THERMAL REQUIREMENTS DURING HIBERNATION

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Abstract

We monitored temperatures for up to 2 years at 15 of the most important sites for hibernation of Indiana bats (*Myotis sodalis*). Comparison of temperatures at successful and unsuccessful sites revealed that populations occupying roosts with midwinter (December–February) temperatures of 3.0–7.2 C increased by 97,339 bats over the past 20 years, whereas populations hibernating at temperatures outside this range decreased by 185,117 animals. In all but the northernmost range of Indiana bats, caves and mines required for successful hibernation must provide chimney-effect air flow between at least two entrances, store sufficient cold air to meet the bats' hibernation needs, and buffer the internal environment to minimize risk of freezing. Protection of caves and mines providing these exceptional characteristics and restoration of appropriate temperatures in altered sites is essential for recovery of the Indiana bat.

Key words: caves, hibernation, Indiana bat, management, mines, *Myotis sodalis*, population, temperature

Introduction

In the early 1800s, the Indiana bat (*Myotis sodalis*) ranked as one of North America's most abundant mammals, with possibly millions occurring in single caves (Silliman et al. 1851, Tuttle 1997). Nonetheless, by 1980, less than 700,000 bats remained, and size of the population fell to 382,000 bats by 2001 (Clawson 2002). The greatest losses occurred in discrete, unrelated episodes that rendered overwintering caves no longer suitable for hibernation, mostly due to reductions in size of a cave's entrance, which ultimately raised internal temperatures (Humphrey 1978). Increases of as little as 2°C resulted in severe reduction of a cave's population (Tuttle 1977). Humphrey (1978), however, concluded that such losses were reversible, because restoration of acceptable temperatures led to prompt recovery at some sites.

Nevertheless, specific temperatures required by Indiana bats during hibernation are not understood completely. Our purpose is to compare annual patterns of temperature in hibernacula where populations of Indiana bats have been successful with temperatures in hibernacula where populations are declining. In addition, we indicate correctable deficiencies at important sites of current and past use and suggest characteristics for evaluating roosts for protection or restoration.

Methods

We evaluated patterns of temperature at 15 of the most important, current and past, hibernating sites of Indiana bats, in caves and mines of Illinois, Indiana, Kentucky, Missouri, Tennessee, and Virginia (Fig. 1). To monitor temperature, we used 60 dataloggers (Model Hobo Pro Temp–RH, Onset Computer Corporation, Pocasset, Massachusetts) in 1998 and 58 instruments in 1999. A datalogger was installed within each hibernaculum, at each site that was favored by hibernating Indiana bats, either currently or in the past. Another datalogger was positioned outside each cave or mine to monitor external conditions, except at the Magazine Mine. All instruments recorded data at 3-h intervals. Although dataloggers recorded temperature and relative humidity, we found no evidence of an effect of humidity beyond that indicated by temperature, so humidity was not included in our analyses.

Most dataloggers were installed in July 1998 and downloaded in July, August, or September 1999 and again in 2000. When dataloggers were installed in 1998 (except at the Magazine Mine), temperatures of the air and wall of the cave also were measured at each roosting site, using a portable digital thermometer (Model 2300-PNC5, IMC Instruments, Inc., Menomonee Falls, Wisconsin) that was recalibrated prior to each field trip. Temperatures indicated by the dataloggers at time of installation differed, on average, by less than 0.3 °C (range = 0.0–0.4°C; n = 31 sites) from wall

