

A review of factors affecting cave climates for hibernating bats in temperate North America

Roger W. Perry

Abstract: The fungal pathogen *Geomyces destructans*, which causes white-nose syndrome in bats, thrives in the cold and moist conditions found in caves where bats hibernate. To aid managers and researchers address this disease, an updated and accessible review of cave hibernacula and cave microclimates is presented. To maximize energy savings and reduce evaporative water loss during winter, most temperate vespertilionid bats in North America select caves with temperatures between 2 and 10 °C, with 60%–100% relative humidity. Generally, the temperature in caves is similar to the mean annual surface temperature (MAST) of a region, which varies by latitude, altitude, and topography. However, MAST for most areas where caves are found in eastern North America is well above 10 °C. Thus, various factors cause cold-air infiltration that reduces temperatures of these caves during winter. These factors include depth of cave, topographic setting, airflow patterns, cave configuration, and water infiltration. Factors affecting humidity, condensation, and evaporation are also addressed. In areas where MAST is above or below the thermal requirements of *Geomyces destructans*, many caves used by bats as hibernacula may still provide favorable sites for optimal growth of this fungus.

Key words: bats, caves, hibernacula, humidity, microclimate, mines, temperature, white-nose syndrome.

Résumé : L'agent pathogène fongique *Geomyces destructans* que casues nez blanc syndrome, se développe dans les conditions froides et humides trouvées dans les grottes où hibernent les chauves-souris. Pour aider les gestionnaires et chercheurs à adresser cette maladie, une revue, mise à jour et accessible, des hibernacles et des microclimats des grottes est présentée. Afin de maximiser les économies d'énergie et réduire les pertes d'eau par évaporation pendant l'hiver, la plus part des chauves-souris vespertilionidés occupants les climats tempérés de l'Amérique du Nord sélectionne des grottes avec des températures entre 2 et 10 °C, avec une humidité relative d'environ 60 % – 100 %. Généralement, la température dans les grottes est semblable à la moyenne annuelle de la température de surface (MATS) d'une région, qui varie selon la latitude, l'altitude et la topographie. Toutefois, la MATS pour la plupart des régions où les grottes se trouvent dans l'Est de l'Amérique du Nord est bien supérieure à 10 °C. Ainsi, divers facteurs entraînent des infiltrations d'air froid qui réduisent la température des grottes pendant l'hiver. Ces facteurs comprennent: la profondeur de la grotte, le contexte topographique, les patrons de circulation d'air, la configuration de la grotte, et l'infiltration d'eau. Les facteurs affectant l'humidité, la condensation et l'évaporation sont également abordés. Dans les zones où la MATS est au-dessus ou en dessous des exigences thermiques de *Geomyces destructans*, de nombreuses grottes utilisées par les chauves-souris comme hibernacles peuvent fournir des sites favorables pour une croissance optimale de ce champignon.

Mots-clés : chauves-souris, grottes, hibernacle, humidité, microclimat, mines, température, nez blanc syndrome.

1. Introduction

Bats that hibernate below ground in caves and mines of temperate regions receive two crucial benefits: relatively stable, above-freezing temperatures at which they can achieve energy-saving long-term torpor; and high humidity, which reduces evaporative water loss during hibernation (Speakman and Thomas 2003). The low temperatures and high humidity that sustain bats during hibernation are also highly conducive for growth of *Geomyces destructans*, the fungus that causes white-nose syndrome (WNS) (Blehert et al. 2009). WNS has decimated bat populations throughout eastern North America. Recent estimates suggest 5.7–6.7 million bats of at least six bat species have died due to WNS (USFWS 2012). Growth requirements of *G. destructans* are similar to temperatures found in most bat hibernacula. Isolates of *G. destructans* grow between 5 and 20 °C, and isolates from the northeastern US grow optimally around 12–13 °C (Blehert et al. 2009; Verant et al. 2012).

The emergence of WNS has refocused interest on the physical factors that influence cave microclimates and how cave microclimates could potentially interact with growth of *G. destructans* and

affect bat survival. Thus, an updated and easily accessible review on the interrelationships among the physical attributes of caves, cave climates, and bat hibernation is beneficial for researchers and managers to respond to this emergent issue. This review may help researchers decipher various questions, such as why caves just a few kilometres apart differ widely in WNS mortality. Recent landscape-scale modeling in the northeastern US suggested that patterns of mortality from WNS are attributed mostly to land cover, mean temperature, elevation, and frequency of precipitation (Flory et al. 2012). All these physical factors affect the climate within individual caves, which could possibly affect the growth of *G. destructans* at those sites.

It has been 35 years since Tuttle and Stevenson (1978) published their synopsis of factors affecting cave microclimates for bats, and almost 60 years since the seminal work of Twente (1955) on cave selection by bats. Much of the original research covering cave climatology was published decades ago in languages other than English and is often hard to obtain. Nevertheless, a summary of

Received 13 August 2012. Accepted 18 October 2012.

R.W. Perry, United States Department of Agriculture Forest Service, Southern Research Station, P.O. Box 1270, Hot Springs, AR 71902, USA.

E-mail for correspondence: rperry03@fs.fed.us.



current knowledge of cave climatology as it relates to bat ecology is needed.

Twente (1955) defined “caves” as having a single entrance, whereas “caverns” have multiple openings, a definition apparently lost over the years. By modern definition, a cavern is simply a large cave. Herein, the term “cave” is used throughout, regardless of cave size or number of openings. Many of the principles that apply to caves also apply to abandoned mines and other below-ground sites used for hibernation, such as culverts, tunnels, storm sewers, cellars, and rock crevices. The importance of abandoned mines should not be overlooked as important bat hibernacula. Thousands of abandoned mines occur throughout North America, and a survey of over 6000 mines in the western US indicated 30%–60% show signs of bat use (Tuttle and Taylor 1998).

In temperate areas, caves can roughly be divided into three principle types based on use by bats: (1) caves used during summer including those used as maternity sites; (2) winter hibernation caves; and (3) transient caves used during migration, autumn swarming, or as staging areas when outside temperatures are variable in spring and autumn (e.g., Barbour and Davis 1969). In most cases, caves used in summer differ from those used in winter (e.g., Tinkle and Patterson 1965; Tuttle and Stevenson 1978), although bats often use the same caves for swarming that they use as hibernacula (e.g., Ingersoll et al. 2010). Female bats that use caves as maternity roosts during summer require warm temperatures for successful rearing of offspring that differ from climates needed for hibernation. However, some males may remain in the same caves during summer they use for hibernation during winter (Barbour and Davis 1969). Some species primarily use trees for roosting during summer but hibernate in caves and mines (e.g., Perry 2012). Because winter hibernation is the period when mortality from WNS is expected, this review focuses on winter cave climates during bat hibernation.

In general, latitude, the physical structure of caves, and airflow are the primary drivers of cave climates in temperate areas, but various biological factors may also affect cave temperature that will not be discussed at length. For example, in caves occupied during the active seasons (e.g., summer), large colonies of bats (>1 million) and their fermenting feces may maintain constant temperatures within a cave, regardless of changes in outside temperature (e.g., Harris 1970; Stoev and Maglova 1993). Heat given off by humans entering caves may also affect temperatures and humidity (e.g., Pflitsch and Piasecki 2003; Domominguez-Villar et al. 2010).

2. Importance of hibernacula temperature to bats

Because of their small size, small mammals can support resting energetic requirements for less than a month on their fat reserves (Humphries et al. 2004). During winter, insect abundance is reduced to near zero in northern latitudes during winter, and insects may not be available for over 150 days in northern areas such as the Canadian Prairies (Lausen and Barclay 2006). In more southerly latitudes such as Florida, insects may be available on warmer (>5.0 °C) nights throughout winter (Frost 1962). Thus, insectivorous bats at northerly latitudes either migrate to warmer climates or hibernate in relatively stable environments to survive periods of food scarcity and avoid remaining active at low temperatures that are energetically costly (e.g., Fleming and Eby 2003). The length of hibernation is dictated by the length of time that bats cannot successfully forage, and bats may hibernate for longer periods at more northerly latitudes. For example, *Myotis lucifugus* (little brown bat) may hibernate for 40% longer in Ontario than in Missouri (Humphries et al. 2005).

Torpor is whereby a bat reduces its metabolism and its body temperature is reduced to near ambient, which results in energy savings. Long-term, deep torpor is considered hibernation. Hibernation allows bats to survive for long periods using relatively little

energy. Bats typically arouse from hibernation periodically and these arousals may account for over 75% of the total energy requirement for hibernation (Thomas and Geiser 1997). Although the exact causes of these periodic arousals are unknown, physiological needs, including the need to excrete waste and replenish water balance, are believed to be involved (e.g., Thomas et al. 1990; Thomas and Geiser 1997). Arousals are also temperature-dependent, with the length and frequency of bat arousals increasing with temperature increases over 10 °C (Brack and Twente 1985; Twente et al. 1985). When torpid bats are exposed to below-freezing temperatures, bats may arouse, increase their metabolic rate to prevent freezing, or maintain body temperatures similar to ambient temperatures and freeze to death (Davis and Reite 1967; Dunbar and Tomasi 2006).

