appear not to have been common at any time since the 1930s. Whether their populations declined prior to the 1930s and have merely maintained themselves at low levels since then is difficult to ascertain.

Two data points in the available records deserve particular attention. Analyzing mark-recapture data of bats over two separate periods (1960-61 and 1961-62), Davis and Hitchcock (1965) estimated the population at Dorset Cave to be $300,000 \pm 30,000$. This estimate is two orders of magnitude greater than any other count made at this hibernaculum. Whether this estimate is accurate has long been a matter of speculation among biologists in Vermont. Davis and Hitchcock (1965) interpreted the estimate to indicate that the portion of the cave accessible to humans, hence the portion included in all other surveys, is only a small part of a vastly greater cave system accessible to the bats. The rapid turnover of bats they observed in the accessible chamber supports this interpretation. For example, on 15 April 1962, Hitchcock banded 186 *M. lucifugus* in this chamber. The next day he captured 83 *M. lucifugus* in the same place, only one of which was banded; all 185 other bats banded the previous day were no longer present. Either the new population of 82 bats entered the cave from the outside as 185 bats departed (which Davis and Hitchcock discount) or they emerged from other locations within the cave.

Davis and Hitchcock (1965) based their estimate on the Lincoln Index, which is sensitive to changes in population size and parameters such as mortality, reproduction, immigration, and emigration. The Lincoln Index assumes a closed population, but studies elsewhere in New England indicate that *M. lucifugus* begins to arrive at maternity colonies by early April (T.H. Kunz personal communication), well before the time during which Davis and Hitchcock made their estimate. Because they did not test their assumptions about mortality, reproduction, and movement in the population at Dorset Cave, but simply assumed values based on studies of other bat populations, their estimate is open to considerable question.

A reasonable interpretation is that, at least in the 1960s, many more bats were in Dorset Cave than were counted at any one time in the portion accessible to humans. Whether this pattern exists today can only be determined by extensive monitoring of movements of banded or otherwise uniquely marked bats through the small passageways at the back of the deepest chamber accessible to humans. From the perspective of understanding trends in wintering populations of bats, however, Davis and Hitchcock's estimate cannot be used as a baseline value for comparison.

In summary, despite the limitations of the available data, it appears that in Vermont since the 1930s, wintering populations of *M. sodalis* have dramatically declined; wintering populations of *M. lucifugus* have increased; and wintering populations of all other species have remained consistently small and stable. The causes of these trends or their relationship to trends prior to the 1930s are unknown.

Biologists who currently survey wintering bat populations in Vermont should consider the following prioritized tasks: First, continue to regularly census all of the hibernacula listed here at a consistent time of year. Each hibernaculum should be censused once every three years, preferably between early January and early February to minimize the chance that counted bats are transient to the hibernaculum (Kunz et al. 1996). Second, investigate hibernacula that anecdotally have been reported, especially mines that have recently been abandoned. Third, continue to work with the Vermont Cavers Association to encourage avoidance of hibernacula during the winter. Last, although it is a formidable task, census maternity colonies (Kunz et al. 1996) to better understand the species present during the summer and the relationship between summer and winter population trends.

ACKNOWLEDGMENTS

This summary was made possible by the countless surveys conducted over many decades. Hal Hitchcock, Don Griffin, and Wayne Davis were responsible for all data collected from 1934 to 1966, and our debt to them for their detailed notes is enormous. Data from the 1980s and 90s were collected by C. Fichtel, J. Freeman, A. Hicks, C.W. Kilpatrick, K. O'Classen, S. Parren, and two authors of this report (SCT and MD). We are grateful to them for their work and for making their data available to us. We also thank S. Parren of the Vermont Nongame and Natural Heritage Program and A. Ruesink of the Vermont Nature Conservancy for their help in searching records housed in their offices. We also thank Tom Kunz and two anonymous reviewers for their many editorial improvements.

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