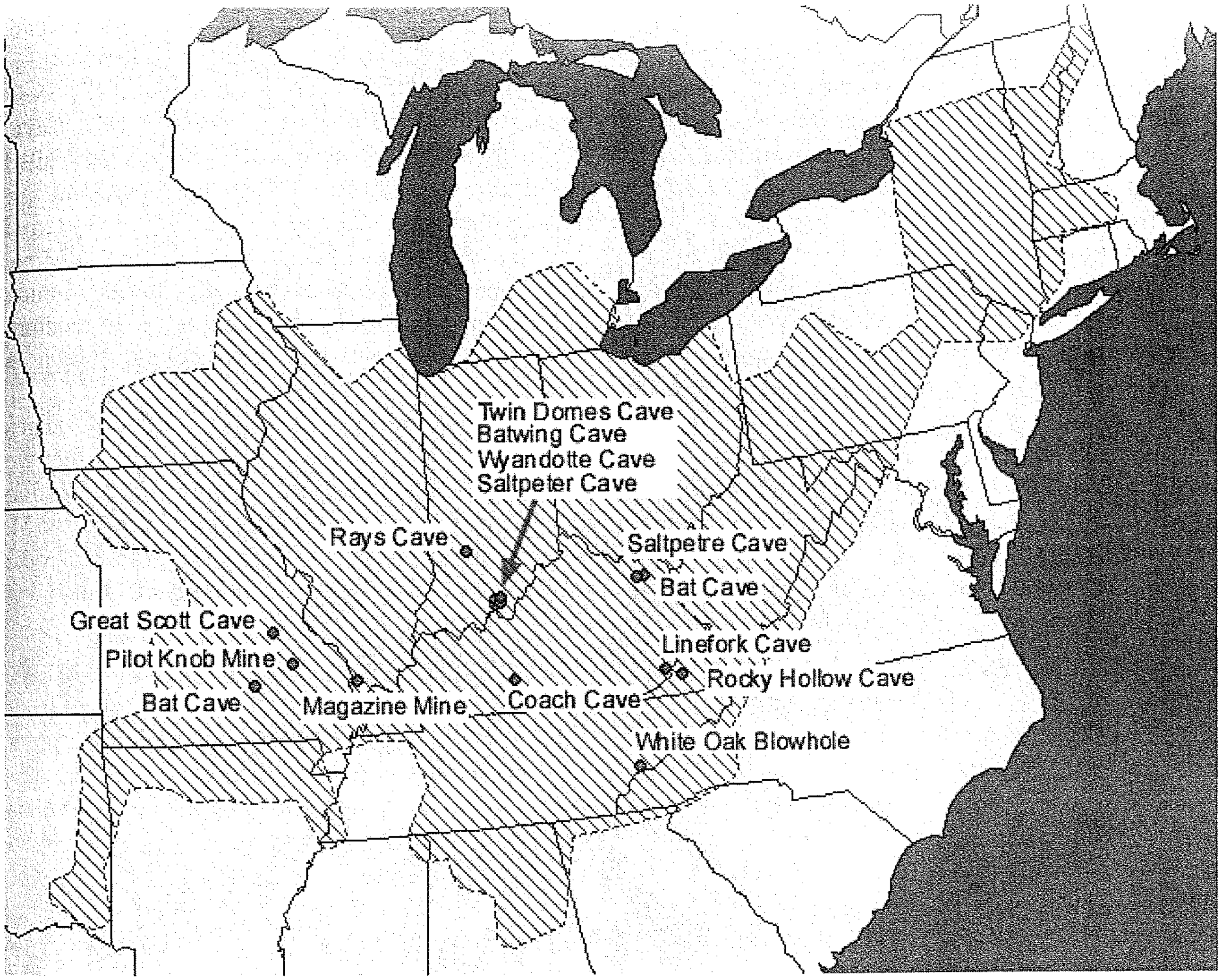

Figure 1.—Range of the Indiana bat and location of hibernacula in which we monitored temperature.

temperatures measured with the digital thermometer. At time of downloading in 1999, a sample of 10 dataloggers from five caves provided readings that again averaged within 0.3°C (0.0–0.7°C) of those obtained with the digital thermometer. In addition, controlled tests of random batches of dataloggers yielded similar average variation (0.3°C).

We also evaluated ability of each hibernaculum to buffer the internal environment against changes in the external environment, using an index of temperature variability:

$$V = (T_{\text{max-roost}} - T_{\text{min-roost}})/(T_{\text{max-surface}} - T_{\text{min-surface}}),$$

where T represents maximum or minimum temperature recorded at the roost or outside the hibernaculum, as indicated by the subscripts. A small value of V indicates a stable internal environment that varies little with changing external conditions; a large value of V indicates a less stable, more variable, internal environment.

Results

In both 1998–1999 and 1999–2000, 43 dataloggers recorded temperatures year-round. Although 17 loggers failed the 1st year and 15 malfunctioned during the 2nd year, only two of 32 malfunctions were caused by operator error. The others were due to problems such as moisture bypassing past dirty seals, moisture entering through cracked housings, or an increased internal resistance that developed within the lithium batteries initially supplied by the manufacturer. Nevertheless, most failures occurred after the hibernation season, thus minimizing loss of data.

Overall, temperatures at the 15 hibernacula in midwinter (December–February) were similar between years (Tables 1–4). Average mean temperature within hibernacula was 6.8°C in 1998–1999 and 6.5°C in 1999–2000, while average mean surface temperatures were

3.5°C and 3.0°C for the same periods. Midwinter means at individual hibernacula varied by less than 1°C between years at all locations, except Great Scott Cave. In addition, changes between years in mean midwinter temperature inside hibernacula always were in the same direction as changes on the surface, again with the exception of Great Scott Cave. Temperature in Great Scott Cave decreased by 3.6°C between years, despite an increase of 0.4°C in surface temperature, following reopening of a previously blocked entrance (Fig. 2). Given the similarity in temperatures between years, we typically restrict further discussion to data obtained in the 1st year for simplicity.

Individual caves differed by almost a factor of eight in ability to buffer changes in external temperature, as indicated by the index of variability. In December–February 1998–1999, the index of variability for Rocky Hollow and Wyandotte caves was 0.05; White Oak Blowhole, 0.06; Saltpeter Cave, 0.08; Saltpetre Cave, 0.09; Bat Cave, Kentucky, 0.10; Pilot Knob Mine, 0.11; Linefork Cave, 0.12; Great Scott Cave, 0.13; Twin Domes Cave, 0.15; Ray's Cave, 0.16; Coach Cave, 0.17; and Bat Cave, Missouri, 0.38. Dataloggers failed during the first winter at Batwing Cave, but the comparable index in 2000 was 0.02. External temperatures were not monitored at the Magazine Mine, so we could not calculate an index for it. Annual temperature profiles for some caves of low-to-medium variability (medium-to-high stability) are shown in Figure 3.