The length of time temperate, insectivorous bats can sustain themselves via torpor is dictated by the temperature at which they hibernate, with low (but above-freezing) temperatures resulting in the most energy savings. McNab (1974) indicated that temperatures below 18 °C are required to allow successful hibernation and only small and solitary-hibernating species (such as *Perimyotis subflavus*, tricolored bat) can hibernate at temperatures above 14 °C in Florida. Solitary bats may also hibernate at higher temperatures than clustered bats of the same species (Clark et al. 1996). Selection of proper cave temperatures is likely important to the physical condition of bats. For example, *Myotis sodalis* (Indiana bat) lose 22% of their body mass when hibernating at 6–10 °C, but only lose 16%–18% of their body mass when hibernating at 0–6 °C over the same period (Richter et al. 1993).

The temperature at which their metabolism is most efficient during hibernation may differ among bat species (Speakman and Thomas 2003). *Myotis lucifugus* may have a minimum metabolic rate at 2 °C (Hock 1951), whereas other species such as *Lasiurus borealis* (red bat) reach their minimum metabolic rate around 5–10 °C (Dunbar and Tomasi 2006; Dunbar and Brigham 2010). *M. lucifugus* increase their energy requirements 3-fold when hibernating at temperatures 3 °C lower or 10 °C higher than their 2 °C metabolic optimum (Humphries et al. 2002). However, minimum metabolic rates may vary within a species based on latitude. *Eptesicus fuscus* (big brown bat) in northern latitudes may have minimum metabolic rates at 2 °C, whereas individuals from southern latitudes may have minimal metabolic rates near 10 °C (Dunbar and Brigham 2010). Thus, bats of the same species hibernating in more northerly climates may be adapted to different hibernation temperatures than those in more southerly locations.

Hibernation has physiological costs, including buildup of metabolic wastes, dehydration, and decreased immune function (e.g., Thomas and Cloutier 1992; Thomas and Geiser 1997; Burton and Reichman 1999). Bats may lessen the adverse effects of long-term torpor by hibernating at warmer temperatures when they can afford to based on fat stores (Humphries et al. 2003) and the length of required hibernation. Bats may select maximum tolerated temperatures for hibernation rather than the minimum temperatures (McNab 1974). In addition, individual bats may select different microsites based on physical condition, with heavier individuals (in better condition) hibernating in warmer sites than individuals in poorer condition (Boyles et al. 2007).

Bats are often found hibernating at a relatively wide range of temperatures, and the literature abounds with references to hibernacula temperatures. Differences among studies in latitude of the study, type of hibernacula surveyed, number and timing of measurements, and variability in temperature at sites selected for hibernation present wide ranges in hibernation temperatures and substantial overlap when examining data from multiple studies. For example, Webb et al. (1996) summarized 16 studies that found *E. fuscus* hibernating between –10 and 20 °C, 14 studies that found *M. lucifugus* hibernating between –4.0 and 13.0 °C, and 10 studies that found *Corynorhinus townsendii* (Townsend's big-eared bat) hibernating between –2.0 and 21.0 °C. Webb et al. (1996) indicated

Table 1. Mean ambient temperatures and relative humidity of hibernation sites for eastern US bats, derived from studies where simultaneous measures of microclimate for different species were taken.

Measure and location	<i>Myotis lucifugus</i>	<i>Myotis sodalis</i>	<i>Myotis septentrionalis</i>	<i>Eptesicus fuscus</i>	<i>Perimyotis subflavus</i>	<i>Corynorhinus rafinesquii</i>	<i>Lasiorycteris noctivagans</i>
Temperature (°C)							
Ohio ^a	7.2	8.4	9.1	9.5	9.6		
Northeast US ^b	7.5	7.0	6.9	7.1	10.9		
South Illinois ^b	8.8		9.7	4.2	10.3	5.1	5.2
Relative humidity (%)							
Northeast US	73.2	78.0	65.2	67.3	84.8		

Note: Data for Ohio are from Brack (2007); data for northeast US are from Raesly and Gates (1987); and data for South Illinois are from Pearson (1962).

^aSubstrate temperature.

^bAmbient temperature.

that the modal hibernacula temperature for 29 vespertilionid species is 6 °C. However, studies suggest different species may favor different temperatures for hibernation (e.g., Nagel and Nagel 1991; Raesly and Gates 1987). Although numerous studies that focused on individual species have quantified the temperatures of hibernacula at a single site or geographic area (e.g., Clark et al. 1996; Briggler and Prather 2003; Hayes et al. 2011), comparative studies of selection for temperature among species at similar latitudes using similar methods may provide better estimates of potential selection of temperature among communities (Table 1). Although bats may hibernate across a range of temperatures within a geographic location, this range may be within the bounds for successful hibernation based on fat stores and length of hibernation period required (Humphries et al. 2002). Energetic-based models on a range of hibernacula temperatures used by little brown bats predict 80% of hibernacula allow survival with minimal fat reserves, whereas all selected hibernacula allow successful hibernation with maximum fat reserves (Humphries et al. 2002).

Based on extensive research, some species appear to favor hibernacula within a narrow temperature range. For example, *Myotis grisescens* (gray bat) hibernate at mean temperatures of 6.7–10.0 °C (Tuttle 1977), *M. sodalis* select sites with mid-winter temperatures of 3–6 °C (Clawson 2000), and clustered *Corynorhinus townsendii ingens* (Ozark big-eared bat) hibernate between 5.5 and 11.2 °C (Clark et al. 1996). Brack (2007) suggested that hibernacula above 10 °C are less than optimal for many species of bats, although he did not account for latitude and length of required hibernation. Substantial information has been published on hibernacula temperatures used by endangered species such as *M. sodalis*, and hibernacula temperatures have been suggested as a possible reason for declines in this species. Among *M. sodalis* populations over a 20-year period, populations in hibernacula that were 3.0–7.2 °C showed substantial increases, whereas populations hibernating at temperatures outside this range decreased (Tuttle and Kennedy 2002). Tuttle (1977) suggested that increasing hibernacula temperatures by 2 °C may have resulted in significant population declines of *M. sodalis*.

Other species, such as *P. subflavus*, may tolerate higher hibernacula temperatures and large fluctuations in temperature compared with other species (Davis 1970). McNab (1974) suggested that *P. subflavus* always select the warmest temperatures available for hibernation, which are as low as 7 °C in Ontario and as high as 13 °C in Kentucky. In Maryland, Pennsylvania, and West Virginia, *P. subflavus* hibernate at sites with significantly warmer temperature than sites for *M. sodalis*, *M. lucifugus*, *Myotis septentrionalis* (northern long-eared bat), and *E. fuscus* (Raesly and Gates 1987). In Arkansas, *P. subflavus* hibernate in caves significantly warmer than random caves, with temperatures ranging from 5.0 to 16.0 °C (mean = 11.8 °C) (Briggler and Prather 2003).

3. Factors affecting cave and mine temperatures

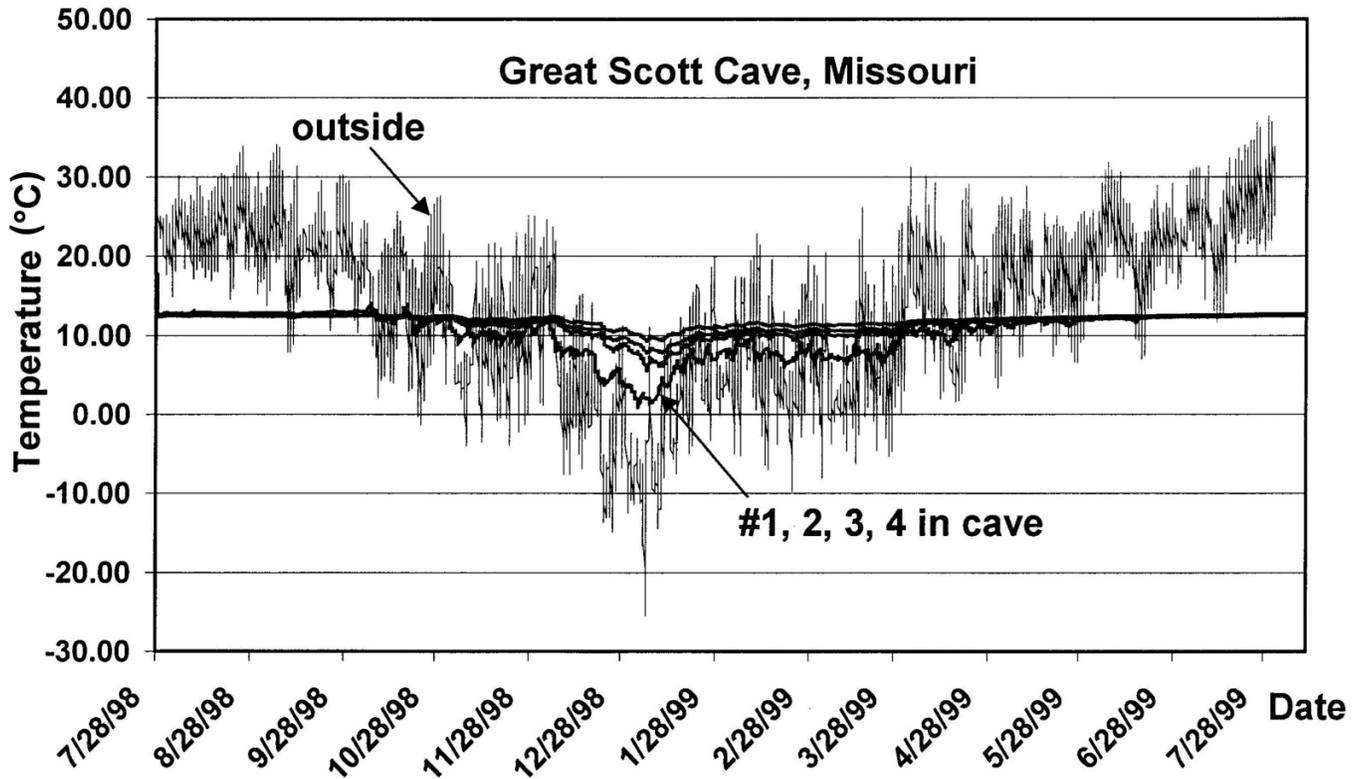
A cave (or mine) is divided into three separate environments: (1) the highly variable twilight zone near the entrance; (2) a middle zone of complete darkness and variable temperature; and (3) a zone of complete darkness and constant temperature in the deep interior (Poulson and White 1969). However, numerous factors affect the climate of an individual cave; and each cave is unique based on its diameter, shape, depth, and its placement in the landscape. The number and size of openings, position of the entrance, passage size, overall cave volume, amount and seasonal timing of water flow, air flow, and outside temperatures are all complicating factors affecting climates within individual caves (Tuttle and Stevenson 1978).

