THE BIOLOGY AND LIFE HISTORY OF THE INDIANA BAT: HIBERNACULA

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Abstract

Hibernating bats allow their body temperature to approximate that of the surrounding environment. They do not produce heat to stay warm, and as body temperature drops, metabolic processes slow, reducing energy requirements. Energy savings can be dramatic, with metabolic efficiency as a log function of temperature; energy consumption at 41.5°C (active working body temperature) is about 112 times that at 2°C. However, there are physiological constraints on minimum body temperatures. If bats get too cold they must use energy to warm themselves or freeze. At 0.5°C, energy expenditure is four times that at 2°C. Bats arouse (awaken) from hibernation periodically and spontaneously during the season of hibernation. The mean length of the period of hibernation between arousals for the Indiana bat under natural conditions is 13.1 days. Arousal is energy expensive, equivalent to about 65 days of hibernation. There are also other physiological costs of metabolic depression. It is likely bats trade off the costs of metabolic depression with costs of less efficient hibernation, using available energy to minimize the duration and depth of hibernation. During arousal, bats select where they will spend the next period of hibernation. It is probable they use behavior and social interaction to help them make this selection. Indiana bats are known for use of large, complex hibernacula; however, they also vertically stratify above areas with freezing temperatures in small, simple, vertical systems. In the past, temperatures of 4 - 8°C, or more narrowly 3 - 6°C, were widely regarded as optimal for the Indiana bat, but increasing populations in Indiana, which now constitute 45% of the total population, hibernate in areas with mean temperatures of 5 - 8°C. Detailed studies in Ohio, Missouri, and Kentucky indicate use of similar temperatures. The only hibernaculum in Indiana with a temperature <4°C has lost 63% of its population over a 29-year period.

Introduction

There are many reasons for mine closure: re-mining, safety, private developments, construction of infrastructure, and improving water quality. However, in winter, the Indiana bat (*Myotis sodalis*), hibernates in limestone caves and some man-made structures, such as underground mines. Listing of the Indiana bat under the Endangered Species Act entitles the species to protection wherever it is found, including mines.

The purpose of this paper is to provide a basic understanding of the biology of hibernation, its importance to this endangered species, and summarize parameters of the environment used by hibernating Indiana bats.

What is Hibernation and Why is it Important?

Hibernation is a physiological state of hypothermia. Hibernating bats allow their body temperature to approximate ambient temperature, i.e., that of the surrounding environment. In the cold environment of a hibernaculum, bats do not produce heat to stay warm and maintain a normal (i.e., active) body temperature. As body temperature drops, the respiration rate, heart rate, and metabolic processes all slow, resulting in a reduced expenditure of energy. Within physiological constraints, a lower body temperature during hibernation equates to lower energy requirement (Stones and Wiebers 1967). Hibernation is an adaptation that reduces energy expenditures during cold portions of the year when food (i.e., insects) is not available and when (liquid) water may not be available.

Bats enter hibernation in autumn when insects are no longer available and emerge in spring when the insects return. This is called the season of hibernation, and for the Indiana bat is roughly the period November - April. All mammalian hibernators arouse (awaken) from hibernation periodically and spontaneously during the season of hibernation (Lyman et al. 1982). The time (period) between arousals spent in hibernation is called the period of hibernation (or a bout of hibernation). The length of the period of hibernation varies by species and temperature (Brack 1979; Brack and Twente 1985; Twente et al. 1985; Fig. 1). Hardin and Hassel (1970) recorded the average length of the period of hibernation for the Indiana bat under natural conditions as 13.1 days, although the variation in most species is great. For example, the range of the period of hibernation of the little brown myotis is 4 – 83 days ($\bar{X}$ = 19.7 at 6°C) under natural conditions (Brack and Twente 1985) and 1 – 76 days ($\bar{X}$ = 12.7 at 5°C) in the laboratory (Twente et al. 1985).