We also examined roost temperatures and changes in population size at seven caves and mines that we monitored, using data on temperature and population provided by the Indiana Bat Recovery Team (Table 5). Hibernacula where populations grew provided roost temperatures of 3.0–7.2°C, whereas populations fell at

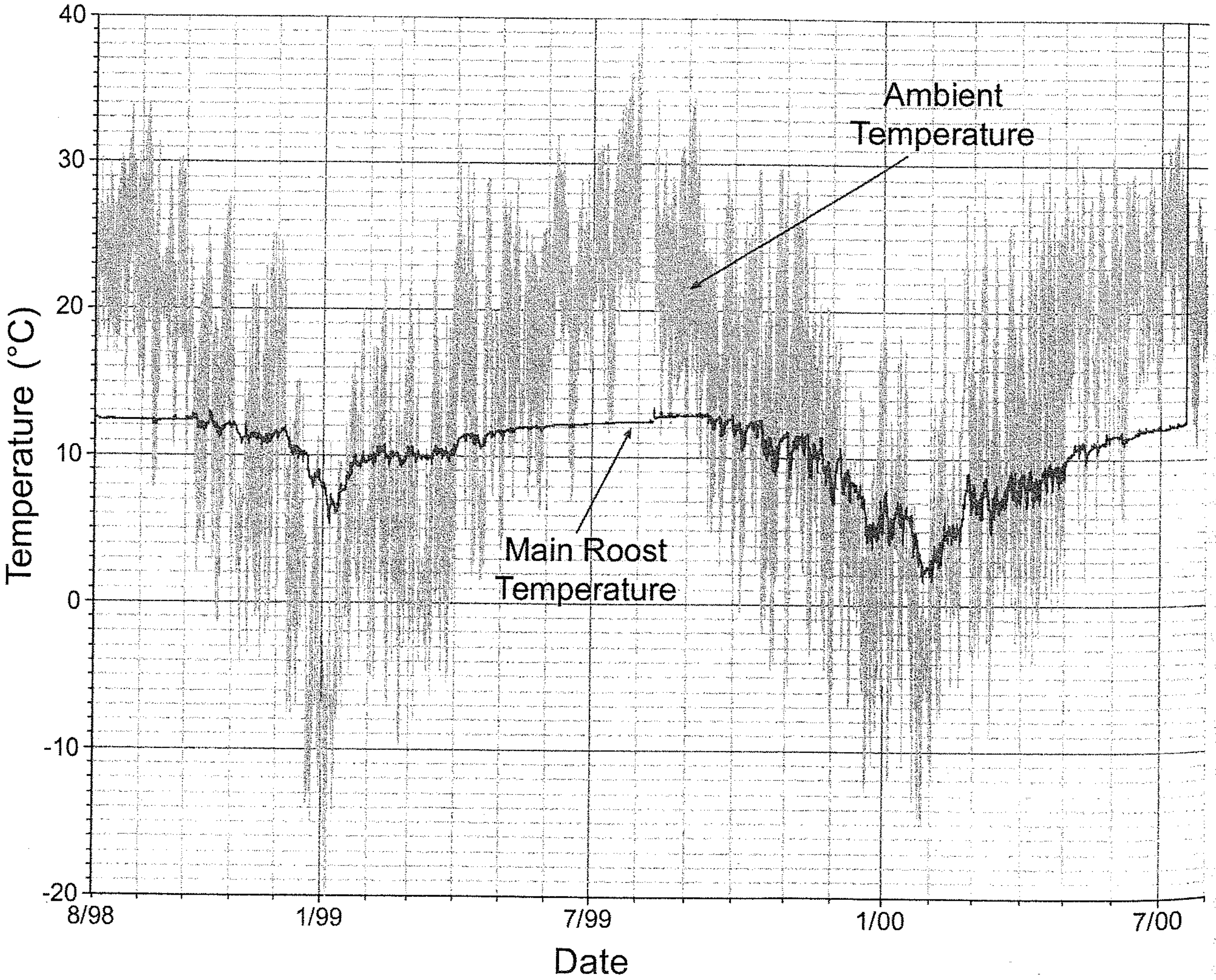

Figure 2.—External ambient temperatures and temperature at the main hibernation site in Great Scott Cave, Missouri, before and after opening a blocked entrance in September 1999.

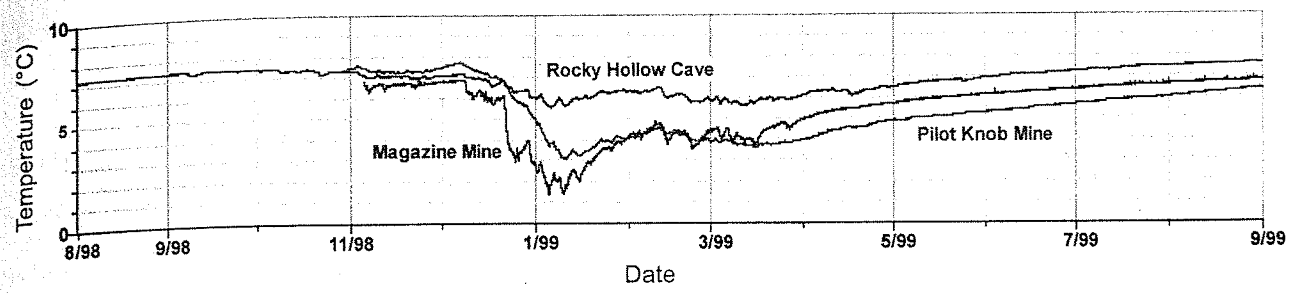

Figure 3.—Annual profiles of temperature for unusually successful hibernacula of the Indiana bat.

hibernacula with temperatures outside that range. At Great Scott Cave, the population increased by 22,800 bats between 1976 and 1979, when internal temperatures averaged 4.8°C, but declined by 46,625 bats between 1980 and 1997, when temperatures averaged 8.1°C, following closure of an entrance.