Temperatures generally increase with an increase in depth below the Earth's surface due to radioactive decay and the Earth's accretion, and this geothermal gradient averages around 2–3 °C/100 m in bore holes and mines (Press and Siever 1978) but varies across regions. Areas that are geologically stable (such as eastern North America) may have lower geothermal gradients (less temperature increase with an increase in depth) than areas that are geologically active such as western North America (Roy et al. 1972). Because of air and water infiltration, temperature gradients in caves are generally less than the geothermal gradient, and geothermal heat flux probably has only a minor effect on cave climates unless caves are very deep (Pflitsch and Piasecki 2003). However, geothermal heat may increase temperatures 2.6 °C above that expected at a depth of only 15 m in Kartchner Caverns, Arizona (Buecher 1999).

Temperature profiles in caves can be divided into two primary zones, the heterothermic zone near the surface and the deeper homothermic zone (Luetscher and Jeannin 2004a). The heterothermic zone occurs from the surface to around 50 m below the surface but may reach depths >100 m (Luetscher and Jeannin 2004a). This zone shows seasonal, and often daily, temperature variations and is greatly affected by outside temperatures (Fig. 1). The influence of outside weather conditions may extend for several hundred metres into caves which have streams or airflow (Cropley 1965). Within the heterothermic zone, there is generally a temperature and moisture gradient, where air characteristics change from outside conditions to reach equilibrium with the cave rock (de Freitas and Littlejohn 1987).

The homothermic zone is an area of temperature stability, where temperature increases with depth below the surface by around 0.4–0.6 °C/100 m, which is often less than the geothermal gradient due to air or water infiltration and is more similar to the lapse rate (see below) above the surface (Pflitsch and Piasecki 2003; Luetscher and Jeannin 2004a). In the absence of complicating factors such as airflow, temperature in the homothermic zone of caves is generally a reflection of the mean annual surface temperature (MAST) (Fig. 2) (e.g., Poulson and White 1969; Wigley and Brown 1976; Luetscher et al. 2008). During summer in temperate

Fig. 1. Typical annual variation in cave temperatures used as a bat hibernaculum in the Missouri Ozarks where the mean annual surface temperature (MAST) of the region is approximately 13 °C. Line Nos. 1–4 correspond with temperature loggers placed at increasing distances from the cave opening (30–150 m). Temperatures deeper in the cave are close to 12 °C but remain below 10 °C near the entrance during most of the winter (line No. 1; lowest line). Internal cave temperatures reach a low in mid-January. Areas closest to the entrance (line No. 1) show the lowest winter temperatures but the greatest temperature variability. *Myotis sodalis* hibernate at location No. 1 but move further into the cave during colder winter periods. From Elliott and Clawson 2001 with permission.



regions, outside temperature is usually greater than MAST, whereas outside temperatures are usually less than MAST during winter. Various factors affect MAST, including latitude, elevation, snow cover, slope angle, aspect, and vegetation cover (Blackwell et al. 1980; Lewis and Wang 1998). Mean temperature of caves typically decreases with an increase in latitude because of decreasing MAST. In areas that experience little fluctuation in annual temperatures such as tropical regions, caves deviate only slightly from the MAST (Luetscher and Jeannin 2004a).

Based on broad MAST estimates alone (Fig. 2), no caves or mines in eastern North America south of Pennsylvania and Iowa should have cave temperatures in the optimal range for most cave-hibernating species (3.0–10.0 °C). However, individual caves and mines with winter temperatures within the optimal temperature range are found throughout this region, from northern Florida to Arkansas and Oklahoma northward (e.g., Saugey et al. 1990; Clawson 2002; Briggler and Prather 2003; Gore et al. 2012). Most of the caves in the region where MAST is 10.1–18.3 °C are unsuitable as bat hibernacula (Tuttle and Stevenson 1978). For example, Tuttle and Stevenson (1978) suggested that *M. grisescens* are limited in their southern distribution by the lack of cold hibernating sites in southern caves, and only about 0.1% of caves in Alabama are known to harbor this species in winter. Thus, physical characteristics, such as cave structure and topographic setting of individual caves, may reduce or increase temperatures compared with MAST.

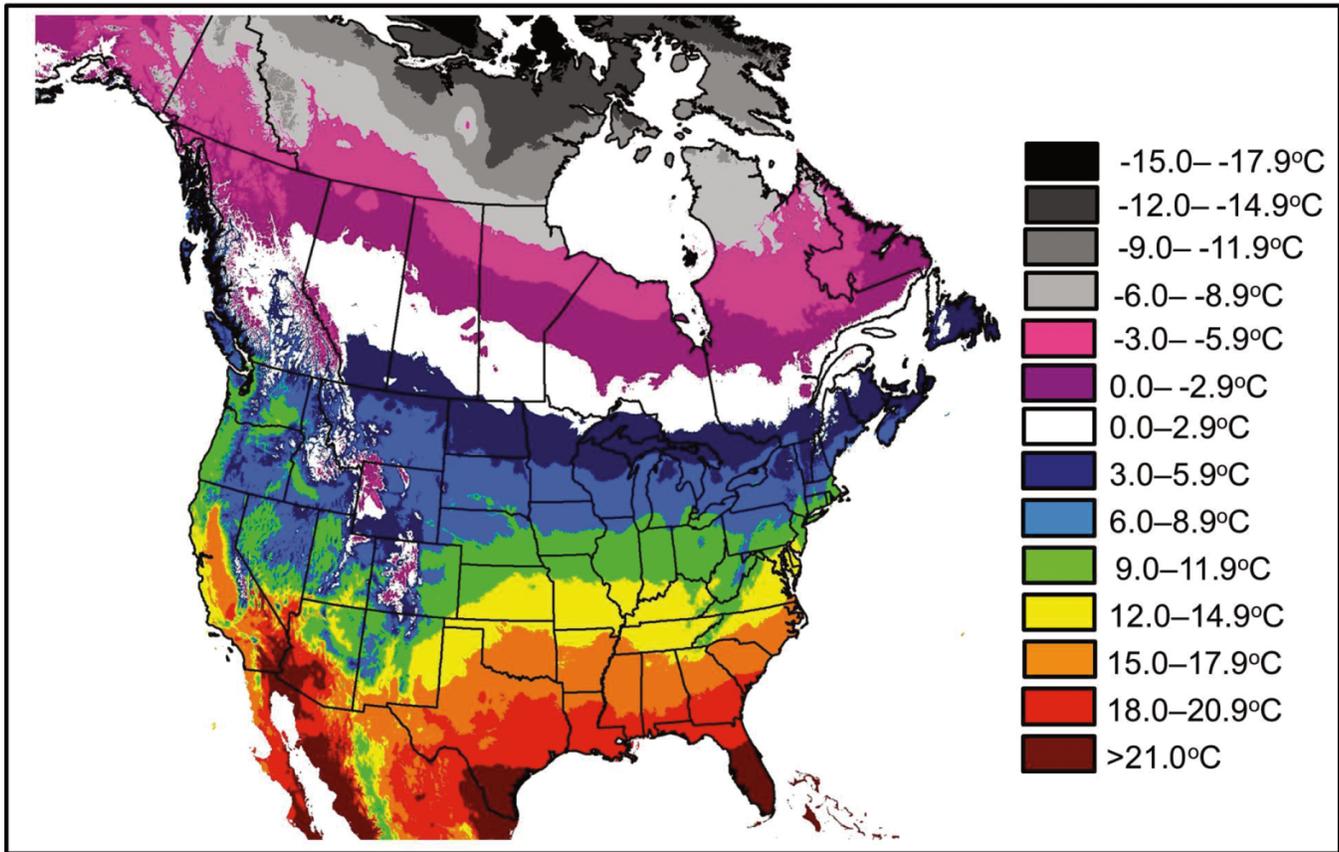
In some caves located in areas where MAST is >10 °C, bats may hibernate close to the entrances where colder outside air mixes with warmer cave air during winter. Twente (1960) examined over 500 caves and mines in Utah and suggested all are either too warm

(>12 °C) or cold for hibernating bats deeper than the twilight zone. However, *Corynorhinus townsendii* may occasionally be found near the entrances of these sites (Davis 1970). Although sites near the entrances of caves may provide colder temperatures than deeper areas of the cave during winter (and warmer temperatures than outside) (Fig. 1), these areas can be highly variable in temperature and occasionally fall below freezing (Elliott and Clawson 2001).

