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The Winter Worries of Bats: Past and Present Perspectives on Winter Habitat and Management of Cave Hibernating Bats

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Abstract

Winter is a time of fascinating changes in biology for cave-hibernating bat species, but it is also a time of vulnerability. Unsurprisingly, assessments of winter habitat for these bats and how they can be managed has been a focus of many researchers involved with the North American Society for Bat Research over the last 50 years. During this time, a paradigm shift has occurred in the way these scientists think about factors driving winter habitat selection. To illustrate this shift, we review three hypotheses seeking to explain microclimate selection in cavernicolous bats. The first, which we call the “Colder is Better Hypothesis”, posits that bats should select cold microclimates that minimize energy expenditure. The second, the “Hibernation Optimization Hypothesis”, posits that bats should select microclimates that reduce the expression of torpor to balance energy conservation against non-energetic costs of hibernation. Finally, the “Thrifty Female Hypothesis” asserts that females should select colder microclimates than males to conserve energy for reproduction. We discuss these hypotheses, and the paradigm shift away from viewing hibernation as a phenomenon driven solely by the need to conserve energy, in the context of hibernacula management in North America. We focus on both historical and recent conservation threats, most notably alteration of thermal regimes and the disease white-nose syndrome. We urge against returning to an over-simplified view of winter habitat selection in response to our current conservation challenges.

Key Words: conservation, ecophysiology, hibernation optimization, physiology, torpor, white-nose syndrome

1 The Winter Worries of Bats

To the uninitiated, hibernation may appear as a relatively uneventful process, at times consisting of weeks of inactivity transpiring in a dark, unchanging environment. However, decades of research have taught us that hibernation is far more interesting. Although the life of a hibernating bat occurs at a much different pace than during summer, the winter lives of bats are dynamic, and the study of winter ecology is both rich in literature and riddled with gaps in knowledge. During winter, bats are not only under selective pressure to conserve energy, but face several competing physiological and ecological demands as well as opportunities (Thomas et al. 1979, 1990; Humphries et al. 2003). Bats respond to these pressures in diverse ways, including periodic arousals, behavioral changes, and habitat selection (Boyles et al. 2007, 2008; Jonasson

and Willis 2012). Unfortunately, while we have learned much about the winter lives of bats in the last 50 years, cavernicolous bats are currently more imperiled than ever, and proper conservation and management of these species will require detailed mechanistic understanding of habitat selection during hibernation.

The first study of hibernation presented at the North American Symposium on Bat Research, “Status, winter habitat, and management of the endangered Indiana bat, *Myotis sodalis*”, was delivered by Stephen Humphrey in 1975. While by no means the first study on the winter worries of bats (Hock 1951; Twente 1955; McNab 1974), this presentation, and a subsequent publication by the same author (Humphrey 1978), articulated concepts that remain relevant in bat conservation to this day. Presenting soon after passage of the Endangered Species Act, Humphrey linked disturbance and habitat degradation to the decline of Indiana myotis. Humphrey correlated events such as closing cave entrances, natural disasters, and disturbances from biologists, recreational cave visitors, and vandals to population declines and temperature changes inside hibernacula. Importantly, he also predicted that if winter disturbance from humans was eliminated, and microclimates were restored to 4–8 °C, Indiana myotis populations would recover and the species could be downgraded from endangered. At the time, a narrow range of cold temperatures was believed to be favorable due to the effect of temperature on metabolism (Hock 1951; Twente 1955; McManus 1974). Humphrey’s connection between energetics and the decline of an endangered species was a pivotal one, and for decades, the belief that suitable winter habitats were those with a narrow range of cold temperatures conducive to maximum energy savings was the dominant paradigm (Richter et al. 1993; Tuttle and Kennedy 2002).

Recent studies have shifted our view of hibernation to emphasize that bats must balance more than energetics during winter (Thomas and Geiser 1997; Humphries et al. 2003; Boyles et al. 2007). These studies benefited from decades of prior research as well as technological advances allowing for more accurate measurements of both bats and their selected microclimates. There is now copious evidence against the caricature of hibernation as a period when bats require stable, cold temperatures (Boyles et al. 2007; Brack 2007; Kurta and Smith 2014). Unfortunately, this knowledge has not always translated to more effective bat conservation because we still lack a fundamental, mechanistic understanding of many important aspects of winter ecology. Failure to recognize the full suite of factors driving winter habitat selection, for example, may result in management plans for hibernacula focused on a narrow range of temperatures that may at times be overly simplistic and focused on the wrong factors. This is supported by varied success of cave restoration exercises and examples of caves with “ideal” microclimates that are unused by hibernating bats (Elliott and Clawson 2007; Gore et al. 2012). Our goal here is to review literature describing our evolving knowledge of winter habitat use and the implications of these studies for bat conservation and management. While our work is not meant to be exhaustive, it aims to put our current knowledge into a theoretical context. We summarize the factors known to contribute to microclimate selection, both within and among species, and across environments. We then review management approaches to date, and the need to adapt these perspectives to the current challenges of WNS.