Discussion

The ideal situation—Caves that historically sheltered the largest populations of hibernating Indiana bats, without exception, were those that provided the largest volumes and structural diversity, ensuring the most stable internal temperatures, over the widest ranges of external temperature, with the least likelihood of freezing. Such caves also provide chimney-effect airflow, typically through multiple entrances, and trap and store cool winter air in low areas (Tuttle and Stevenson 1978). Within such caves, hibernating Indiana bats prefer temperatures of 3–6°C in midwinter (Hall 1962, Henshaw and Folk 1966). Although metabolism of hibernating bats is lowest at temperatures slightly above 0°C, Indiana bats are forced to increase production of metabolic heat or arouse from torpor as temperatures fall to 0°C and below. They also arouse in response to abrupt changes in ambient temperature (Davis and Reite 1967, Henshaw and Folk 1966). Thus, roosts with the most stable temperatures should result in fewest arousals, thereby minimizing energy expenditure (Thomas et al. 1990).

Recent and historic populations of hibernating Indiana bats support these conclusions. For example, Mammoth Cave is the world's largest and most complex cave system, with a length of 571 km. Staining left on walls and ceilings of Mammoth Cave (Toomey et al. 2002) suggests that this cave once sheltered the largest hibernating population of Indiana bats, conservatively estimated at ca. 10 million animals (Tuttle 1997). In addition, comparison of other populations of Indiana bats that remained stable or increased with those that declined over the past 20 years (Table 5) strongly implies that inappropriate temperatures at hibernating sites are a primary cause of decline, as suggested by Humphrey (1978).

We believe that temperature profiles documented for Rocky Hollow Cave, Magazine Mine, and Pilot Knob Mine (Fig. 3) most closely approximate ideal hibernating conditions for the Indiana bat. Through the entire annual cycle (not just midwinter) of 1998–1999, Rocky Hollow Cave remained at 5.6–7.6°C; Magazine Mine, at 1.4–6.9°C; and Pilot Knob Mine, at 3.1–7.7°C. Such stability within the Indiana bat's preferred range of hibernating temperatures is achieved through the buffering effects of very large volume.

Not surprisingly, these three sites have histories of extraordinary success at supporting hibernating populations of Indiana bats. Rocky Hollow Cave contained one of North America's largest populations prior to the onset of intense human disturbance, and the population of Indiana bats at the Magazine Mine grew to nearly 15,000 bats in only a few years after the mine closed (Kath 2002). Pilot Knob Mine also rapidly attracted a hibernating population of at least 100,000 Indiana bats soon after it became available, though subsequent collapse has prevented further censuses (Clawson 2002).

Effects of restoring airflow—Comparison of annual cycles before and after reopening a blocked entrance illustrates that management efforts can restore unacceptably altered roost temperatures. The population at Great Scott Cave (Fig. 2, Tables 1, 3, and 5) was growing prior to blockage of its second entrance in summer 1978, after which roost temperature rose by at least 3.3°C and the population decreased by 80%. After the entrance was reopened in September 1999, average internal temperatures decreased by 3.6°C, even though outside temperatures averaged 0.4°C higher in winter 1999–2000 than in the previous winter. Consequently, temperatures at the roost were within the ideal, 3–6°C

Table 1.—Ambient temperatures (°C) from 1998–1999, measured at roosting sites within major hibernacula of the Indiana bat.

Hibernaculum	October–November		December–February		March–April	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Illinois						
Magazine Mine	6.7	6.3–6.9	4.2	1.4–6.9	4.9	3.7–5.7
Indiana						
Batwing Cave	8.1	8.0–8.2	7.6	7.3–8.2	7.1	7.0–7.3
Rays Cave[a]	10.5	8.6–12.5	8.1	3.6–11.4	—	—
Saltpeter Cave	10.3	9.5–11.0	8.2	6.5–10.1	8.1	7.3–8.9
Twin Domes Cave[a]	8.7	7.1–9.9	5.7	2.5–9.2	—	—
Wyandotte Cave	10.3	9.9–10.8	9.2	8.2–10.5	9.3	8.8–9.8
Kentucky						
Bat Cave	10.0	8.2–11.6	8.2	5.8–10.2	8.7	7.4–9.8
Coach Cave	9.1	7.4–10.5	5.8	2.4–9.5	6.4	4.0–8.6
Linefork Cave	8.2	7.4–8.9	6.1	4.0–8.1	5.9	4.4–7.0
Saltpetre Cave	9.7	8.3–12.4	7.2	5.6–9.7	6.7	5.5–8.4
Missouri						
Bat Cave	7.9	3.0–11.7	1.9	-8.3–8.0	4.6	-0.7–7.3
Great Scott Cave	11.8	10.8–13.1	9.4	5.4–12.0	10.7	9.5–11.8
Pilot Knob Mine	7.4	7.3–7.6	5.0	3.1–7.7	4.2	3.6–4.9
Tennessee						
White Oak Blowhole	9.8	9.1–10.1	8.8	7.4–9.6	8.7	8.0–9.3
Virginia						
Rocky Hollow Cave	7.2	7.0–7.5	6.3	5.6–7.2	6.1	5.6–6.5

[a] Missing data resulted from premature failure of datalogger.

