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COMMENT

Cooling subterranean environments for climate adaptation and disease management: reply to Meierhofer et al.

Brent J. Sewall[1] | **Gregory G. Turner**[2] | **Michael R. Scafini**[2] | **Joseph S. Johnson**[3]

[1]Department of Biology, Temple University, Philadelphia, Pennsylvania, USA

[2]Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA

[3]Department of Biological Sciences, Ohio University, Athens, Ohio, USA

Correspondence
Brent J. Sewall, Department of Biology, Temple University, 1900 N. 12th Street, Philadelphia, PA 19122, USA.
Email: bjsewall@temple.edu

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Climate change has become increasingly evident globally, especially in more northerly regions, with warming trends virtually certain to continue over the coming decades (IPCC, 2021). Meierhofer et al. (2022) note that current and predicted future climate trends are likely to cause particular harm to specialized species in subterranean environments because such species often have narrow physiological tolerances and limited ability to disperse (Mammola et al., 2019).

To date, conservation efforts designed to maintain biodiversity or promote ecological resilience in the face of climate change have focused primarily on identifying, protecting, and restoring climate refugia (e.g., Maxwell et al., 2019) or facilitating community shifts to favor species well adapted to current or expected environmental conditions (e.g., Hylander et al., 2021). In contrast, the application of climate adaptation—anthropogenic modification designed to cope with current and future climate changes (IPCC, 2018)—to natural systems has rarely been undertaken and systematically evaluated, apart from in a few iconic animal species (Mason et al., 2021). Current efforts and tools for climate adaptation therefore remain far too limited to conserve the diversity of species and communities that will be harmed by climate change. In this context, we greatly appreciate Meierhofer et al.'s essay noting that the techniques we recently described for manipulating underground environments to conserve bats threatened by an invasive pathogen (Turner et al., 2022) could also be applied to protect other subterranean species from the worst effects of climate change.

In Turner et al. (2022), we examined how hibernacula microclimates modify bat responses to white-nose syndrome (WNS), a deadly infectious disease that has caused widespread, precipitous declines in several hibernating bat populations across eastern North America (Cheng et al., 2021). We found that, in the 8 years following mass mortality and pervasive regional contamination of hibernacula, 4 of the 5 bat species we studied increased or were found in higher numbers in hibernacula that were relatively colder or drier or both (i.e., hibernacula with midwinter temperatures of 3–6 °C and water vapor pressure deficits of 1–1.6 kPa). We further evaluated whether manipulative cooling of relatively warm, little-used hibernacula could benefit bats and found that within 2–5 years after cooling, bat numbers increased in at least 3 bat species due to population growth, immigration, roost shifts, or a combination. Together, these results suggest that bat population response to WNS is mitigated by microclimatic conditions in hibernacula and that, under appropriate conditions, hibernating bat species respond favorably to microclimate manipulation.

Our work on disease mitigation took advantage of the different ways in which microclimates affect the pathogen and the bat host. Relatively cold, dry conditions are less favorable for growth of *Pseudogymnoascus destructans* (Pd), the invasive fungal pathogen that causes WNS (Verant et al., 2012; Marroquin et al., 2017), yet such conditions are often suitable for bat hibernation (Haase et al., 2021). Thus, cooling may provide bats a microclimatic refuge from Pd. Meierhofer et al. note, however, that our technique of one-time engineering of entrance geomorphology to modify interior microclimates could be adopted for a different conservation goal. Specifically, manipulative cooling could be extended to proactively or reactively protect sensitive cave species or even entire subterranean communities from harmful effects of climate change. In the same vein, we add that manipulative cooling to counteract climate change could similarly benefit bats, by keeping hibernacula within optimal temperature ranges for hibernation. Temperature decreases we obtained (2.1 °C on average, maximum 6.3 °C) are of a sufficient scale to offset observed climate changes (atmospheric surface temperatures over land have increased 1.59 °C above the 1850–1900 average [IPCC, 2021]) and those expected in the coming decades. Thus, although managers have few tools to shield local biodiversity from warming in most terrestrial, freshwater, or marine habitats, manipulative cooling could feasibly counteract warming climates in some subterranean environments. Manipulations of entrance geomorphology are unlikely to address some effects of climate change on subterranean communities, such as alterations of hydrological regimes. Still, if carefully calibrated, such manipulations could retain interior temperatures close to historical baselines, despite the warming underway outside.

Meierhofer et al. also sound a strong note of caution about this type of manipulation. They argue that, whether for disease or climate change mitigation, manipulations themselves could have unintended consequences, including alterations to other factors beyond temperature, such as airflow, relative humidity, and water chemistry, to which diverse native biota may also be sensitive. We strongly agree that a precautionary approach is needed when considering manipulation of sites that harbor sensitive species or intact subterranean communities, given that troglobitic and troglophilic organisms are poorly understood.