2 Factors Driving Microclimate Selection in Winter

To illustrate how thought on winter habitat selection has evolved over the last several decades, we describe three hypotheses representing previous and contemporary views on the topic. The

earliest hypothesis explaining microclimate selection by hibernating bats, which we call the Colder is Better Hypothesis, posits that bats select hibernacula with ambient temperatures (T_a) that minimize their torpid metabolic rate (TMR), thus minimizing energy spent during hibernation (Figure 1a). This hypothesis is built on the assumption that overwinter survival is negatively correlated with energy spent during hibernation, and that this selective pressure alone drives winter habitat use. Because TMR decreases with T_a down to a threshold below which hibernators must increase TMR to avoid freezing (T_{min}), hibernating bats can maximize their energetic savings during winter by hibernating at T_{as} slightly above T_{min} (Buck and Barnes 2000; Boyles and McKechnie 2010). Energy savings are maximized at $T_{as} > T_{min}$ because hibernacula microclimates vary during winter, and periodic drops in T_a below T_{min} cause hibernators to incur greater energetic costs than hibernating at T_{as} consistently above T_{min} . Hibernation at cold T_{as} also saves energy because these temperatures are associated with longer torpor bouts (McNab 1974; Brack and Twente 1985; Dunbar and Tomasi 2006). Given that energetic cost of arousals constitutes the majority of a hibernating bat's winter energy budget, increasing torpor bout duration can significantly reduce energy use (Thomas et al. 1990; Jonasson and Willis 2012).

Numerous studies during the 20th century reported observations of bats hibernating at cold T_{as} , seemingly in support of the Colder is Better Hypothesis (McManus 1974; Nagel and Nagel 1991; Tuttle and Kennedy 2002). However, such studies still often reported variation in T_{as} selected, and over time variation within and among species became apparent (Webb et al. 1996). Also evident were numerous examples of cold hibernacula with absent or declining bat populations, and warmer sites where populations were not declining, apparently at odds with Colder is Better but without a framework for understanding why (Tuttle and Kennedy 2002; Elliott and Clawson 2007; Gore et al. 2012). An explanation began to emerge by the turn of the century with the realization that maintaining higher rates of metabolism during hibernation may be beneficial for non-energetic reasons (Humphries et al. 2003). This understanding, combined with recognition of the costs of torpor, led to the recognition that colder is not necessarily better. Costs of torpor are likely not fully understood, but include reduced immune function, disruptions of homeostatically controlled process such as sleep, exposure to predation and abiotic events, and loss of the physiological advantages of euthermy (Humphries et al. 2003; Heller and Ruby 2004; Bouma et al. 2010). Thus, successful hibernators balance competing costs and benefits of torpor, and this revelation led to the articulation of new hypotheses predicting winter habitat selection (Boyles et al., *In Review*).

The Hibernation Optimization Hypothesis posits that bats should select microclimates where they can survive while reducing the use of torpor (Boyles et al. 2007). This hypothesis considers energetic constraints during hibernation, predicting that bats should select cold T_{as} when energy is scarce, but also predicts bats should avoid cold T_{as} when possible to minimize torpor costs (Figure 1b). Implicit to this hypothesis is the expectation that individuals vary in habitat selection based on their unique ecology and physiology. Boyles and colleagues (2007) were among the first to find support for this hypothesis, finding that little brown myotis (*M. lucifugus*) with greater energy reserves – fat – select warmer T_{as} because they can afford more frequent periodic arousals than bats with smaller energy reserves. This hypothesis could also be used to assess interspecific differences in habitat use. For example, although it is well known that different species often exhibit differences in microclimate preference, we currently lack suitable explanations for why some species prefer warmer or colder T_{as} (McNab 1974; Raesly and Gates 1987; Brack 2007; Kurta and Smith 2014; Johnson et al. 2017). Comparisons of different species selecting where to hibernate from the same range of available microclimates may reveal

important differences in ecology, such as energy needed for reproduction or migration, or physiology, such as metabolism or heat and water loss.

