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Original investigation

Long-term microclimate measurements add further evidence that there is no “optimal” temperature for bat hibernation

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ABSTRACT

Hibernation has long been known to be an energy bottleneck for temperate-zone bats. As such, considerable research effort has been expended to understand the physiological ecology of bat hibernation and the microclimates necessary for successful hibernation. Still, few long-term datasets of microclimate in bat hibernacula are available, and most descriptions of “optimal” hibernation sites are based on temporally or spatially limited datasets. Here, we summarize a long-term dataset of microclimate data from caves used by hibernating Indiana bats (*Myotis sodalis*) to draw conclusions about our understanding of microclimate selection of hibernating bats more generally. Ambient temperature varied among and within most hibernation microsites across the season of hibernation. Microsites near entrances were strongly and rapidly affected by external climatic conditions, while sites deeper in caves were more weakly related to external temperatures and show a greater lag time in response to those conditions. Comparison of microclimate and concurrent population counts suggests that bats select mid-winter microsites with a wider range of environmental conditions than is often stated; mid-winter survey counts increased between 1983 and 2011 in both cold and warm microsites. This extensive dataset provides some of the most exhaustive evidence yet that not all bats within a species choose (or likely require) microsites with the same microclimatic conditions. We argue that too often researchers and land managers have viewed microclimate selection through the lens of “optimal” conditions, and in doing so, often miss important variation that may actually be preferred by some bats.

Introduction

Populations of many species of cave-dwelling bats have been in a general decline for decades or centuries. Prior to the recent rise of White-nose Syndrome (WNS) in bats, habitat loss, pesticide use, and human persecution all played a role (Fenton, 1997), but anthropogenic disruption to the hibernation cycle likely has the most significant long-term impact on cavernicolous species. Hibernation is an energy and water bottleneck, and anthropogenic disturbances may increase the rate of energy use and water loss (Boyles and Brack, 2009; Thomas et al., 1990). Many fat-storing mammals, including small bats, must survive 4–9 months with few opportunities to forage. While more southerly populations forage occasionally during winter (Boyles et al., 2006), winter energy balance in temperate regions is likely determined by the rate of energy expenditure during hibernation for most populations and species. Energy expenditure during hibernation is determined by metabolic rate during torpor and euthermy, and frequency of euthermic arousals, all of which are strongly affected by ambient temperature (Hock, 1951). Water is also often limiting during the season of hibernation, and torpor is a water-conservation strategy for many species. Euthermic arousals further affect water balance, but the relationship is less clear than with energy. On one hand, respiratory and cutaneous water losses are higher during euthermy than torpor, suggesting that arousals may increase the chance of desiccation (Thomas and Cloutier, 1992). In contrast, many hibernacula have either standing water or enough condensation that bats may be able to drink during arousals.

In addition to chronic threats faced by hibernating bats, the recent addition of WNS as an acute threat to bats in North America may drive several species to extinction in the foreseeable future (Frick et al., 2010). To some degree, WNS exacerbates both energy

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and water bottlenecks, hastening energy expenditures and dehydration (Boyles and Willis, 2010; Cryan et al., 2010, 2013; Storm and Boyles, 2011; Warnecke et al., 2013; Willis et al., 2011). WNS has increased the urgency to understand how microclimates drive energy expenditure and water balance in hibernating bats in natural settings.

It is important to understand microclimatic conditions of microsites used by hibernating bats because of its importance in determining energy expenditure and water loss. Still, an oversimplified view of hibernation energetics and water balance is misleading, with important conservation implications (Boyles and Brack, 2014). Traditionally, hibernation was viewed as a discrete event largely disconnected from the rest of the life cycle. As such, most observers discussed "optimal" hibernation conditions as those that minimized energy expenditure during hibernation and presumably maximized survival (Day and Tomasi, 2014; Kokurewicz, 2004; Nagel and Nagel, 1991). However, hibernation is, in a sense, a starvation response that may impose considerable ecological and physiological costs during other portions of the life cycle (Boyles et al., 2007; Humphries et al., 2003a; Humphries et al., 2003b). Overexpression of hibernation (i.e., hibernating too deeply or for too long) may reduce lifetime reproductive output or survival. Thus, over a life spanning several decades (Wilkinson and South, 2002), bats must balance the benefits of survival within winters against reproductive output and survival across a lifetime. This trade-off necessitates that truly optimal hibernation conditions lead to a balance that maximizes lifetime fitness (Boyles et al., 2007). The optimal hibernation temperature is likely to vary among individuals, throughout the season of hibernation, and across seasons. Observations have long suggested that not all individuals within a species hibernate at a single temperature (Beer and Richards, 1956; Brack, 2007; Daan and Wichers, 1968), and experimental evidence suggests this variation is strongly related to variation in body condition among individuals (Boyles et al., 2007; Wojciechowski et al., 2007). Bats also move within hibernacula across time (Brack and Twente, 1985; Daan and Wichers, 1968), suggesting optimal conditions for hibernation are not static throughout winter or year-to-year (Brack, 2007).