Table 2.—Surface temperatures (°C) from 1998–1999, measured outside major hibernacula of the Indiana bat.

Hibernaculum	October–November		December–February		March–April	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Illinois						
Magazine Mine[a]	6.1	1.5–8.1	1.6	-9.5–8.6	4.4	-1.3–7.3
Indiana						
Batwing Cave[b]	12.9	-0.8–24.8	—	—	—	—
Rays Cave	10.0	-5.0–26.7	1.7	-24.7–22.8	8.6	-6.6–29.1
Saltpeter Cave	11.7	-3.4–26.8	3.7	-19.5–23.1	10.5	-6.3–29.1
Twin Domes Cave	11.1	-3.3–24.8	3.2	-19.2–24.3	10.2	-6.8–33.7
Wyandotte Cave	11.7	-3.4–26.8	3.7	-19.5–23.1	10.5	-6.3–29.1
Kentucky						
Bat Cave	9.7	-6.1–27.5	2.9	-18.0–26.6	9.2	-8.8–32.2
Coach Cave	12.7	-1.4–28.4	4.9	-14.9–25.8	11.4	-3.5–30.8
Linefork Cave	12.1	-1.0–25.7	4.5	-13.2–20.2	9.9	-6.0–30.5
Saltpetre Cave	9.7	-6.1–27.5	2.9	-18.0–26.6	9.2	-8.8–32.2
Missouri						
Bat Cave	13.2	-1.9–29.0	4.5	-17.0–25.4	11.5	-6.2–32.3
Great Scott Cave	11.8	-4.1–27.7	3.2	-25.5–24.7	10.4	-8.1–31.3
Pilot Knob Mine	10.5	-1.3–33.3	3.3	-18.1–24.5	11.3	-6.7–35.4
Tennessee						
White Oak Blowhole	12.0	-2.6–33.8	6.4	-10.9–27.6	12.0	-4.7–43.5
Virginia						
Rocky Hollow Cave	10.9	-2.2–23.9	3.0	-14.4–17.4	8.1	-7.0–17.0

[a] Datalogger was not installed until 5 November 1998. Temperatures are for the entrance passage, and they are not actual surface temperatures.

[b] Missing data resulted from premature failure of datalogger.

Table 3.—Ambient temperatures (°C) from 1999–2000, measured at roosting sites within major hibernacula of the Indiana bat.

	October–November		December–February		March–April	
Hibernaculum	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	Range
Illinois						
Magazine Mine[a]	6.9	5.8–7.4	—	—	5.4	4.4–6.0
Indiana						
Batwing Cave	8.2	8.1–8.3	7.6	7.1–8.2	7.4	7.3–7.5
Rays Cave	10.1	5.7–11.9	7.1	3.4–10.3	9.3	7.2–10.5
Saltpeter Cave	10.2	9.1–10.7	8.0	6.4–9.6	8.4	7.9–9.0
Twin Domes Cave[b]						
Wyandotte Cave	10.3	9.8–10.6	9.1	8.2–10.1	9.5	9.1–9.8
Kentucky						
Bat Cave	10.0	8.1–11.4	7.5	4.5–9.8	9.3	8.3–10.2
Coach Cave	9.2	6.5–11.0	5.6	2.2–8.5	7.4	5.5–8.9
Linefork Cave	8.3	6.9–8.9	5.7	3.3–7.4	6.5	5.7–7.2
Saltpetre Cave	9.6	8.1–12.2	6.9	4.4–8.7	6.9	6.0–9.0
Missouri						
Bat Cave	6.4	0.3–9.0	1.4	-3.9–5.9	4.6	-0.4–6.4
Great Scott Cave	10.8	6.9–12.6	5.8	1.7–10.8	8.6	5.0–9.8
Pilot Knob Mine	7.4	7.2–7.7	5.5	3.9–7.6	4.9	4.5–5.4
Tennessee						
White Oak Blowhole	9.9	9.0–10.3	8.2	6.9–9.3	8.5	8.1–8.9
Virginia						
Rocky Hollow Cave	77.3	6.8–7.5	6.2	5.4–7.0	6.4	6.1–6.7

[a] Dataloggers were not recording during periods with missing data.

[b] Missing data resulted from premature failure of datalogger.

Table 4.—Surface temperatures from 1999–2000, measured outside major hibernacula, past and present, of the Indiana bat.