Within species, there are additional drivers of variation in torpor use and habitat selection beyond existing fat reserves. Jonasson and Willis (2011) developed the Thrifty Female Hypothesis based on their observations of different patterns of body mass loss between males and females during winter. The Thrifty Female Hypothesis posits that females should express torpor to a greater degree during winter because they face greater selective pressure to maximize energy savings than males (Figure 1c). Unlike males, female bats need additional fat reserves to ovulate upon emergence from hibernation and successfully fertilize with sperm stored over winter (Kunz et al. 1998). Thus, females have less energy available to mitigate the costs of torpor than males and are predicted to select colder microclimates within hibernacula than males with the same amount of fat. Since its articulation, this hypothesis has become a widely accepted aspect of Hibernation Optimization where each sex balances costs and benefits differently. However, data demonstrating that females use both relatively warm and cold regions within the same hibernacula (Boyles et al. 2007) despite pressure to maximize energy reserves, demonstrates that females still respond to the need to minimize costs of torpor to at least some degree. Bats may be unique among hibernators in their adherence to the Thrifty Female Hypothesis based on their reproductive strategy or inability to cache food during winter, but studies seeking to apply this hypothesis outside of bats are scarce.

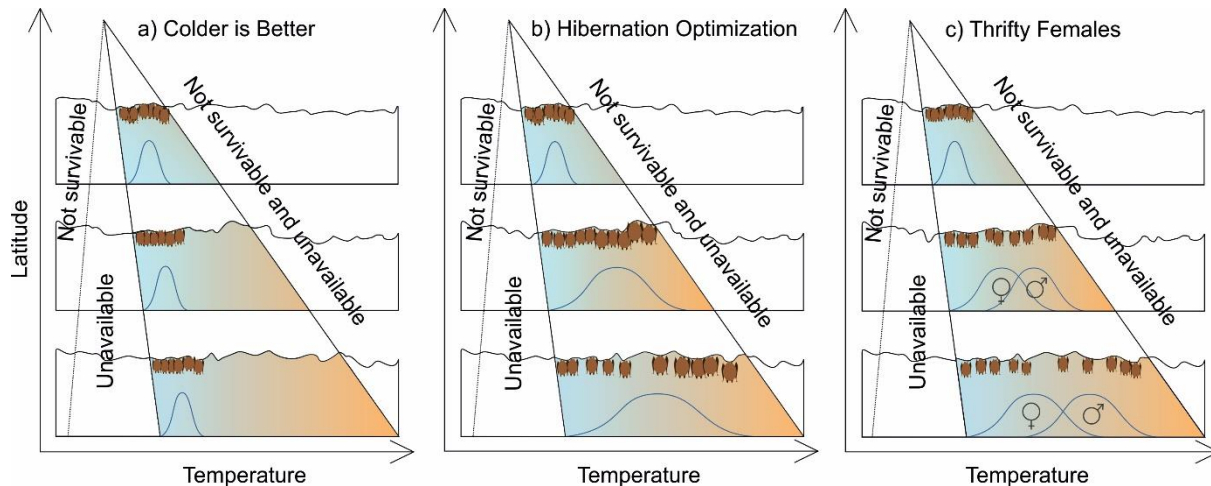


Figure 1. Conceptual diagrams of hypotheses predicting winter microclimate selection in cavernicolous bats. Each panel shows the hypothesized distribution of bats across a thermal gradient within a single hibernaculum (x-axis), which is expected to vary latitudinally (y-axis). The Colder is Better Hypothesis (A) posits that bats should select cold microclimates to maximize energy savings. The Hibernation Optimization Hypothesis (B) posits that bats should select microclimates that allow for survival while also reducing torpor expression. The Thrifty Female Hypothesis (C) posits that females should select colder microclimates than males because for females, fitness will be influenced not only by winter survival, but also emerging from hibernation with the fat stores needed for ovulation.

The latter two hypotheses reflect the importance of a range of thermal environments during winter. However, it is not well documented how available temperatures vary across large geographic areas, and how this variation affects hibernators. One such study, conducted across the unique temperature gradient present in Florida, demonstrates the potential impact of research

in this area (McNab 1974). This study paired measurements of hibernacula microclimates available in Florida with observations of where gray myotis (*M. grisescens*) and tri-colored bats (*Perimyotis subflavus*) were found hibernating. Finding that the larger gray myotis was limited to northern Florida, where colder temperatures were available, McNab (1974) concluded that subtropical temperatures in Florida pose challenges to obligate hibernators, species in which females must hibernate to store sperm over winter. That the smaller tri-colored bat can be found hibernating at more southern latitudes in Florida reflects important differences in ecology or physiology, although the nature of that difference has not been tested. Thus, available temperatures vary with latitude, influencing opportunities for bats to reduce torpor use given their energetic constraints (Figure 1). This, in turn, may result in local adaptation and acclimatization in populations of species with large geographic ranges (Dunbar and Brigham 2010). Unfortunately, few studies have examined variation in hibernacula temperatures across in North America and the potential for this to interact with selective pressures driving microhabitat selection, and more research is needed in this area.