3.1. Topographic setting of caves

Cave climates may vary based on the topography where those caves are located due to topographic effects on MAST. In northern latitudes, southern aspects receive greater solar radiation than both horizontal sites and north slopes, and radiation received depends on the steepness of the slope (Barry 1992). Alternatively, north slopes may remain cooler because the ground is often shaded and persistent snow cover may enable frost to penetrate deep into the ground (Barry 1992). Caves on north slopes may remain cooler than those on south slopes because of lower MAST (Tuttle and Stevenson 1978; Pflitsch and Piasecki 2003). Orientation of the entrance may also affect temperatures, with cooler north winds or warmer south winds flowing directly into caves (e.g., Smithson 1991). Sinking cold air on hillsides (slope drainage) into small enclosed valleys during clear, calm nights may create temperature inversions up to 30 °C (frost hollows or frost pockets) (Barry 1992), which are sometimes demarcated by visible bowls of mist or fog. Inversions are temperature increases at higher altitudes instead of decreases as is typical. Thus, entrances in valleys may draw in colder air masses than entrances on hill tops during winter (Pflitsch et al. 2010). Forest cover may also reduce MAST

Fig. 2. Broad-scale mean annual surface temperature (MAST) in temperate North America.



and ground temperatures may be 2 °C cooler in forests that in adjacent clearings (Blackwell et al. 1980).

It is generally known that air temperature decreases with an increase in elevation. The rate at which temperature decreases with an increase in height is termed “lapse rate.” Lapse rates may vary by season, time of day, aspect, wind direction, humidity, topography, presence of snow, atmospheric stability (tendency of air to move vertically), cloud cover, and ground cover (Barry 1992). Mean lapse rates are around $-0.6\text{ }^{\circ}\text{C}/100\text{ m}$ rise in elevation (Barry 1992). Higher elevations typically have lower MAST and lower cave temperatures than the surrounding area (e.g., Davis et al. 2000; Nagy and Postawa 2011).

Bat hibernation studies that examined elevation of caves or mines suggest effects of elevation may vary by region, and studies of caves in different temperate areas have found different results. Bats have been found hibernating in caves or mines as high as 3200 m in mountainous areas (Szewczak et al. 1998). Kryštufek (2007) suggested bats use caves at low elevations because that is where the caves tend to be located in his study area. Others suggest that different species may prefer different elevations, resulting from their species-specific hibernation preferences for temperature (Rehák 2006; Nagy and Postawa 2011). For example, Nagy and Postawa (2011) suggested that among bats hibernating in Romanian caves, some species hibernate at the higher temperatures found at lower elevations, while other species hibernate in caves with colder temperatures found at mid- to higher elevations. In coastal areas of western Canada, *Myotis* spp. may hibernate primarily in deep portions of higher elevation caves where temperatures remain cold but stable (Davis et al. 2000).

Drastic changes in elevation may occur over relatively short distances in mountainous areas, which make predicting favorable cave structure across these regions more difficult. For example,

sites <80 km apart may differ in MAST by over 8.4 °C in western areas such as New Mexico and Arizona (Fig. 2). Cave configurations that are favorable for hibernacula in one area may make them unfavorable a short distance away at a different elevation. Mean temperature of hibernacula used by bats may remain relatively constant even though caves may be at considerably different elevations. For example, mean temperature of bat hibernacula is 4.7 °C at 550 m and 4.6 °C at 850 m, even though MAST differs by 2.6 °C (Nagel and Nagel 1991). Further, mean elevation of abandoned mines used as hibernacula by *C. townsendii* in Colorado (1900 m) are similar in elevation to unoccupied mines (Hayes et al. 2011). Thus, bats likely seek out individual caves or mines with the appropriate temperatures, regardless of elevation.

3.2. Temperature fluctuations in caves

In temperate regions, many caves undergo an annual temperature cycle, whereby temperatures are typically lower in winter than in summer (Fig. 1). The amplitude of change in annual cave temperature may be only a fraction of the variation in outside temperatures. For example, the range in temperature variation in Kartchner Caverns, Arizona, is only 1%–2% of the variation in outside temperature (Cigna 2002). Heat transferring through solid rock such as limestone is relatively slow. Daily fluctuations in outside temperature of 30 °C are reduced to <1 °C at a depth of 0.5 m in solid limestone, and annual temperature differences of 30 °C result in changes <1 °C below 11 m (Moore and Sullivan 1997). Thus, annual variation in cave temperature typically results from other factors such as air circulation or water infiltration. A delay often occurs between the coldest yearly outside temperatures and lowest annual temperatures in the cave, which may range from a few days to many months (Cigna 2002).

Although the temperature at a spot where a bat roosts may vary widely within a given day (Twente 1955), variability in cave temperatures during winter is an important quality affecting successful hibernation by bats. Some species may arouse after abrupt changes in temperature during hibernation (e.g., Davis and Reite 1967). Hibernacula that often fall below 0 °C may be detrimental because hibernating bats must produce metabolic heat to prevent freezing. Bats hibernating too close to the entrances may freeze to death during severe winters (Humphrey 1978). Caves that vary greatly in temperatures during winter may be marginal habitats. For example, Elliott and Clawson (2001) monitored cave temperatures in a Missouri cave that had experienced high bat mortality previously and found highly fluctuating temperatures, which declined to -8 °C after passage of a cold front.

3.3. Cave structure and airflow

Thermal convection (the movement of air caused by differing temperatures or densities) probably causes most air circulation in caves (Plummer 1962; Tuttle and Stevenson 1978). Rising warm air and sinking cold air are the primary drivers of these air movements. Thermal convection takes place due to differences between cave-wall temperature (generally close to MAST) and the outside air temperature. Thermal convection may occur by many means based on the structure of individual caves.

Caves or mines that consist of a single horizontal tunnel may have little airflow (Fig. 3A) and relatively static temperatures past the entrance (Twente 1955; Tuttle and Stevenson 1978). Caves with small entrances may have reduced or very little air circulation (Tuttle and Stevenson 1978). However, cold air intrusion may occur during winter in single-opening caves with large openings that are generally funnel-shaped. When outside temperatures are below MAST (winter), air warmed by cave walls escapes along the ceiling, which draws in cooler air along the floor (Fig. 3B) (e.g., McLean 1971). The rate of airflow in these caves is determined by the slope of the floor and ceiling (de Freitas et al. 1982).

Caves with a single entrance or multiple entrances at the same elevation that slope downward (or vertical) may act as cold sinks when temperatures are above MAST (summer) (Fig. 3C) (e.g., Geiger et al. 2003; Cigna 2004; Luetscher and Jeannin 2004b). Air cooled by cave walls sinks and may remain near the bottom without substantial circulation. During winter, these caves may also be cooler than MAST due to air circulation. Air warmed by the cave walls may rise out of vertical shafts, drawing in cold air (Fig. 3D) (Luetscher and Jeannin 2004b). Similarly, in caves with two vertical openings at the same elevation, air warmed by the cave walls can rise out one opening, drawing in cold outside air from another opening during winter (Fig. 3E) (Luetscher and Jeannin 2004b). Caves with down-sloping entrances located at the bottom of valleys may have enhanced cold infiltration (Geiger et al. 2003). Caves with up-sloping entrances may act as warm air traps when outside temperatures are less than cave-wall temperatures (winter) (Fig. 3F) (Cigna 2004). Warm air rising off cave walls may become trapped at upper reaches of these caves.