However, manipulative cooling of sites with currently low biodiversity value may often be sufficient for disease or climate change mitigation in bats. Meierhofer et al. focus primarily on caves harboring relatively intact subterranean communities. However, precisely to avoid or minimize potential negative effects on these communities, we targeted anthropogenic sites (mines and tunnels) and caves that have been heavily affected by past human use. Such sites may be less likely than intact natural caves to harbor sensitive species because they may be of relatively recent origin, may have undergone more extensive or recent anthropogenic disturbance, may be less complex in structure, and may have different substrate types. Such sites are common. In Pennsylvania (U.S.A.) alone, there are >5000 abandoned mines (PASDA, 2021), and most that have been surveyed have no sensitive invertebrate or vertebrate species and are not used by bats. To be clear, some anthropogenic sites do have high biodiversity value. Thus, a candidate site should be comprehensively surveyed for sensitive or rare species, and it should not be assumed that such species are absent due to a site's anthropogenic origin or history of heavy modification. The point is that careful selection of sites for cooling should often enable disease or climate change mitigation in bats while avoiding potential risks to broader biodiversity in subterranean ecosystems.

Other reasons for caution about such manipulation relate to bats themselves. For instance, the coldest and driest locations we studied were most suitable for most hibernating bat species (Turner et al., 2022), but we did not examine very cold (<3 °C) or dry (>1.6 kPa) sites or sites that were highly variable. We hesitate to extrapolate our results to such sites because hibernacula microclimates that are too cold or variable can impose large costs on bats (Boyles et al., 2020), and environments that are too dry increase bats' evaporative water loss and can be unsuitable for bat species not adapted to hibernating in unsaturated environments (Haase et al., 2021). Furthermore, not all bat species benefit equally from manipulative cooling. *Perimyotis subflavus* declined in the coolest sites and sought out warmer sections of manipulated sites (Turner et al., 2022). In Pennsylvania, though, relatively warm sites are abundant, and cooling a small portion of these sites seems unlikely to harm *P. subflavus* at the landscape level, but could expand the limited availability of winter habitat for other locally hibernating species. Thus, a clear-eyed evaluation of which species will benefit from microclimate manipulations and where and how this fits into a broader management picture should be completed prior to implementing a manipulation project.

Moreover, the need for caution does not necessarily imply that no action should be taken, and we acknowledge the perils of failing to take advantage of subterranean habitats for conservation. In bats, WNS has caused mass mortality events at thousands of hibernacula in North America, resulting in severe or pervasive threats to multiple bat species (Cheng et al., 2021). Even before WNS affected North American bats, the number of underground habitats with conditions suitable for hibernation was low in some areas. For instance, in Pennsylvania, the mean annual surface temperature (MAST) is about 11.8 °C (PRISM Climate Group, 2022), meaning most underground sites there are unsuitable or at best marginal for bat hibernation, except where geomorphology or other factors drive internal temperatures below MAST (McClure et al., 2020). This, combined with bats' ongoing shift to colder roosts after the onset of WNS (Johnson et al., 2016; Turner et al., 2022), means some bat species have increasingly aggregated in a few cold sites (Turner et al., 2022), a trend that seems set to continue as warming of existing refugia increases both bat energy expenditure during hibernation and *P. destructans* growth rates. Similarly, the risk of taking no action to protect other sensitive cave species and subterranean communities from climate change should be carefully balanced against potential risks of manipulative cooling. Maintaining or expanding habitat for bats and other sensitive cave species may alleviate extinction risk by reducing the probability that a large portion of the population is lost by stochastic events (e.g., flooding or entrance collapse) or human disturbance at one or a few sites.

Importantly, insectivorous cave bats of North America are keystone species both in subterranean ecosystems, where they provide energy and nutrient subsidies to many troglobitic and troglophilic species, and in aboveground environments, where they regulate arthropod populations and provide pest control services vital to the agricultural sector (Kunz et al., 2011). Management steps favoring bat persistence and recovery in light of invasive pathogens and climate change therefore can contribute important secondary benefits to subterranean and aboveground ecological communities and to people. We urge further investigations of the effectiveness of manipulative cooling in mitigating accelerating threats from disease and climate change in bats and sensitive subterranean communities.

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ORCID

Brent J. Sewall https://orcid.org/0000-0001-8714-571X
Gregory G. Turner https://orcid.org/0000-0002-5022-9554
Joseph S. Johnson https://orcid.org/0000-0003-2555-8142

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