	October–November		December–February		March–April	
Hibernaculum	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	Range
Illinois						
Magazine Mine[a]	6.9	-1.0–9.4	—	—	5.3	-0.8–7.1
Indiana						
Batwing Cave	10.6	-7.9–25.9	2.3	-17.3–24.1	10.8	-5.1–27.5
Rays Cave	10.1	-7.4–24.9	1.2	-17.4–22.4	9.7	-9.0–25.9
Saltpeter Cave	12.1	-6.5–27.8	3.3	-16.1–25.7	11.9	-3.8–31.8
Twin Domes Cave[b]	11.5	-6.6–25.4	2.9	-16.8–27.5	11.6	-3.6–31.1
Wyandotte Cave	12.1	-6.5–27.8	3.3	-16.1–25.7	11.9	-3.8–31.8
Kentucky						
Bat Cave	10.0	-6.5–28.4	2.2	-19.2–28.7	11.0	-6.4–31.6
Coach Cave	12.6	-3.3–28.6	4.2	-13.2–30.1	12.8	-2.9–34.3
Linefork Cave	10.7	-2.6–18.7	2.5	-11.5–16.3	9.7	-1.6–20.4
Saltpetre Cave	10.0	-6.5–28.4	2.2	-19.2–28.7	11.0	-6.4–31.6
Missouri						
Bat Cave[c]						
Great Scott Cave	12.4	-8.4–29.8	3.6	-15.2–27.5	11.6	-9.2–32.8
Pilot Knob Mine	13.9	-4.4–38.9	4.2	-13.2–33.2	13.3	-3.7–35.6
Tennessee						
White Oak Blowhole	11.6	-3.4–31.8	5.4	-12.3–33.6	12.0	-2.8–38.8
Virginia						
Rocky Hollow Cave	10.0	-7.2–20.8	2.1	-16.4–22.3	9.6	-4.5–25.6

[a] Temperatures are for the entrance passage, and they are not actual surface temperatures.

[b] Dataloggers were not recording during periods with missing data.

[c] Datalogger was stolen, and data were not recovered.

range on 61 days during 1999–2000, greatly improving from only 1 day in the entire previous hibernating season.

We anticipate that the population at Great Scott Cave, with return of more appropriate hibernating temperatures, will again begin to grow, as happened at Wyandotte Cave. The entrance to this cave was mostly blocked by a masonry wall that was removed in 1977 (see fig. 4 in Currie 2002). Afterwards, temperatures in Wyandotte Cave decreased, and the population grew by 90% (Johnson et al. 2002, Richter et al. 1993). Nevertheless, temperatures in Wyandotte Cave (Tables 1 and 3) remain too high, in our opinion, to permit reestablishment of a historic-sized population of Indiana bats.

Staining on the walls and ceiling in Wyandotte Cave suggest a much larger past population that possibly numbered in the millions. The current population, despite encouraging recovery, is no more than a small fraction of its presumed former size. Results of temperature monitoring strongly suggest that this population could be expanded substantially with further lowering of internal temperature. Stability of internal temperature in Wyandotte Cave already is similar to that of Rocky Hollow Cave ($V = 0.05$ for both; Tables 1 and 3), probably contributing greatly to the level of recovery already achieved at Wyandotte Cave. An additional decrease of 5°C would further enable large numbers of bats to hibernate in traditional roosts beyond areas now disturbed by commercial tours in winter (Johnson et al. 2002), probably permitting even greater recovery.

Are we protecting marginal sites?—Knowledge of energetics during hibernation, historical conditions chosen by the largest hibernating populations, and temperature profiles that we provide, strongly suggest that a large proportion of currently protected sites are marginal, at best, in terms of long-term survival of the Indiana bat. To understand better what is required to rebuild historically large populations, one must consider the impact of known factors on the species' annual energy budget. When inappropriate temperatures or rapid fluctuations in temperature cause arousal and increase the cost of hibernation, less energy remains for surviving unusually stressful winters or unpredictable weather during spring migration.

Summer nursery roosts that provide marginally warm temperatures or that are distant from good feeding habitat result in extra energy expenditure and slower growth of young in insectivorous bats (Tuttle 1975, 1976a). Late fledging leads to low body mass in autumn (Humphrey et al. 1977), and this can make the cost of long-distance migration, already an important mortality factor, prohibitive (Tuttle 1975, 1976b; Tuttle and Stevenson 1977). Hibernation sites sheltering the largest populations of Indiana bats require the longest average migrations from suitable summer habitats, because these hibernacula serve animals from the largest geographic areas. Also, long autumn migrations may require as much energy as an entire winter of hibernation (Tuttle 1976b), so it seems that the very substantial costs of marginal hibernating conditions cannot be borne by bats having to make long migrations.

When hibernating conditions deteriorate and large populations decline due to significant disturbance and/or altered roost temperatures, a small proportion of the population usually survives in the now-marginal hibernaculum. Size of this proportion undoubtedly is determined by the amount of added costs that are imposed by the disturbance or altered microclimate during hibernation. In contrast, the relatively few bats that summer in more ideal conditions near the hibernaculum avoid the costs of autumn and spring migration, thereby conserving substantial energy that can be spent on hibernation, as well as on surviving unpredictable spring weather. Those that use less-than-optimal summer habitat or migrate long distances may not have sufficient energy available to meet the new demands and may succumb over winter.

Also, some small populations that continue using marginal caves appear stable only because of annual immigration of bats from more successful populations at more ideal hibernacula. For example, ca. 1,000–2,000 Indiana bats hibernated in Wyandotte Cave each winter before 1978, i.e., before removal of the wall that elevated winter temperatures. Richter et al. (1993), based on body-mass dynamics, estimated that survivorship of hibernating individuals at this time was not high enough to sustain the population and that apparent stability of the population at Wyandotte Cave actually was due to an influx of bats each year from other hibernacula. Their data suggested annual mortality rates of 45% during hibernation in Wyandotte Cave, compared with 1% in a cooler hibernaculum, Twin Domes Cave, which was located nearby.