Physiological Parameters of Hibernation

During hibernation, metabolism is reduced to a fraction of the euthermic metabolic rate. This reduction is commonly explained by a reduction in biochemical reactions, described as a Q10 effect. However, a second mechanism, metabolic inhibition (and suppression of heat production), reduces energy expenditures below that attributable to temperature alone (Geiser 1988, 2004; Snyder and Nestler 1990; Heldmaier and Ruf 1992). The costs of metabolic depression may include oxidative stress, reduced immunocompetence, and perhaps neuronal tissue damages, so trade-offs between the benefits of energy conservation and physiological costs of metabolic depression should cause hibernators to minimize the depth and duration of periods (bouts) of hibernation (Humphries et al. 2003), i.e., bats should hibernate at the highest temperatures they can and still have enough fat to survive.

Energy savings from hibernation can be dramatic and metabolic efficiency is a log function of temperature. Early studies by Hock (1951), though limited in precision, are nevertheless instructive:

- At 10°C, energy expenditures are twice that at 2°C
- At 20°C, energy expenditures are five times that at 10°C
- At 30°C, energy expenditures are five times that at 20°C
- At 37°C, energy expenditures are 1.5 times that at 30°C
- At 41.5°C, energy expenditures are 1.5 times that at 37°C

Total Savings ➔ ➔ ➔ ➔ ➔ 112 times

Thus, while bats should hibernate where it is cold, efficiencies gained at very low temperatures (e.g. <5°C) are disproportionately small because energy expenditures are curvilinear and asymptotic to zero (Geiser 2004). In addition, bats must also avoid freezing (Davis 1970). Hock (1951) also found that at 0.5°C, energy expenditure was four times that at 2°C, because bats were thermoregulating, ostensibly to avoid freezing.

Arousal (warming, being awake, and reentering hibernation) is energy expensive. The amount of time spent awake between periods of hibernation and the frequency of arousal also affect the energy expended during the season of hibernation (Speakman et al., 1991; Thomas, 1995). Arousal represents 80 – 90% of the cost of hibernation and each episode is equivalent to about 65 days of hibernation (Thomas et al. 1990). The cost of arousal also increases at lower temperatures because the bat must warm over a greater range of temperatures to reach working body temperature, and at colder temperatures, heat produced for warming dissipates more rapidly. At temperatures near freezing, bats often appeared to have difficulty warming, and I have observed bats that could not arouse at these temperatures when wet.

In summary, bats face constraints and must hibernate within specific environmental parameters, most notably temperatures that are cold enough to conserve enough energy to survive the winter, but not so cold they freeze or expend additional energy thermoregulating. They must also balance the physiological costs of metabolic depression with hibernating efficiently enough to survive winter (Fig. 2).

Ecological Parameters of Hibernation

During arousal, bats select where they will spend the next period of hibernation, i.e. somewhere that will not be too hot or too cold. A bat can select an area that is the appropriate temperature now, but how can a bat select a location that will have temperatures suitable for hibernation in the future? One mechanism may be social interactions. If bats return to sites they have used successfully in the past, then better sites should be used by more bats. Indeed,

- Across years, bats concentrate use into specific caves and mines
- Across years, bats concentrate use into specific areas of caves or mines
- Within the season of hibernation, larger and larger concentrations of bats hibernate in specific portions of caves and mines

Presumably, areas where bats concentrate are the best, or at least good for hibernation. Raesly and Gates (1987) examined numerous variables to determine which physical feature or attribute of a cave was associated with the location used for hibernation. They found that the best predictor of the use of an area was the presence of other bats.

Hibernacula Used by the Indiana Bat

Indiana bats typically hibernate in areas of caves and mines where temperatures are cold but stable (Fig. 3). Many large populations of hibernating Indiana bats use large cave (or mine) systems. These systems often have large entrances or multiple entrances with differences in elevation to allow an influx of cold winter air. Several variations on this theme were presented by Humphrey (1978). An influx of cold air is necessary to cool the hibernaculum and allow efficient hibernation, but if cold air enters too quickly, the hibernaculum may get too cold. Large complex systems allow air flow, but their volume and complexity often buffer, or slow, changes in temperatures. However, Indiana bats have also been found in a second general type of smaller system (Fig. 4). In these cases, cold air falls through a steep vertical system while bats hibernate above areas affected by freezing temperatures. A dramatic example of this is a cave shaped like a jug; the entrance is a karst window in the mouth to the jug (Fig. 4a). Air falls through the entrance and 23 m to the floor, and then through cracks in the floor. The bats roost high on the ceiling of the jug, to the side of and bypassed by the influx of freezing air.