Thus, research conducted in the nearly 50 years following Humphrey's study of winter habitat selection in Indiana myotis has demonstrated the phenomenon is not the product of a single variable, but rather a collection of variables, with hibernators balancing costs and opportunities given limited energy. Viewed in this context, it is not surprising that winter habitat selection in well-studied species shows considerable variation. Unfortunately, the need for management recommendations on how to best provide, protect, and restore winter habitat is more pressing than ever, and extends to many more species. Below, we discuss how knowledge of factors behind winter habitat selection has been used in management in the past, how new data have challenged old assumptions, and how WNS has added an additional dimension to this challenge.

3 Management Challenges

When Humphrey presented his work in 1975, the newly minted Endangered Species Act directed agencies to avoid adversely affecting critical habitat. Humphrey noted that closing caves or obstructing their airflow was tantamount to their degradation or destruction, and recommended their restoration (Humphrey 1978). There are notable examples where these recommendations, when enacted, were followed by significant growth of winter populations (Richter et al. 1993; Tuttle and Kennedy 2002). While these successes were invaluable, it must be noted that not all such efforts have resulted in population responses, suggesting a fundamental disconnect between our understanding of hibernation ecology and population recovery. Indeed, unless the causes of population trends are clearly identified, management actions should not be expected to succeed (Figure 2). Given this disconnect, and the changing paradigm surrounding winter habitat selection, there clearly is a need to reconsider hibernacula management practices. Although all possible management actions merit attention, we focus our discussion solely on microclimates.

Restoration or improvements of thermal habitats within hibernacula revolves around efforts to reduce T_a (Richter et al. 1993; Tuttle and Kennedy 2002; Johnson et al. 2017). Unintended warming of hibernacula is well-known to occur at sites modified with walls and gates, which impede inflow of cold air during winter (Humphrey 1978; Richter et al. 1993). Restoration of airflow is straightforward in instances where large walls or doors meant to keep humans out impede airflow, but the impacts on bat populations are less straightforward than they may appear. Perhaps the most famous example comes from Wyandotte Cave, Indiana, where