Buffering climatic extremes—Although suitable roost-temperature profiles are important, a roost's ability to buffer climatic extremes is also critical. For example, our temperature profiles from Bat Cave, in Missouri, illustrate that it is a mortality trap. Although

Table 5.—Ambient temperature and population change at hibernacula of the Indiana bat obtained from the Indiana Bat Recovery Team.

			Number of Indiana bats		Population change at caves with different temperatures	
Hibernaculum	Period	Mid-winter temperature[a] (°C)	Beginning of period	Ending of period	3.0–7.2°C	8.1–10.9°C *or* 0.0–1.9°C
Indiana						
Ray's Cave	1985–1997	5.9, 4.2–7.5	12,200	51,365	+39,165	
Twin Domes Cave	1983–1998	3.7, 2.3–5.7	70,750	67,100	-3,650	
Wyandotte Cave	1952–1977[b]		12,500	2,500		-10,000
	1978–1997[c]	7.2, 6.0–8.0	2,500	25,424	+22,924	
Kentucky						
Bat Cave	1957–1997	4.5, 2.5–7.0	45,300	28,200	-16,500	
Coach Cave	1957–1960	4.5, 4.0–5.0	100,000	100,000	0	
	ca. 1965–1993	10.9, 10.5–11.4	100,000	33		-99,967
Missouri						
Bat Cave	1976–1979	4.6, 3.5–6.0	46,000	76,700	+30,700	
	1980–1989	1.9, 0.4–5.0	32,800	4,275		-28,525
	1991–1997	3.7, 1.8–5.9	4,275	6,175	+1,900	
Great Scott Cave	1976–1979	4.8, 2.8–8.2	46,600	69,400	+22,800	
	1980–1997	8.1, 4.5–11.8	58,500	11,875		-46,625
Total change in population					+97,339	-185,117

[a] Mean is given followed by the range. Data were obtained from the Indiana Bat Recovery Team; temperatures represented spot recordings made during censuses and were not the result of continuous recordings that were reported in Tables 1 and 3.

[b] Wall was installed in entrance in 1952 resulting in higher, but unrecorded temperatures.

[c] Wall was removed in 1977, restoring airflow.

Bat Cave provides ideal temperatures in autumn, it often falls well below freezing in winter, and Indiana bats attracted to this cave in autumn risk freezing to death before spring (Tables 1 and 3).

Our data suggest that some caves with currently stable or growing populations also are mortality traps that more seriously threaten survival of the species than do sites like Bat Cave, Missouri. Small, simple sites, such as Ray's Cave and Twin Domes Cave, may provide ideal internal temperatures over long-enough periods that a large population develops between lethal, external extremes in temperature. Range of internal temperatures at these two caves, during December–February 1998–1999, was 7.8 and 6.7°C, respectively, compared with nearby Wyandotte Cave, with a range of 2.3°C (Table 1). By comparing indices of temperature variability at these sites, we see that Ray's ($V = 0.16$) and Twin Domes (0.15) caves are 3.2 and 3.0 times less stable than Wyandotte Cave (0.05), which probably was the traditional, primary hibernaculum for the region.

Differences in stability were even more pronounced during January, when temperatures within Ray's and Twin Domes caves were 4.3 and 5.0 times less stable, respectively. Average surface temperature for January 1999 at Ray's Cave was 0.8°C higher than in 2000, and consequently, internal temperatures were 0.7°C higher. In contrast, a 1.3°C external rise at Wyandotte Cave raised roost temperatures only 0.2°C. Mean temperatures for January over the past 100 years in that area of Indiana ranged from 4.9°C, in 1950, to -10.2°C, in 1977, a difference of 15.1°C (http://www.wrcc.dri.edu/spi/divplot2map.html, South Central Indiana Division). This large difference among years suggests that sites like Ray's and Twin Domes caves are extremely vulnerable over several decades, and emphasizes the importance of restoration efforts at former key bastions of survival, such as Wyandotte, Rocky Hollow, and Mammoth caves (e.g., Toomey et al. 2002), that are more stable.

Comments on other hibernacula—Efforts to restore temperature are also in progress at Coach Cave, the former home of at least 100,000 Indiana bats. Internal temperatures appear suitable, but fluctuations in December–February 1999–2000 (Table 3) are still 3.2 and 3.5 times greater than those at Wyandotte and Rocky Hollow caves, respectively. Such instability, along with rapid airflow through roosting areas, may explain current failures to restore the population at this site (Currie 2002). Cooler temperatures and airflow may be due to an artificial entrance that remains open, although past enlargement of passages for use by tourists also may be a factor. This is definitely a correctable problem that should receive high priority.

Linefork Cave is another site of a large past population, and it appears to have an adequate temperature profile to justify a population larger than it currently has. We suspect that disturbance remains an issue here. The cave is popular with cavers, and an entrance (Dungeon Entrance) that leads through the primary area of past use by bats, remains unprotected.