In the past, temperatures of 4 - 8°C, or perhaps more narrowly 3 - 6°C, during mid-winter were widely regarded as optimal for the Indiana bat (USFWS 1999). Hall (1962), Henshaw and Folk (1966), and Humphrey (1978) stated that mid-winter temperatures of hibernacula used by the Indiana bat were 4 - 5°C, 2 - 3°C, and 4 - 8°C, respectively, but did not provide supporting documentation. However, 25 years of studies in many of the caves in Indiana addressed by Hall (1962) and Humphrey (1978) have documented increasing populations of Indiana bats (Brack et al. 2003) hibernating in areas with mean temperatures of 5 - 8°C (Table 1). The single large population in Indiana hibernating at <4°C has experienced a 63% in 29 years. In Missouri, Myers (1964) found Indiana bats in hibernacula with temperatures of 4.4 - 16.7°C, but considered 7.8°C a mean representative of the species. He provided data on mid-winter temperatures at clusters in three caves that were 5.0 - 9.2°C ($n = 6$; $\bar{X} = 7.1$; $SD = 1.4$). Also in Missouri, Clawson et al. (1980) found that Indiana bats used portions of caves with rock temperatures of 6 - 8°C in late January. Hassell (1967) and Hardin and Hassell (1970) reported mean hibernaculum temperatures of 8.3 and 7.6°C, respectively, for areas used by 90,000 Indiana bats in Bat Cave, Kentucky, although temporal variation was large, including temperatures below freezing. Indiana bats froze in this cave during hibernation (Davis 1970). The largest population of Indiana bats in Ohio (9,500 bats) hibernates in a limestone mine at a mean temperatures of 8.4±1.7°C (Table 1; Brack upubl. data).

Table 1. Temperatures used by Indiana bats hibernating in caves in Indiana and a limestone mine in Ohio. Indiana data are garnered from 25 years of surveys with increasing populations of bats (160%) in caves with temperatures >4°C. As of 2005 only a single large population in Indiana used a hibernaculum at ≤4°C. This population suffered a 63% decline over the past 29 years. Data from Ohio are for the period 1996 to 2002.

Location	% of Population	≤4°C	>4 - <5°C	≥5°C
Indiana	45%	28%	2%	71%
Ohio	2.5%	<<1%		100%

Hibernation Strategies and Tactics

A variety of trade-offs can be made by individuals and by species of bats to ensure successful hibernation. Some species hibernate in areas that are warm and stable, assuring they will not freeze. However, hibernation at warmer temperatures is less efficient. Species that use this strategy, such as the eastern pipistrelle (*Pipistrellus subflavus*), can offset the cost of less efficient hibernation by arousing less frequently (Fig. 1). Species that hibernate in colder areas face the physiological costs of hibernating at and arousal from lower temperatures, and the ecological cost of an unstable thermal regime and potentially freezing temperatures. The Indiana bat uses areas of moderate temperatures, balancing cold temperatures and thermal stability.

Individual bats can decrease exposure to fluctuating air temperatures by increasing surface contact with the cave (rock) or by increasing contact with other bats. Big brown bats (*Eptesicus fuscus*) and northern myotis (*Myotis* *septentrionalis*) often wedge themselves into tight cracks and crevices, putting most of their body surface area in contact with the cave. The Indiana bat clusters tightly. Beads of moisture often collect on guard hairs of the little brown myotis (*M. lucifugus*) and eastern pipistrelle as they hibernate. This water may act as a thermal sink, dampening fluctuations in air temperature. Finally, individuals may adjust to seasonal temperature changes by making inter- or intra-cave movements. Locations of clusters of Indiana bats change over the season (Clawson et al. 1980; Myers 1964); numerous researchers throughout temperate portions of the world have documented intra-cave and intra-mine movements by many species of bats during the season of hibernation. Whitaker and Rissler (1992) documented winter movements of several species of bats into and out of a mine in Indiana.