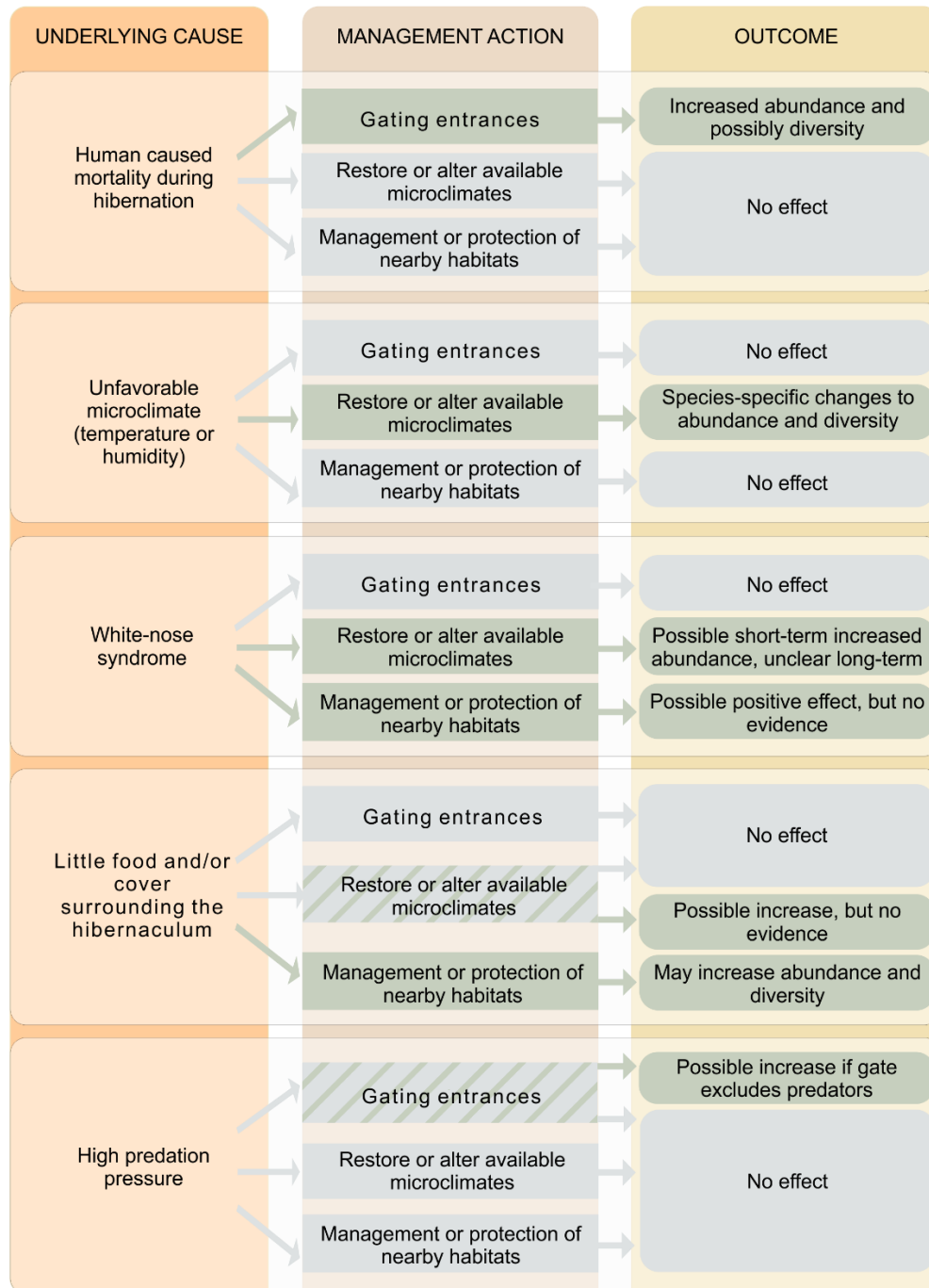


Figure 2. A flow-diagram depicting a list of possible causes for low abundance or species diversity at bat hibernacula, which may be an impetus for management actions. Because we lack a strong empirical connection between abundance and diversity within hibernacula (white-nose syndrome being an exception), management actions taken sometimes fail to address the underlying conservation concern and therefore fail to achieve the desired result. To illustrate this, we provide a flow diagram of the direct effects that three possible management actions would have given the underlying cause of low abundance or diversity at site, assuming these actions are implemented properly (e.g., gating did not change microclimates inadvertently).

rapid growth of Indiana myotis occurred following removal of stone wall at the cave entrance (Richter et al. 1993). Although the cooling that occurred following manipulation was credited as leading to this growth, counts from nearby hibernacula suggest that Wyandotte was the recipient of bats moving in from nearby sites, including sites where microclimates were presumed more favorable (Brack et al. 2003). Most notably, the population at Twin Domes steadily declined following modification of Wyandotte, despite the hibernaculum having cooler T_{as} within the range of “preferred” temperatures (Richter et al. 1993; Tuttle and Kennedy 2002). Thus, while the cooling at Wyandotte improved conditions at the site, the movement of bats from even colder hibernacula clearly indicates that colder is not necessarily better. Furthermore, efforts to replicate results from Wyandotte at Great Scott Cave, Missouri, did not meet with population growth following the reopening of a blocked entrance to the site (Elliott and Clawson 2007).

Cooling hibernacula has, therefore, met with equivocal results. While this conservation strategy is likely effective in many cases, we urge caution when basing management solely on cooling hibernacula to supposed “optimal” temperatures. Such an approach is over-simplified and will not always lead to population recovery, as evidenced from the studies above and additional accounts of sites with suitable microclimates that go unused by bats (Gore et al. 2012). Perhaps more importantly, the two accounts reviewed above focused on a single species, which will not likely be inclusive of the needs of all cave-hibernating bats. This realization is essential for management at the time of this review, as one hibernating species, the northern myotis (*Myotis septentrionalis*) was recently listed as federally threatened, and additional species may follow as WNS continues to spread and cause mortality in affected areas.

Although restoring cool hibernacula T_{as} does not always result in population growth, limited evidence suggests that cooling unused hibernacula with warm T_{as} can improve otherwise unfavorable habitat. To our knowledge, the only published record of this comes from Pennsylvania, where state biologists created soil mounds to prevent cold air from flowing out of an abandoned mine with an entrance that slopes uphill (Johnson et al. 2017). Prior to the arrival of WNS, this effort to trap cold air in the mine resulted in an increase in the number of hibernating little brown myotis as well as an increasing species richness at the site. This example demonstrates how understanding factors determining T_a within a site (for review, see Perry 2013) can be leveraged to improve marginal sites. However, we note that cooling hibernacula in this way comes from a southern perspective. In a survey of abandoned mines in Michigan’s Upper Peninsula, Kurta and Smith (2014) found that occupied sites were warmer than unoccupied sites, and lacked chimney-effect airflow other studies have found are important to other species at lower latitudes (Tuttle and Kennedy 2002). Kurta and Smith (2014) also found that occupied sites were more complex than unoccupied sites, and likely had a wider range of microclimates available than unoccupied sites as a result, although the authors did not report the amount of thermal diversity within the sites. Thus, while the importance of sites that are relatively warm or cold T_{as} may vary latitudinally, hibernacula offering a diversity of thermal habitats are likely of high value at all latitudes.