Our data suggest that Bat Cave, Kentucky, is a site of secondary importance, compared with nearby Saltpetre Cave, which is another apparently essential hibernaculum of the past. Staining indicates a historic population of perhaps a million Indiana bats at Saltpetre Cave prior to extensive mining of nitrate during the War of 1812, followed by use of the cave for commercial tours. Remnants of its population of Indiana bats apparently reside in Bat Cave. Physical alterations resulting from mining and commercialization probably cause temperatures to be slightly higher than the optimum for Indiana bats (Tables 1 and 3), but Indiana bats still should prefer Saltpetre Cave to Bat Cave because of Saltpetre's lower and more stable internal temperatures ($V = 0.08$ for Saltpetre Cave and $V = 0.10$ for Bat Cave; Tables 1 and 3). A cessation of commercial tours during hibernation, beginning in winter 1998–1999, likely is responsible for an increase in population, from 475 bats in 1999 to 1,225 bats in 2001. Research on how best to restore ideal temperatures is underway, and we believe this site offers excellent potential for further recovery.

Conclusions

Available evidence strongly suggests that protection of hibernacula from disturbance by humans is critically important, yet it is insufficient if not accompanied by restoration of appropriate temperatures. All populations of which we are aware, which are not jeopardized by inappropriate temperatures, disturbance, or flooding, are stable or growing, indicating that problems during hibernation likely are a key factor in the species' overall decline. Degradation of summer feeding and roosting habitats is probably a contributing factor in decline of Indiana bats. Nevertheless, restoration of required temperatures and protection of essential hibernating sites is vital to recovery, and we agree with Humphrey (1978) that losses are reversible through restoration.

We suggest that resource managers make immediate efforts to identify and correct deficiencies in temperature at major caves of past or current use. In addition, we suggest that abandoned mines now provide some of the best options for large-scale restoration of the population, due to the enormous size of some mines, the resulting stability of temperature, and the multiple entrances to many mines that cause chimney-effect airflow (e.g., Kath 2002). Furthermore, we emphasize that significant hibernacula of the past may not be occupied currently and that other sites of historic use remain undiscovered. Such sites easily are identified by a combination of temperature, roost staining, and a structure that traps cold air; these caves may need nothing more than protection from disturbance or removal of material blocking the entrance to restore large populations of Indiana bats. Finally, all cave entrances essential to proper cooling of key hibernating sites must be identified and protected from inadvertent closures, including those that may occur naturally. Most caves that once served as bastions of survival for Indiana bats already have been lost to commercialization or closure, and those that remain require careful management if this species is to recover.

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Literature Cited

Clawson, R. L. 2002. Trends in population size and current status. *In* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Currie, R. R. 2002. Response to gates at hibernacula. *In* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Davis, W. H., and O. B. Reite. 1967. Responses of bats from temperate regions to changes in ambient temperature. Biological Bulletin 132:320–328.

Hall, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading Public Museum and Art Gallery, Scientific Publications 12:1–68.

Henshaw, R. E., and G. E. Folk, Jr. 1966. Relation of thermoregulation to seasonally changing microclimate of two species of bats (*Myotis lucifugus* and *M. sodalis*). Physiological Zoology 39:223–236.

Humphrey, S. R. 1978. Status, winter habitat, and management of the endangered Indiana bat, *Myotis sodalis*. Florida Scientist 41:65–76.

Humphrey, S. R., A. R. Richter, and J. B. Cope. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58:334–346.

Johnson, S. A., V. Brack, Jr., and R. K. Dunlap. 2002. Management of hibernacula in the state of Indiana. *In* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Kath, J. A. 2002. An overview of hibernacula in Illinois, with emphasis on the Magazine Mine. *In* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Richter, A. R., S. R. Humphrey, J. B. Cope, and V. Brack, Jr. 1993. Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Conservation Biology 7:407–415.

Silliman, B., Jr. 1851. On the Mammoth Cave of Kentucky. American Journal of Science and Arts (Second Series) 11:332–339.

Thomas, D. W., M. Dorais, and J. M. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. Journal of Mammalogy 71:475–479.

Toomey, R. S., III, M. L. Colburn, and R. A. Olson. 2002. Paleontological evaluation of past use of caves by: a significant tool for restoration of hibernacula. *In* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Tuttle, M. D. 1975. Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. University of Kansas, Occasional Papers of the Museum of Natural History 36:1–24.

Tuttle, M. D. 1976a. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. Ecology 57:587–595.

Tuttle, M. D. 1976b. Population ecology of the gray bat (*Myotis grisescens*): philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. University of Kansas, Occasional Papers of the Museum of Natural History 54:1–38.

Tuttle, M. D. 1977. Gating as a means of protecting cave-dwelling bats. Pp. 77–82 *in* 1976 National Cave Management Symposium proceedings (T. Aley and D. Rhodes, eds.). Speleobooks, Albuquerque, New Mexico.

Tuttle, M. D. 1997. A Mammoth discovery. Bats

15:3–5.

Tuttle, M. D., and D. Stevenson. 1977. An analysis of migration as a mortality factor in the gray bat based on public recoveries of banded bats. American Midland Naturalist 97:235–240.

Tuttle, M. D., and D. Stevenson. 1978. Variation in the cave environment and its biological implications. Pp. 108–121 *in* 1977 National Cave Management Symposium proceedings (R. Zuber, J. Chester, S. Gilbert, and D. Rhodes, eds.). Adobe Press, Albuquerque, New Mexico.

U.S. Fish and Wildlife Service. 1999. Agency draft. Indiana bat (*Myotis sodalis*) revised recovery plan. Fort Snelling, Minnesota.