A common type of convection is the chimney effect (Fig. 3G) found in caves that have multiple openings that differ in elevation (e.g., Plummer 1962). When the outside temperature is below MAST (winter), air warmed by the cave walls rises and exits via upper openings, which draws colder outside air into the lower entrance. Alternatively, when outside temperatures are above MAST (summer), air cooled by cave walls may sink out of the lower entrances of the cave, which draws warm air into the higher openings. This process may create constant airflow. During winter in cold climates, upper entrances typically exhale air, whereas these entrances inhale air during summer. During spring and fall, the direction of flow may change between day and night, when outside air temperatures fluctuate above and below MAST. There is typically a thermal gradient in these caves with lower reaches

typically cooler than upper portions. Greater differences between outside temperature and cave-wall temperature, and greater differences in elevation of the openings result in greater airflow rates (Cigna 1968; Wigley and Brown 1976; de Freitas et al. 1982). Upper or lower entrances may not always be obvious in chimney caves and may simply consist of cracks or fissures (Plummer 1962; Wigley and Brown 1976), causing a chimney airflow that is not obvious. Texture of cave walls may also affect airflow. Rough walls create friction that reduces airflow whereas smooth walls may facilitate airflow (e.g., Twente 1955; Wigley and Brown 1976; Atkinson et al. 1983).

Tuttle and Stevenson (1978) suggested that caves with adequate structure for hibernacula can be easily predicted, with chimney types and cold-air traps having the most potential unless the caves are at high elevations or high latitudes. These types of caves may create ideal thermal conditions for many bat species, such as *M. sodalis*, *M. lucifugus*, and *Corynorhinus townsendii ingens* that require relatively cold caves in areas where MAST is generally >10 °C. However, in more northern latitudes and mountainous areas where MAST is <10 °C, chimney caves and cold-air traps are likely too variable or too cold for hibernation. In these areas, caves with little airflow or warm air traps probably provide the best climates for hibernation.

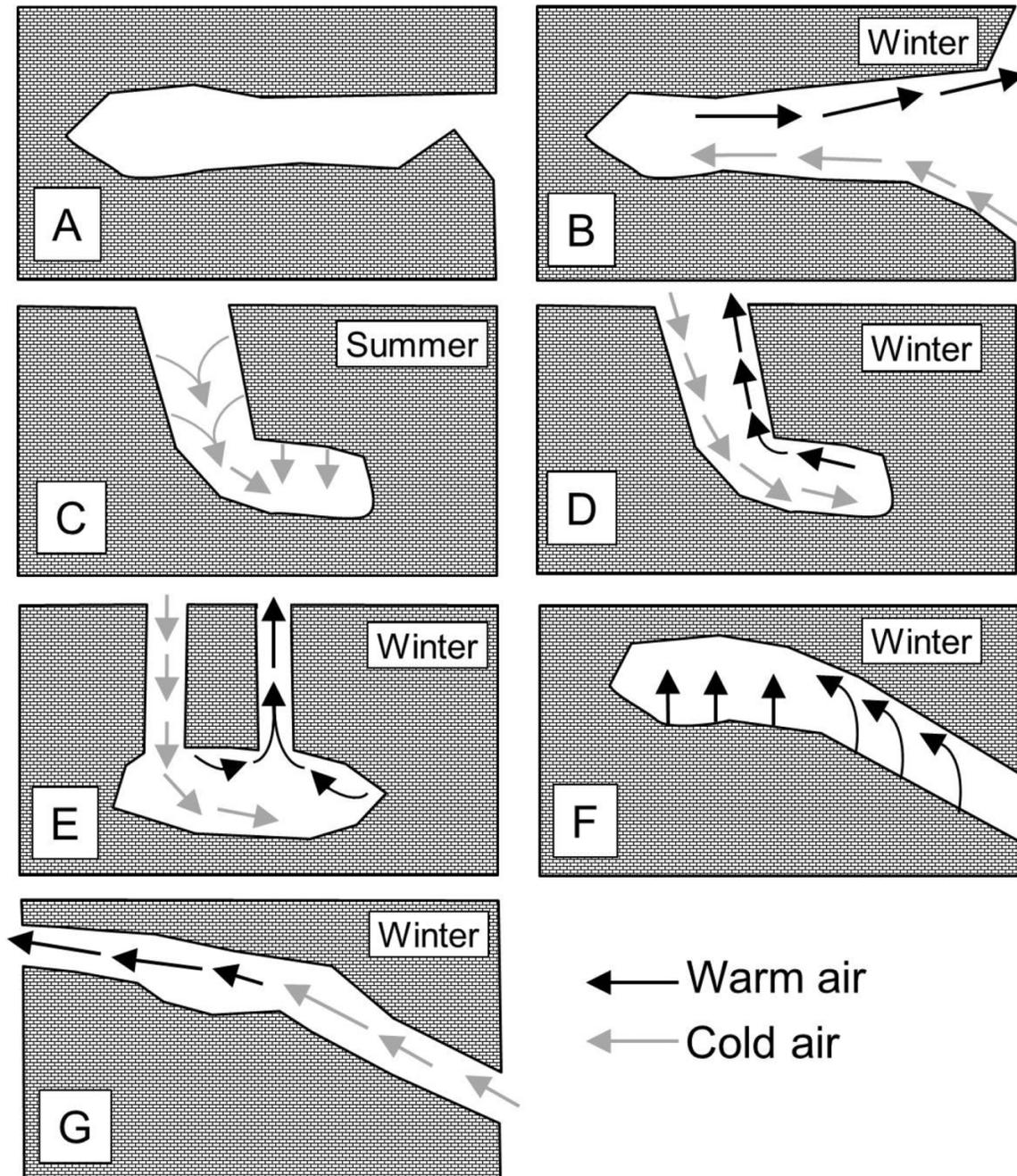
3.4. Airflow in caves from barometric pressure

Differences in atmospheric pressure outside a cave and air pressure within a cave can cause air to flow in an effort to equalize the pressure. Changes in barometric pressure can affect airflow (and temperature) into caves but is likely not as widespread a factor as thermal convection in most caves (Tuttle and Stevenson 1978). Because thermal and barometric processes are happening concurrently in many caves, the exact processes driving air movements can be difficult to discern (Pflitsch et al. 2010). In most caves (especially small caves or caves with large openings), airflows due to barometric changes are hardly measurable because of the small amounts of air being exchanged and the almost immediate equalization between outside and inside pressure (Pflitsch et al. 2010). In large caves, barometric airflow may be noticeable at small entrances and narrow tunnels between large chambers (Cigna 1968; Lewis 1991; Pflitsch et al. 2010). Changes in barometric pressure outside large cave systems such as Lechuguilla Cave, New Mexico, can create airflows >96 km/h at openings (Richards 2001).

Large- and small-scale changes in atmospheric air pressure occur frequently. Large changes occur due to weather, with cyclonic (low pressure) and anticyclonic (high pressure) systems dominating barometric pressure changes (Lewis 1991). Smaller changes in barometric pressure or pressure waves may be caused by solar cycles, atmospheric tides, the jet stream, and low-frequency sounds (Herman and Goldberg 1978; Lewis 1991). Atmospheric tides are due to heating by the sun and move in a westward direction with the movement of the sun, causing a 12-h cycle in pressure peaks (Lewis 1991). Short-duration barometric changes (generally <3 min) may occur from many natural and man-made sources, including low-frequency waves created by storms, explosions, vehicles, and the aurora borealis (Lewis 1991). Many cases of oscillations in intake and exhale of air (cave breathing) may be the result of external air pressure waves that cause fluctuations in outside barometric pressure (Lewis 1991).

Frequency, timing, and direction of barometric-driven airflows in caves differ from temperature-induced airflows such as those found in chimney caves. Airflows in chimney caves are greatly affected by season, often reversing between summer and winter, with oscillations during fall and spring (Pflitsch et al. 2010). Barometric airflows show little difference between summer and winter but can reverse direction frequently (in seconds or days) with changes in outside barometric pressure (Pflitsch et al. 2010). In chimney caves, air enters some entrances at the same time it exits others, whereas

Fig. 3. Simplified cave configurations showing air movements in various types of caves. Summer represents times when outside temperatures are above the mean annual surface temperature (MAST) and winter represents times when outside temperatures are below MAST. (A) single tunnel with little airflow; (B) air circulation in a cave with a single large opening during winter; air warmed by cave walls exits near the ceiling which draws in cold outside air near the floor; (C) cold air sink during summer whereby air is cooled by cave walls and sinks into lower portions of the cave; (D) airflow during winter in a single entrance vertical cave; air warmed by cave walls flows vertically out of cave, drawing in cold air; (E) cave with two vertical openings; air warmed by the cave walls exits one opening and the other opening draws in cold air; (F) warm air trap during winter whereby air warmed by cave walls rises to upper portion of the cave and little circulation occurs; and (G) chimney flow cave during winter; air warmed by the cave exits top opening, drawing in cold air at lower entrance. Configurations (B), (D), (E), and (G) may maintain cave temperatures below MAST during winter, whereas configuration (F) may maintain temperature near or above MAST.



barometric airflows produce simultaneous inflows or simultaneous outflows at all openings (Pflitsch et al. 2010).

Temperature distribution in chimney caves also differs from barometric caves. In chimney caves, temperatures near lower entrances are cooler than upper entrances and equilibrium in temperatures may be reached at some point between the upper and lower openings (Pflitsch et al. 2010). In barometric caves, inflow is

typically warmer than MAST during summer and cooler than MAST during winter, and the temperature gradient from openings to the inner parts of the cave is similar among all openings.