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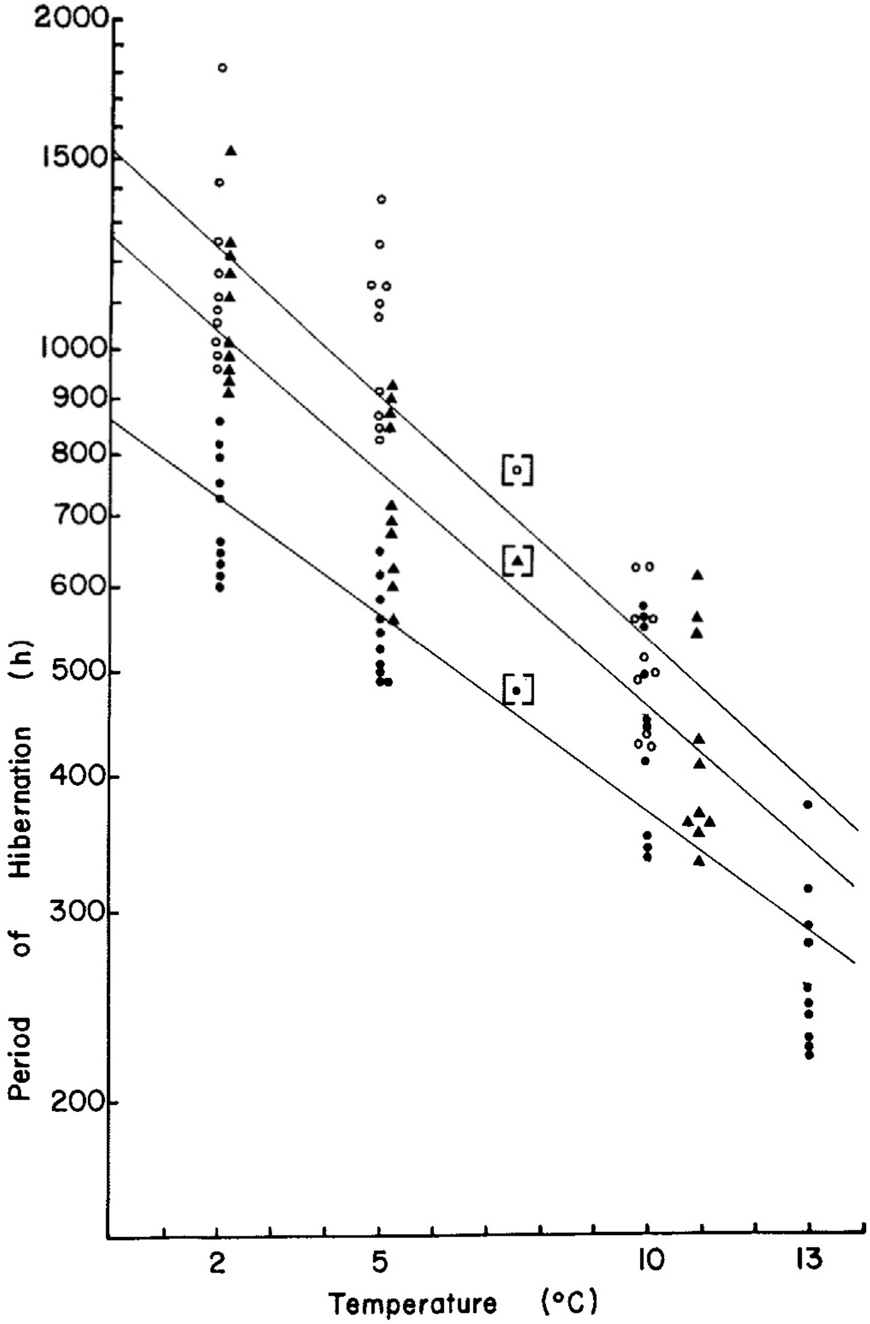

Fig. 1. The 10 longest periods of hibernation at 2, 5, 10, and 13°C for the big brown bat (solid triangles), eastern pipistrelle (solid circle), and little brown myotis (empty circle; from Twenty et al. 1985).