That hibernacula management is not as simple as maintaining and restoring cold T_{as} should not be surprising given bats’ need to balance the conflicting pressures described above. Unfortunately, WNS adds an additional variable to winter habitat selection and further complicates management. A full review of WNS is outside of the scope of this chapter, but its intersection with microhabitat selection and hibernacula management merits attention. The fungus causing WNS, *Pseudogymnoascus destructans*, has a temperature-dependent growth rate, growing optimally from 12.5–15.8 °C, with rapidly decreasing rates at colder and warmer

temperatures (Verant et al. 2012). WNS mortality also varies with hibernacula T_a , with colder temperatures conferring a survival benefit (Langwig et al. 2012; Johnson et al. 2014; Lilley et al. 2016). In addition to being associated with slower fungal growth, colder T_a s likely benefit WNS-affected bats because they promote increased use of torpor, providing energetic savings and limiting arousals and costly, potentially maladaptive, immune responses (Lilley et al. 2017).

WNS has therefore altered the costs and benefits of hibernating at the various T_a s discussed above. Bats' response to this change can be used to test the hypotheses shown in Figure 1, and potentially guide management. Specifically, a shift in habitat selection by both sexes towards colder T_a s would broadly support the Hibernation Optimization Hypothesis, as bats would receive less benefit from minimizing torpor when suffering from WNS. Potentially more interesting, however, is whether females continue to select colder T_a s than males, or if the effects of WNS are so great as to drive both sexes to similar microclimates. Finally, because the Colder is Better Hypothesis already predicts bats select cold T_a s, it predicts no shift in habitat selection. Although data from WNS-positive hibernacula in Pennsylvania show remnant populations of little brown myotis, tri-colored bats, and big brown bats (*Eptesicus fuscus*) have responded to the disease by moving to colder areas within sites (Johnson et al. 2017), sex-specific data have not yet been reported.

The shift in habitat selection by bats in response to WNS raises questions over how the need to increase short-term survival impacts long-term fitness. This question is a critical one, because although protecting cold hibernacula, or cooling those that are too warm, may yield short-term benefits for survival in WNS-affected areas (Johnson et al. 2017), hibernating at cold T_a s comes at a physiological cost that bats should reduce where possible. It is for this reason that cooling hibernacula has met with mixed success in the past, and although the balance of costs and benefits to during hibernation has changed, the cost of cold T_a s will still be incurred and potentially vex management efforts. We suggest that this realization, well supported in recent literature, be remembered in the years ahead. For example, if bats are hibernating at cold T_a s in response to WNS, an important follow-up question is at what cost such an adaptation comes. Costly behavioral adaptations in response to invasive species have been documented elsewhere and are worthy of investigations in the context of WNS (Thawley and Langkilde 2017), although standing genetic variation and phenotypic plasticity may mitigate the process and contribute as population level pre-adaptations (Messer and Petrov 2013). Finally, because different species select different T_a s during hibernation, and individuals do not necessarily show a consistent preference throughout winter, it is unlikely that narrow recommendations for hibernacula conditions will meet with success in the years ahead. Careful consideration of the life history of hibernators in an area, the availability of thermal habitats, and the costs and benefits of hibernating across this range of conditions, are needed if hibernacula management is to succeed in mitigating WNS mortality.

4 Conclusion and Future Directions

Winter is a complex and dangerous time for cavernicolous species. At temperate latitudes, many species appear to be obligate hibernators and often migrate not in search of warmer climates, but of suitable hibernacula. Hibernating bats are not dormant until spring, but are periodically active to copulate, minimize the physiological consequences of torpor, and to select appropriate microclimates. This habitat selection is driven by factors both internal (e.g., physiology) and external (e.g., availability) to hibernators, the interaction of which are not fully understood. Our

review of what is known draws significantly on research presented and planned at the North American Symposium on Bat Research over the past 50 years, and illustrates a clear shift away from a conceptualizing hibernation as a simple process geared towards conservation of energy towards a dynamic period during which bats balance costs and opportunities given their limited energy reserves.