Another type of barometric effect is when two entrances are a substantial distance apart and a difference exists in barometric pressure at the two entrances (Plummer 1962). These differences in pressure lead to airflow inside the cave similar to winds caused

by differences in barometric pressure outside the cave. The Sinks of Gandy (West Virginia), a cave with two entrances approximately 1 km apart, demonstrates this effect (Plummer 1962).

3.5. Microhabitat differences within caves

Temperatures can vary greatly within an individual cave and a single temperature measure taken at one spot may not be indicative of the temperature range found throughout a cave. Climatic conditions within a cave can vary based on the distance from the entrance, height of the ceiling, and amount of air circulation (Twente 1955). Dead-end passages may be warmer and more humid, and temperature may be stratified such that colder air remains near the floor and warmer air remains near the ceiling (Twente 1955; Smithson 1993). There may be warm air traps and cold air sinks within an individual cave (Tuttle and Stevenson 1978), and direction of airflow in a tunnel may differ near the ceiling versus the floor (e.g., Toomey 2009). Cooling from evaporation of water from cave walls and temperature differences between cave walls and air can cause temperatures to vary based on distance from walls. Twente (1955) found air temperature 1 cm from cave walls is 1 °C cooler than air 5–7 cm from the wall.

Bats can behaviorally regulate the length and depth of torpor by selecting favorable microsites (Brack and Twente 1985). Bats can discern coarse changes in temperature during hibernation, especially abrupt changes (Davis and Reite 1967); and bats may be able to detect changes in temperature as small as 1 °C (Hall 1982). Bats hibernating in caves or mines may change locations in response to changes in cave climate, and microhabitat selection in a cave may change throughout the season (Twente 1955). Twente (1955) suggested bats locate hibernation spots in a cave by trial and error. However, bats often return to the same spots year after year, suggesting prior experience, learning from others, or olfactory clues may also be involved in microhabitat selection. Bats have also been shown to move within a cave, following specific temperature zones. Henshaw and Folk (1966) found *M. sodalis* move throughout the winter season as temperatures in the cave decline, following the 2–3 °C temperature zone. Thus, a complex cave or mine with multiple tunnels, rooms, and shafts may provide a range of thermal habitats that benefit hibernating bats (Tuttle and Taylor 1998), and the ideal bat cave is one that offers a large thermal range among its microhabitats (Tuttle and Stevenson 1978).

3.5. Water effects on cave temperatures

Water may affect both humidity and temperature of caves. Because of the high specific heat of water, large bodies of water such as subterranean lakes may greatly affect cave temperatures. Water flow from surface runoff and subterranean streams entering caves may increase or decrease cave temperatures compared with MAST (Bögli 1978; Tuttle and Stevenson 1978; Moore and Sullivan 1997), and cold water entering caves, such as snow melt, may lower cave temperatures. Streams entering caves that are warmed by ambient air and sunlight may radiate warmth into caves even at considerable distances from the stream (Tuttle and Stevenson 1978). Turbulent water flow may pull air currents along the surface of the water (entrainment) by causing friction with the air, which may produce air currents over 1 m/s (Wigley and Brown 1976). Rapidly rising flood waters may displace air and create air currents (Wigley and Brown 1976). Waterfalls may draw in air, affecting cave temperatures as well (Cigna 1968). Evaporation and condensation may also affect cave temperatures (see below).

4. Bat water balance

Bats have high rates of evaporative water loss compared with other mammals because of their relatively large, naked wing membranes and large lungs (Licht and Leitner 1967; Hattingh 1972; Bassett 1980), which makes them susceptible to dehydration

during hibernation (Thomas and Cloutier 1992). Because 99.7% of water loss is through the skin, individuals can reduce this loss by selecting hibernacula with high humidity and (or) clustering to reduce exposure of their skin to hibernacula air (Thomas and Cloutier 1992). Some species that do not cluster during hibernation, such as *P. subflavus*, often roost in areas where condensation occurs (such as near cave entrances) and are often covered with water droplets.

High relative humidity is often suggested as an important factor in cave microsite selection by bats, although Twente (1955) suggested caves with the highest humidity are rarely occupied by torpid bats in Kansas and Oklahoma, likely because these areas have the greatest temperatures. Relative humidity at hibernation sites often ranges from 60% to 100% (Davis 1970; Thomas and Cloutier 1992), and bats of different species may select sites with different levels of humidity (e.g., Twente 1955; Davis 1970; Raesly and Gates 1987; Siivonen and Wermundsen 2008) (Table 1). Raesly and Gates (1987) suggested differences in relative humidity of spots where bats hibernate may better separate individual species than temperature. However, within- and among-group overlap is considerable for both temperature and relative humidity as demonstrated by clusters of bats containing different species (Raesly and Gates 1987). Davis (1970) suggested that *P. subflavus*, *M. lucifugus*, and *M. leibii* (small-footed bat) select areas with the greatest humidity, whereas *E. fuscus* and *M. sodalis* select sites with lower relative humidity. However, comparative studies on humidity selection among species are less straightforward (Table 1). Cryan et al. (2010) suggested that the species most affected by WNS are the ones that select the highest humidity (*M. lucifugus*, *M. septentrionalis*, and *P. subflavus*). There is currently no information on the relationship between moisture in caves and growth of *G. destructans*, but Langwig et al. (2012) found declines of *M. sodalis* from WNS are greater when they hibernate in locations of greater humidity.

Evaporative water loss rates depend on temperature and humidity (see below). Because relative humidity depends on temperature, it is often difficult to distinguish between effects of temperature and humidity on roost selection. Unlike temperature, detailed studies on selection for humidity or evaporation rates are rare. At relatively constant absolute humidity, evaporative water loss by bats increases with an increase in temperature and is more pronounced in bats not in torpor (Cryan and Wolf 2003).

Arousal from torpor during hibernation uses substantial energy reserves (Thomas and Geiser 1997). It is suggested that one of the primary reasons (among others) for periodic arousals by hibernating bats is to restore water balance (Thomas et al. 1990; Thomas and Geiser 1997). Bats exposed to dry air have shorter bouts of torpor than bats exposed to more humid air (Thomas and Cloutier 1992), and dehydration may be the best predictor of arousal frequency (Thomas and Geiser 1997). Dehydration may cause mortality directly or may indirectly kill bats by increasing arousals and energy depletion (Willis et al. 2011), and water loss has been hypothesized as one of the primary avenues of mortality in bats affected with WNS (Cryan et al. 2010). Bats affected with WNS may have shorter bouts of torpor (Reeder et al. 2012). Further, some species (e.g., *M. lucifugus*) may be more susceptible to water loss than others even when hibernating at sites with high humidity (Cryan et al. 2010). Bat species most susceptible to water loss may be those experiencing the greatest mortality from WNS (Willis et al. 2011). During arousal, bats roosting in areas where condensation occurs have a readily available supply of water. These bats have been observed licking condensed water off their fur during arousals in hibernacula (Davis 1970). Further, winter flight of bats outside of hibernacula may result from the need to drink (e.g., Speakman and Racey 1989; Hays et al. 1992).

5. Cave moisture

5.1. Humidity

Temperature affects the amount of water vapor that can be held in air, with warm air capable of holding more water vapor than cold air. At sea level, 1 m³ of air can hold around 8 g of water at 10 °C and around 30 g of water at 30 °C. Dew point temperature is the temperature at which the air is 100% saturated with water vapor and cannot hold any more. Humidity can be expressed in a number of ways. Relative humidity (%) is the amount of water vapor in the air divided by the amount of water the air can hold when saturated at a certain temperature. Absolute humidity is the amount of water vapor in a given volume of air (e.g., g/m³ of air), but density of air in a given volume can change based on barometric pressure and elevation. Specific humidity is a ratio of the mass of water vapor to mass of air (mass of water vapor/(mass of air + mass of water vapor)). Although relative humidity is often reported in studies of cave microclimate, relative humidity and absolute humidity are biased by temperature or pressure. Consequently, specific humidity is a better measure of air moisture availability (de Freitas 2010). Use of different humidity measures may influence the perceived amount of moisture within an environment. For example, Tuttle and Stevenson (1978) found relative humidity is 99% in a cave during winter and 92% in summer, but the absolute humidity is twice as high in summer as in winter. Further, they suggested that high relative humidity at low temperatures may be more desiccating than lower relative humidity at higher temperatures because there is less water vapor per unit of air at lower temperatures.