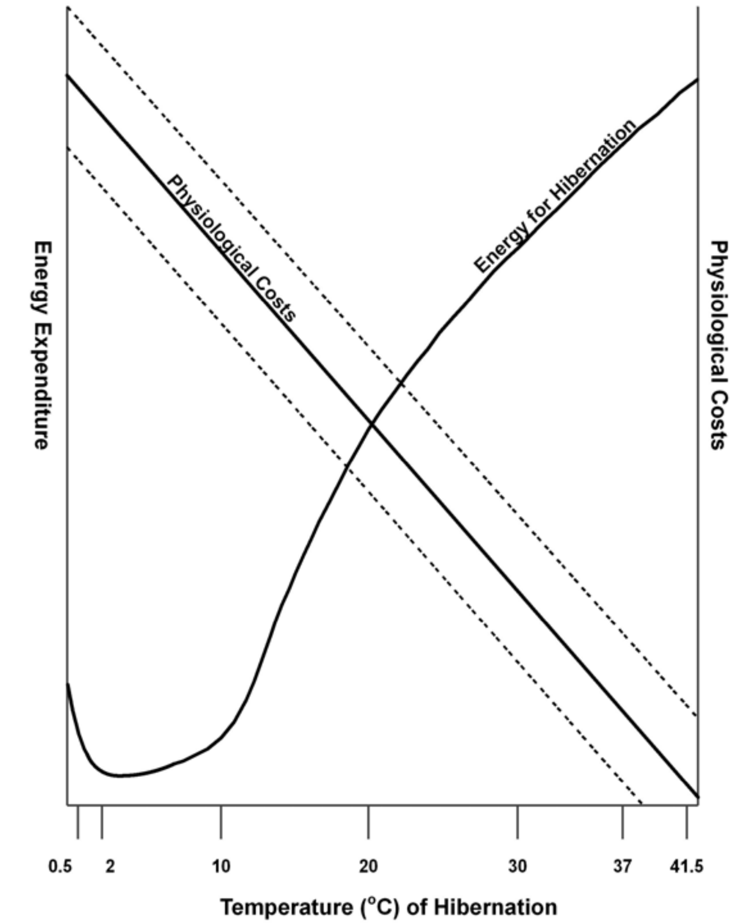

Fig. 2. As body temperature decreases from active (41.5°C) to 2°C, energy savings accrue; below 2°C, energy costs again increase. The "Energy for Hibernation" line reflects relative values (Hock 1951). There are other physiological costs, undefined, that accrue inversely proportional to temperature (Humphries et al., 2003). Placement and slope of the "Physiological Costs" line was arbitrary (it may be concave and curvilinear), but as illustrated by dashed lines, as physiological costs at any temperature increase, benefits of hibernation decrease and the optimum temperature of hibernation increases.