Unfortunately, the need to fill the remaining gaps in our knowledge of winter habitat selection has been made more urgent since the discovery of WNS. Carefully designed experiments are needed to better understand the causes and consequences of winter habitat selection of cave-hibernating species, and to determine how hibernacula management must be adapted in WNS-affected regions. Correlative studies, while valuable, are inherently limited in inferential scope and will never fully explain how conditions in hibernacula affect hibernating bats. In the absence of well-designed manipulative experiments, we run risk of once again viewing winter habitat selection one-dimensionally, only this time through the lens of WNS. For example, although selecting colder T_{as} may be adaptive for surviving infection with *P. destructans*, the fact that bats did not always select the coldest T_{as} prior to the arrival of WNS indicates that such an adaptation may also come at a cost. Moreover, a better understanding of winter ecology, including the use of alternative hibernacula is needed. Species such as the eastern small-footed (*Myotis leibii*) and northern myotis are suspected to hibernate in rock piles in addition to caves and mines, and even western populations of *M. lucifugus* are thought to rely on these sites not traditionally considered hibernacula (Lemen et al. 2016; Moosman et al. 2016; Neubaum 2018). This behavior is poorly understood but may be associated with different disease dynamics and require different management approaches than traditional hibernacula, and merits research attention.

When Humphrey presented his work on Indiana myotis in 1975, poor management of hibernacula temperatures and human disturbance were the greatest threats to North American bats during winter. Nearly 50 years later, the role of microclimate during winter remains a central focus of winter research and management. Bat researchers and managers today are faced with changing climates and the continued spread and impact of WNS. Successful management of winter habitats will require that these professionals avoid returning to our previous, over-simplified understanding of winter habitat selection. To continue to grow our understanding on winter habitat selection, we recommend the use of experimental studies and investigations of the physiological, ecological, and fitness consequences of habitat selection at different T_{as} beyond energy conservation.

5. References

- Bouma HR, Carey H V., Kroese FGM (2010) Hibernation: the immune system at rest? *J Leukoc Biol* 88:619–624. doi: 10.1189/jlb.0310174
- Boyles JG, Dunbar MB, Storm JJ, Brack VJ (2007) Energy availability influences microclimate selection of hibernating bats. *J Exp Biol* 210:4345–4350. doi: 10.1242/jeb.007294
- Boyles JG, McKechnie AE (2010) Energy conservation in hibernating endotherms: Why “suboptimal” temperatures are optimal. *Ecol Modell* 221:1644–1647. doi: 10.1016/j.ecolmodel.2010.03.018
- Boyles JG, Storm JJ, Brack V (2008) Thermal benefits of clustering during hibernation: A field test of competing hypotheses on *Myotis sodalis*. *Funct Ecol* 22:632–636. doi:

10.1111/j.1365-2435.2008.01423.x

- Brack VJ (2007) Temperatures and Locations Used by Hibernating Bats, Including *Myotis sodalis* (Indiana Bat), in a Limestone Mine: Implications for Conservation and Management. *Environ Manage* 40:739–746. doi: 10.1007/s00267-006-0274-y
- Brack VJ, Johnson SA, Dunlap RK (2003) Wintering populations of bats in Indiana, with emphasis on the endangered Indiana myotis, *Myotis sodalis*. *Proc Indiana Acad Sci* 112:61–74
- Brack VJ, Twente JW (1985) The duration of the period of hibernation of three species of vespertilionid bats. I. Field studies. *Can J Zool* 63:2952–2954
- Buck CL, Barnes BM (2000) Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. *Am J Physiol Integr Comp Physiol* 279:R255–R263. doi: 10.1152/ajpregu.2000.279.1.R255
- Dunbar MB, Brigham RM (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. *J Comp Physiol B Biochem Syst Environ Physiol* 180:885–893. doi: 10.1007/s00360-010-0457-y
- Dunbar MB, Tomasi TE (2006) Arousal patterns, metabolic rate, and an energy budget of eastern red bats (*Lasiurus Borealis*) in winter. *J Mammal* 87:1096–1102. doi: 10.1644/05-MAMM-A-254R3.1
- Elliott WR, Clawson RL (2007) Gray and Indiana bat population trends in Missouri. In: *Proceedings of the National Cave and Karst Management Symposium*. pp 46–61
- Gore JA, Lazure L, Ludlow ME (2012) Decline in the winter population of gray bats (*Myotis grisescens*) in Florida. *Southeast Nat* 11:89–98
- Heller HC, Ruby NF (2004) Sleep and Circadian Rhythms in Mammalian Torpor. *Annu Rev Physiol* 66:275–289. doi: 10.1146/annurev.physiol.66.032102.115313
- Hock RJ (1951) The metabolic rates and body temperatures of bats. *Biol Bull* 101:289–299
- Humphrey SR (1978) Status, winter habitat, and management of the endangered Indiana bat, *Myotis sodalis*. *Florida Sci* 41:65–76
- Humphries MM, Thomas DW, Kramer DL (2003) The Role of Energy Availability in Mammalian Hibernation: A Cost-Benefit Approach. *Physiol Biochem Zool* 76:165–179. doi: 10.1086/367950
- Johnson JS, Reeder DM, McMichael JW, et al (2014) Host, pathogen, and environmental characteristics predict white-nose syndrome mortality in captive little brown myotis (*Myotis lucifugus*). *PLoS One* 9:. doi: 10.1371/journal.pone.0112502
- Johnson JS, Scafani MR, Sewall BJ, Turner GG (2017) Hibernating bat species in Pennsylvania use colder winter habitats following the arrival of white-nose syndrome
- Jonasson KA, Willis CKR (2012) Hibernation energetics of free-ranging little brown bats. *J Exp Biol* 215:2141–2149. doi: 10.1242/jeb.066514