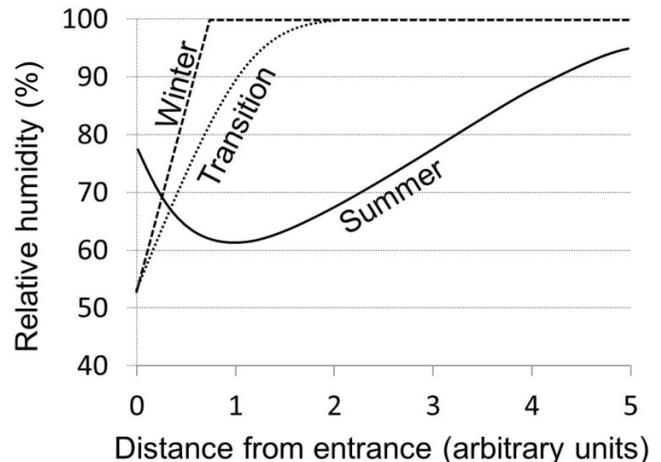
In most caves, relative humidity far from the entrance is close to 100% (Wigley 1969; Cigna 2004). This humidity comes from evaporation of cave moisture and humid air drawn into caves, especially during summer. The water in caves comes from a variety of sources, including condensation, surface runoff, precipitation seeping into caves, and subterranean streams and lakes. After rainfall, meteoric water is temporarily stored in soils and weathered rock layers before seeping into caves, and a lag of days or weeks may occur between rain and seepage (e.g., McLean 1971; Williams 1983; Hill 1987). Heavy rainfall may cause surface runoff to enter caves via conduits or stream channels. During dry years, a cave may lose more moisture from evaporation than is resupplied by surface precipitation (McLean 1971; Buecher 1999). Dripping water from cave ceiling and splashing water from waterfalls creates large hydroaerosol particles with increased surface area, which fosters evaporation into cave air (Dublyansky and Dublyansky 1998) and increases humidity.

Like temperature, humidity can vary widely within a cave and can differ near the ceiling versus near the floor (Hill 1987). A gradient of increasing relative humidity generally occurs from the entrance into farther reaches of a cave (Wigley and Brown 1976) (Fig. 4). Humidity profiles in caves are often affected by airflow. In caves with substantial air exchange with outside air, changes in cave humidity may parallel those of the outside air, with nighttime humidity greater than that during the day, although humidity within caves is typically greater than outside humidity during all seasons (Twente 1955). In caves with seasonally reversing airflow, areas near entrances with high humidity in one season may have lower humidity in another (Tuttle and Stevenson 1978). Extensive air exchange with outside air may be problematic in arid climates (Buecher 1999), which may dry out caves. Furthermore, changes in airflow resulting from anthropogenic manipulations of opening size or number of openings may dry caves out (e.g., McLean 1971; Buecher 1999), as well as change cave temperatures. To hibernate at lower temperatures, bats may use caves with winter airflow in areas where MAST is above 10 °C; however, this airflow may reduce cave moisture, resulting in higher rates of evaporative water loss.

5.2. Condensation and evaporation in caves

Patterns of condensation and evaporation in caves are complex (Dublyansky and Dublyansky 1998). In general, warm air entering

Fig. 4. Theoretical relative humidity with increasing distance from the entrance in well-ventilated caves during three time periods (summer, winter, and the transition period). Distance from entrance is arbitrary units. During winter, relative humidity in caves is typically greater than outside, and cool dry air entering caves increases in humidity quickly. During summer, relative humidity generally falls off near the entrance due to warm air meeting cold cave walls, which creates condensation on the walls of the cave entrance and removes moisture from the air; humidity rebounds due to cooler temperatures deeper in the cave that holds less water vapor. Adapted from Wigley and Brown (1976) with permission.



caves during summer meets cooler rocks (or air) near the entrance which causes condensation, whereas cooler air meeting warmer rocks during winter causes evaporation (Wigley and Brown 1976). Consequently, condensation generally dominates during summer and evaporation generally dominates during winter in temperate areas (Dublyansky and Dublyansky 1998). Caves typically experience a net gain in moisture via condensation and humidity during summer and a net loss (drying) during winter (McLean 1971; de Freitas 2010). The evaporation rate during winter near the entrance of Mammoth Cave, Kentucky, may be 200 times greater than that of summer (Barr 1967).

Evaporation rates depend on airflow, humidity, temperature, and air pressure. Air near the surface of a wet object is saturated; and when the air is constantly replaced with air of lower humidity (via air flow), the rate of moisture removal from the surface is intensified. Thus, greater rates of airflow increase evaporation rates. Caves with low humidity may have relatively high amounts of evaporation (Hill 1987), and slight changes in humidity can drastically change evaporation rates. Decreasing the relative humidity from 99.5% to 99.0% doubles the evaporation rate (Buecher 1999), and evaporation may occur even though relative humidity suggests the air is nearly saturated (McLean 1971; de Freitas and Schmekal 2005). Evaporation rates are also affected by temperature, with higher temperatures increasing evaporation rates. At 90% humidity, the evaporation rate in a cave at 25 °C is 2.5 times greater than that in a cave at 10 °C (Howarth 1980). During winter, cold air moves into a cave from the outside and is warmed along a gradient from the entrance. As the air warms, the water-holding capacity of the air increases, which causes evaporation even though relative humidity may be 100% (de Freitas and Schmekal 2005). Evaporation rates also increase at reduced air pressures (Rygalov et al. 2004). Thus, evaporation and condensation rates may change with the passing of weather fronts or differ among various elevations because of differences in air pressure (Dublyansky and Dublyansky 1998).

Condensation typically occurs when the dew point temperature of the cave air is higher than the temperature of the rock

(de Freitas and Schmekal 2005). Because rock-surface temperature is relatively stable near MAST, air temperature is the main factor that influences condensation rates (de Freitas and Schmekal 2005). In large caves, condensation is generally isolated near the entrance of the cave, whereas small caves and mines may have abundant condensation throughout.

When warm moist air entering caves meets colder cave air, it can condense into aerosol particles visible to the naked eye and produce fog (Dublyansky and Dublyansky 1998). In caves where warm air is stratified near the ceiling, a distinct vertical transition from dry to condensation-soaked walls may appear (Badino 2010), and condensation may be abundant only in the upper reaches or near the ceiling of a cave. A thin layer of condensation fog may appear in caves when cave air is stratified by temperature (Buecher 1999). Warm air rising may condense and fall back to the floor as water droplets; the water droplets evaporate near the floor, further cooling lower portions of the cave (Buecher 1999; Badino 2010).

Condensation produces heat, whereas evaporation removes heat (evaporative cooling). Condensation of water on cave walls is accompanied by a significant yield of heat (585 kcal/kg) that can affect cave temperature and humidity (Dublyansky and Dublyansky 1998). Heat production from condensation may lead to oscillations of air movement direction (breathing) in caves (Dublyansky and Dublyansky 1998). Alternatively, cave breathing may also occur due to oscillation or waves in outside barometric pressure or resonance created by the size and shape of the cave (Plummer 1962; Lewis 1991). The heat release due to condensation can create warm zones near the entrance during summer, where temperature is greater than both cave and outside air temperatures (Wigley and Brown 1971, 1976). Likewise, evaporation of moisture at the cave entrance may super cool air during winter, creating “cold zones” close to the cave entrance; these cold zones may retain ice when temperatures both inside and outside the cave are above freezing (Wigley and Brown 1971, 1976).

6. Cave size

Larger (or longer) caves may be used more readily by hibernating bats than smaller caves (Raesly and Gates 1987; Briggler and Prather 2003; Kryštufek 2007) and may have a greater diversity of bats due to a greater range of microhabitats (e.g., Tuttle and Stevenson 1978). However, small caves may be equally important to many species. Because the majority of caves are relatively small, the overall contribution of these caves to some bat populations may be great. Of the approximately 1300 known caves in Iowa, it is estimated that approximately 90% are 50 m or less in length (Dixon 2011). Some species are commonly found in small caves. For example, *Corynorhinus townsendii ingens* may be found hibernating in relatively small, cold caves with vertical or down-sloping entrances in Arkansas and Oklahoma (Prather and Briggler 2002). *P. subflavus* are often found hibernating in small caves (e.g., Briggler and Prather 2003; Dixon 2011), and surveys of 27 small (typically 30–150 m in length) abandoned mines in Arkansas found all held hibernating populations of *P. subflavus*, with as many as 800 hibernating in a single 70-m long adit (Heath et al. 1986). Small caves with substantial airflow are likely more variable in temperature and humidity than large caves. Because of the decreased surface area of rocks and short length of time passing air is exposed to rock in small caves, thermal equilibrium between rocks and air may not occur, and a homothermic zone may not be present.

7. Conclusions

Most bat species in temperate North America require hibernacula with high humidity and stable temperatures between 2 and 10 °C for successful hibernation. However, these temperature requirements likely vary based on the condition of individuals

(fat stores), latitude, and bat species. Where MAST is above 10 °C, caves or mines used as hibernacula by species such as *M. sodalis* and *M. grisescens* typically have configurations that lower the cave temperatures below MAST during winter, primarily by allowing significant air infiltration. These caves are often chimney-effect caves with multiple openings at different elevations; caves with vertical openings that trap or circulate cold air; high elevation caves; and caves with large, funnel-shaped entrances. Alternatively, bats in these areas may hibernate near the entrances of caves where temperatures are typically lower but more variable and occasionally fall below freezing. Unfortunately, the temperature requirements for many hibernating species are within the range of optimal growth of *G. destructans*. Thus, in areas where MAST is outside the thermal range of *G. destructans* growth, some caves may still provide favorable environmental conditions for growth.