Variation in ambient temperature further complicates its effect on energy expenditure. To date, essentially all estimated energy budgets for hibernating bats assume that ambient temperature is stable at a site across the season of hibernation. However, because the relationship between ambient temperature and metabolic rate is non-linear and asymmetrical, even small variations in temperature can produce large changes in energy expended across winter (Boyles and McKechnie, 2010). Although it is generally understood that temperatures, and likely water content of air, vary more near cave entrances, few attempts have been made to characterize this variation and how it relates to selection of microsites by hibernating bats (but see Elliott and Clawson, 2001). This may be, in part, because most studies of microclimate selection relied largely on point measurements of temperature taken during bat surveys (Clawson et al., 1980; Nagel and Nagel, 1991).

The effects of humidity on roost-site selection by hibernating bats are largely unknown. It generally appears that most species choose hibernation sites with nearly saturated air (Beer and Richards, 1956; Clawson et al., 1980; Thomas and Cloutier, 1992). Still, it is clear that at least some variation exists, both intra- and interspecifically, in selection of roost sites with different levels of humidity. Like temperature, this variation probably imposes a trade-off on hibernating bats. High humidity slows evaporative water loss (Thomas and Cloutier, 1992), which leads to longer torpor bouts (Thomas and Geiser, 1997) and decreased energy expenditure. However, longer torpor bouts may be detrimental because of negative physiological effects of hibernation (Humphries et al., 2003b) and lessened ability to fight off infections (Luis and Hudson, 2006). Differential mortality rates among bats hibernating in roosts and caves with different levels of air moisture suggest WNS may affect this trade-off (Ehlman et al., 2013), but a more thorough understanding of the dynamics of microclimate selection before WNS is vital to understanding basic bat biology and effects of this devastating epizootic.

We took advantage of a unique, long-term dataset of microclimate measurements within hibernacula used by Indiana bats (*Myotis sodalis*) in southern Indiana and concurrent winter population counts to address several objectives. We completed descriptive analyses of thermal stability and temporal variation within and across the season of hibernation at each microsite, and analyses of bat use in relationship to internal and external conditions. We use these analyses to discuss problems with the current paradigms of microclimate selection in bats and present considerations for resource managers and regulatory agencies as they struggle to conserve the most important elements of the natural environment for the long-term benefit and survival of bats.

Methods

Data

Microclimate data were collected by two entities: the Indiana Department of Natural Resources (IDNR) and the Indiana Karst Conservancy (IKC). The IDNR sampled widely across 27 microsites in 10 hibernacula, but generally for short periods (<10 yr). They recorded ambient temperature and relative humidity at 60-min intervals using Hobo ProV2 dataloggers (Onset Computer Corporation, Bourne, MA), accurate to 0.2 °C over the range of temperatures in hibernacula. Manufacturer reported accuracy of relative humidity measurements is <3.5%, but it is generally accepted these dataloggers perform poorly over long periods at high humidities, which is common in bat hibernacula. The Hobo ProV2 dataloggers were not calibrated between seasonal deployments.

The IKC sampled fewer microsites but over a longer time (up to 21 yr). They recorded temperatures at 192-min intervals using HoboXT dataloggers (Onset Computer Corporation), which are accurate to 1% but do not measure relative humidity. These dataloggers were calibrated to 0 °C before and after use by submersing them in an ice bath for several hours. During some years, they were only calibrated before the season. We used these calibrations to correct for absolute offset in temperature, when only one calibration was done, or offset and drift in temperature when pre- and post-deployment calibrations were performed. We used Program Expedata (Sable Systems, Las Vegas, NV) for corrections. We tested several correction types, but simple linear (2nd order polynomial) corrections were most appropriate. In some cases, data still appeared to drift even after calibration. This error was likely caused by variation in water bath temperatures. Where a calibration before or after winter was obviously incorrect, we used only one calibration point, but there are several microsites where error (drift) is still evident, and in some cases, drift may have been introduced by calibration itself.

We refer to hibernacula (e.g., Ray's Cave, Wyandotte Cave, Grotto Cave) as sites and datalogger locations within them (e.g., Ray's-Location A, Wyandotte-Bat's Lodge) as microsites. We defined the season of hibernation as 15 September-15 May, and removed years when data were missing for substantial portions of this period. There is considerable inter-individual variation in both immergence and emergence of bats from hibernation, but these dates facilitate comparison among sites and years. We notate year as the year when hibernation began (e.g., winter 2013–2014 is referred to as 2013). Population counts were typically completed in January or February; thus, microclimate data are notated as one