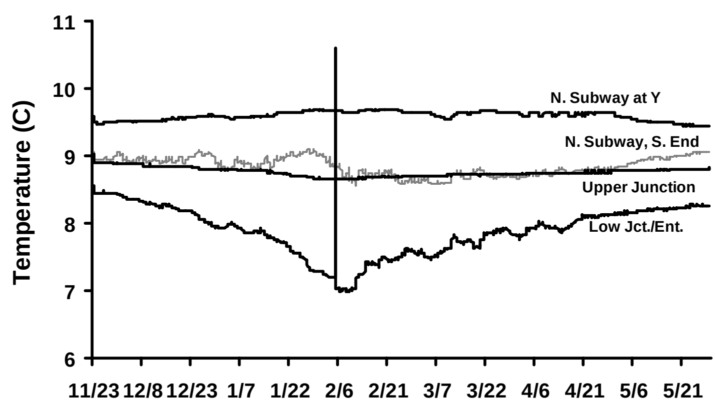

Fig. 3. Temperatures during the season of hibernation at four locations in a cave in Bland County, Virginia. Indiana bats hibernated in the area designated by the lowest line (Low Jct/Ent), illustrating the compromise between using areas that are both cool (allowing more efficient hibernation) and stable (to avoid freezing or an increase in thermoregulatory expenditures). Colder, but more thermally variable, locations were available for hibernation.

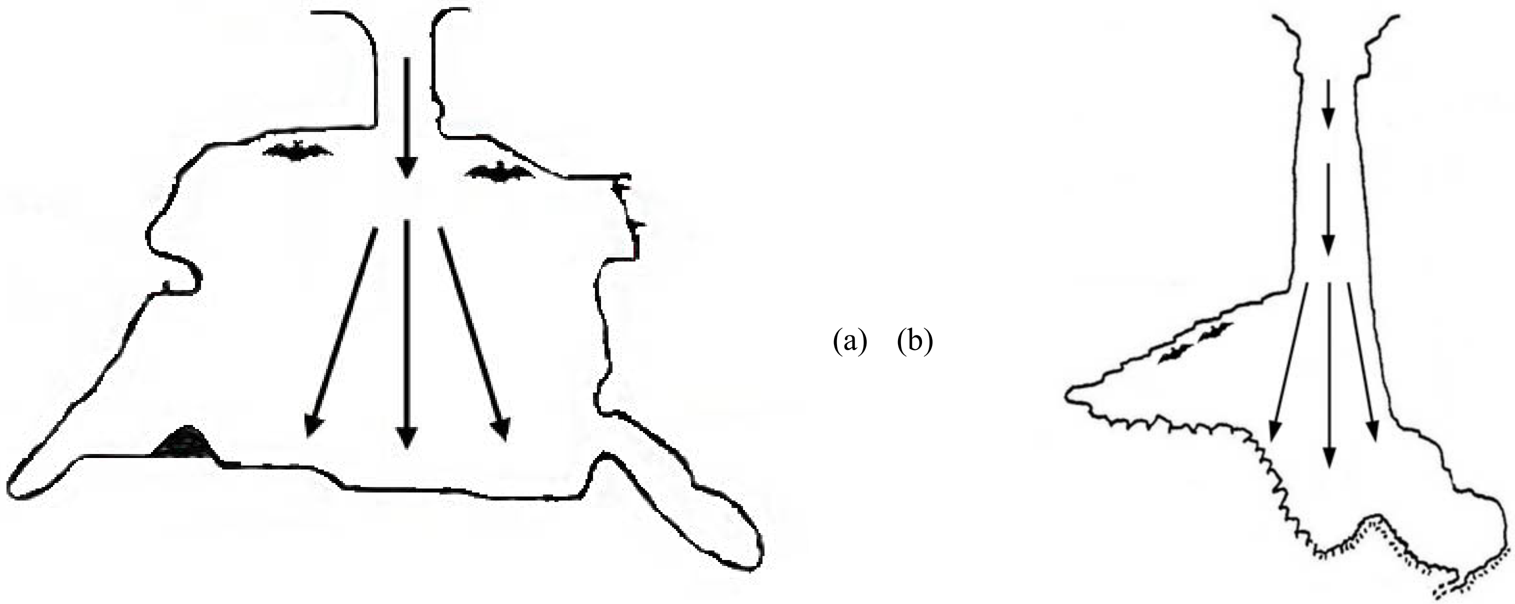

Fig 4. Indiana bats are known for use of large, complex hibernacula (illustrated in Humphrey 1978). However, they also vertically stratify above freezing temperatures in small, simple, vertical systems. In Fig. a, bats hibernate high, and to the side of the entrance of a jug-shaped cave, where cold air falls through a karst window and to the floor. Fig. b shows a variation on this theme.