- Jonasson KA, Willis CKR (2011) Changes in body condition of hibernating bats support the thrifty female hypothesis and predict consequences for populations with white-nose syndrome. PLoS One 6:. doi: 10.1371/journal.pone.0021061
- Kunz TH, Wrazen JA, Burnett CD (1998) Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). Ecoscience 5:8–17
- Kurta A, Smith SM (2014) Hibernating Bats and Abandoned Mines in the Upper Peninsula of Michigan. Northeast Nat 21:587–605
- Langwig KE, Frick WF, Bried JT, et al (2012) Sociality , density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecol Lett 15:1050–1057. doi: 10.1111/j.1461-0248.2012.01829.x
- Lemen CA, Freeman PW, White JA (2016) Acoustic evidence of bats using rock crevices in winter: A call for more research on winter roosts in North America. Trans Nebraska Acad Sci Affil Soc 36:9–13
- Lilley TM, Johnson JS, Ruokolainen L, et al (2016) White-nose syndrome survivors do not exhibit frequent arousals associated with *Pseudogymnoascus destructans* infection. Front Zool 13:1–8. doi: 10.1186/s12983-016-0143-3
- Lilley TM, Prokkola JM, Johnson JS, et al (2017) Immune responses in hibernating little brown myotis (*Myotis lucifugus*) with white-nose syndrome. Proc R Soc B Biol Sci 284:20162232. doi: 10.1098/rspb.2016.2232
- McManus JJ (1974) Activity and thermal preference of the little brown bat, *Myotis lucifugus*, during hibernation. J Mammal 55:844–846
- McNab BK (1974) The Behavior of Temperate Cave Bats in a Subtropical Environment. Ecology 55:943–958. doi: 10.2307/1940347
- Messer PW, Petrov DA (2013) Population genomics of rapid adaptation by soft selective sweeps. Trends Ecol Evol 28:659–669. doi: 10.1016/j.tree.2013.08.003
- Moosman PR, Warner DP, Hendren RH, Hosler MJ (2016) Potential for monitoring eastern small-footed bats on talus slopes. Northeast Nat 22:1–13. doi: 10.1656/045.022.0102
- Nagel A, Nagel R (1991) How do bats choose optimal temperatures for hibernation? Comp Biochem Physiol Part A Physiol 99:323–326
- Neubaum DJ (2018) Unsuspected retreats: autumn transitional roosts and presumed winter hibernacula of little brown myotis in Colorado. J Mammal 99:1294–1306. doi: 10.1093/jmammal/gyy120
- Perry RW (2013) A review of factors affecting cave climates for hibernating bats in temperate North America. Environ Rev 21:28–39
- Raesly RL, Gates JE (1987) Winter habitat selection by north temperate cave bats. Am Midl Nat 118:15–31
- Richter AR, Humphrey SR, Cope JB, Brack VJ (1993) Modified cave entrances: Thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Conserv

Biol 7:407–415

- Thawley CJ, Langkilde T (2017) Attracting unwanted attention: generalization of behavioural adaptation to an invasive predator carries costs. *Anim Behav* 123:285–291
- Thomas DW, Dorais M, Bergeron, Jean-Marie (1990) Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *J Mammal* 71:457–479
- Thomas DW, Fenton MB, Barclay RMR (1979) Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behavior. *Behav Ecol Sociobiol* 6:129–136
- Thomas DW, Geiser F (1997) Periodic arousals in hibernating mammals: is evaporative water loss involved? *Funct Ecol* 11:585–591
- Tuttle MD, Kennedy J (2002) Thermal requirements during hibernation. In: Kurta A, Kennedy J (eds) *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Austin, pp 68–78
- Twente JW (1955) Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology* 36:706–732
- Verant ML, Boyles JG, Waldrep WJ, et al (2012) Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. *PLoS One* 7:e46280. doi: 10.1371/journal.pone.0046280
- Webb PI, Speakman JR, Racey P a. (1996) How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Can J Zool* 74:761–765. doi: 10.1139/z96-087