Quantitative studies of cave and microsite selection by hibernating bat communities in North America are relatively few in number. Even fewer studies have examined humidity, condensation, and evaporation of cave microsites selected by bats. Most studies that measured humidity have reported relative humidity, which is biased by temperature. Measuring the important climate factors of an individual cave for hibernating bats is more complicated than a single temperature measure taken at one location and one date. Because caves selected as hibernation sites by bats may vary both spatially and temporally in climate, measures of cave variability (spatial and temporal) should be assessed. Further, the amount of time during winter that caves fall above or below specified thresholds important to bats during hibernation (based on metabolic rates, fat loss, or dehydration) would demonstrate whether a cave is a potential source or sink to populations.

There are research needs in many areas of cave selection and bat hibernation. Quantitative studies on cave and microsite selection are needed for most species at various latitudes, including temperature and humidity preferences for most species. The relationship between minimum metabolic rates and temperature is not established for most North American species. Effects of latitude and elevation (in mountainous areas) on selection of caves by bats need further study. Research on effects of changing hibernation temperature on bat survival and bat condition among various species is also needed. Potential selection by bats for humidity, evaporation, and condensation needs further study along with growth of *G. destructans* under various moisture conditions. The interaction of latitude, temperature, minimum metabolic rates, and minimum and maximum number of days needed to survive hibernation under different fat stores also need study. Lastly, because MAST is changing across North America due to climate change, research is needed on potential changes in cave climates, bat distributions, and selection of caves under this changing climate.

Acknowledgments

Thanks to W. Mark Ford and David Leslie, Jr. (U.S. Geological Survey, Blacksburg, Va.), Richard E. Sherwin (Christopher Newport University, Newport News, Va.), and two anonymous reviewers for review of an earlier draft. Murray M. Humphries and Manuelle Landry-Cuerrier (McGill University, Montréal, Que.) provided editing of the French translation of the abstract. Also, Nicholas L. Crookston (U.S. Forest Service, Moscow, Idaho) provided help with geographic information system (GIS) files of North American temperature data.

References

- Atkinson, T.C., Smart, P.L., and Wigley, T.M.L. 1983. Climate and natural radon levels in Castleguard Cave, Columbia Icefields, Alberta, Canada. *Artic Alpine Res.* 15: 487–502. doi:10.2307/1551235.
- Badino, G. 2010. Underground meteorology – “What’s the weather underground?” *Acta Carsologica*, 39: 427–448.

- Barbour, R.W., and Davis, W.H. 1969. *Bats of America*. University Press of Kentucky, Lexington, Ky.
- Barr, T.C., Jr. 1967. Observations on the ecology of caves. *Am. Midl. Nat.* **101**: 475–491.
- Barry, R.G. 1992. *Mountain weather and climate*, second edition. Routledge, Chapman, and Hall Inc., New York, N.Y.
- Bassett, J.E. 1980. Control of postprandial water loss in *Myotis lucifugus lucifugus*. *Comp. Biochem. Physiol.* **65A**: 497–500. doi:10.1016/0300-9629(80)90066-3.
- Blackwell, D.D., Steele, J.L., and Brott, C.A. 1980. The terrain effect on terrestrial heat flow. *J. Geophys. Res.* **85**: 4757–4772. doi:10.1029/JB085iB09p04757.
- Bleher, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T.H., Darling, S.R., Gargas, A., Niver, R., Okoniewski, J.C., Rudd, R.J., and Stone, W.B. 2009. Bat white-nose syndrome: an emerging fungal pathogen? *Science*, **323**: 227. doi:10.1126/science.1163874.
- Bögli, A. 1978. *Karsthydrographie und physische speleologie*. Springer, Berlin, Germany.
- Boyles, J.G., Dunbar, M.B., Storm, J.S., and Brack, V., Jr. 2007. Energy availability influences microclimate selection of hibernating bats. *J. Exp. Biol.* **210**: 4345–4350. doi:10.1242/jeb.007294.
- Brack, V., Jr. 2007. Temperature 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, V., Jr., and Twente, J.W. 1985. The duration of the period of hibernation in three species of vespertilionid bats I: field studies. *Can. J. Zool.* **63**: 2952–2954. doi:10.1139/z85-442.
- Briggler, J.T., and Prather, J.W. 2003. Seasonal use and selection of caves by the eastern pipistrelle bat (*Pipistrellus subflavus*). *Am. Midl. Nat.* **149**: 406–412. doi:10.1674/0003-0031(2003)149[0406:SUASOC]2.0.CO;2.
- Buecher, R.H. 1999. Microclimate study of Kartchner Caverns, Arizona. *J. Cave Karst Stud.* **61**: 108–120.
- Burton, R.S., and Reichman, O.J. 1999. Does immune challenge affect torpor duration? *Funct. Ecol.* **13**: 232–237. doi:10.1046/j.1365-2435.1999.00302.x.
- Cigna, A.A. 1968. An analytical study of air circulation in caves. *Int. J. Speleol.* **3**: 41–54.
- Cigna, A.A. 2002. Modern trend in cave monitoring. *Acta Carsologica*, **31**: 35–54.
- Cigna, A.A. 2004. Climate of caves. In *Encyclopedia of caves and karst science*. Edited by J. Gunn. Taylor and Francis Group, Oxford, UK. pp. 228–230.
- Clark, B.K., Clark, B.S., Leslie, D.M., Jr., and Gregory, M.S. 1996. Characteristics of caves used by the endangered Ozark big-eared bat. *Wildl. Soc. Bull.* **24**: 8–14.
- Clawson, R.L. 2000. Implementation of a recovery plan for the endangered Indiana bat. In *Proceedings of Bat Conservation and Mining: A Technical Interactive Forum*. Edited by K.C. Vories and D. Throgmorton. 14–16 November, St. Louis, Mo. pp. 239–250. Available from <http://www.techtransfer.osmre.gov/ntmain/site/Library/proceed/bat2000/session5.pdf>.
- Clawson, R.L. 2002. Trends in population size and current status. In *The Indiana bat: biology and management of an endangered species*. Edited by A. Kurta and J. Kennedy. Bat Conservation International, Austin, Tex. pp. 2–8.
- Cropley, J.B. 1965. Influence of surface conditions on temperatures in large cave systems. *Bull. Nat. Speleol. Soc.* **27**: 1–10.
- Cryan, P.M., and Wolf, B.O. 2003. Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasius cinereus*, during its spring migration. *J. Exp. Biol.* **206**: 3381–3390. doi:10.1242/jeb.00574.
- Cryan, P.M., Meteyer, C.U., Boyles, J.G., and Bleher, D.S. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. *BMC Biol.* **8**: 135. doi:10.1186/1741-7007-8-135.
- Davis, M.J., Vanderberg, A.D., Chatwin, T.A., and Mather, M.H. 2000. Bat usage of the Weymer Creek cave system on northern Vancouver Island. In *Proceedings of the Conference on the Biology and Management of Species and Habitats at Risk*. Edited by L.M. Darling. 15–19 February 1999, Kamloops, B.C. pp. 305–312.
- Davis, W.H. 1970. Hibernation: Ecology and physiological ecology. In *Biology of bats*. Vol. 3. Edited by W.A. Wimsatt. Academic Press, New York, N.Y. pp. 265–300.
- Davis, W.H., and Reite, O.B. 1967. Responses of bats from temperate regions to changes in ambient temperature. *Biol. Bull.* **132**: 320–328. doi:10.2307/1539637. PMID:6046026.
- de Freitas, C.R. 2010. The role and importance of cave microclimate in the sustainable use and management of show caves. *Acta Carsologica*, **39**: 477–489.
- de Freitas, C.R., and Littlejohn, R.N. 1987. Cave climate: assessment of heat and moisture exchange. *J. Climatol.* **7**: 553–569. doi:10.1002/joc.3370070604.
- de Freitas, C.R., and Schmokal, A. 2005. Prediction of condensation in caves. *Speleogen. Evol. Karst Aquifers*, **3**: 1–9.
- de Freitas, C.R., Littlejohn, R.N., Clarkson, T.S., and Kristament, I.S. 1982. Cave climate: assessment of airflow and ventilation. *Int. J. Climatol.* **2**: 383–397. doi:10.1002/joc.3370020408.
- Dixon, J.W. 2011. The role of small caves as bat hibernacula in Iowa. *J. Cave Karst Stud.* **73**: 21–27. doi:10.4311/jcks2010sc0145.
- Domomínguez-Villar, D., Fairchild, I.J., Carrasco, R.M., Pedraza, J., and Baker, A. 2010. The effects of visitors in a tourist cave and the resulting constraints on natural thermal conditions for palaeoclimate studies. *Acta Carsologica*, **39**: 491–502.
- Dublyansky, V.N., and Dublyansky, Y.V. 1998. The problem of condensation in karst studies. *J. Cave Karst Stud.* **60**: 3–17.
- Dunbar, M.B., and Brigham, R.M. 2010. Thermoregulatory variation among populations of bats along a latitudinal gradient. *J. Comp. Physiol.* **180**: 885–893. doi:10.1007/s00360-010-0457-y.
- Dunbar, M.B., and Tomasi, T.E. 2006. Arousal patterns, metabolic rate, and an energy budget of eastern red bats (*Lasius borealis*) in winter. *J. Mammal.* **87**: 1096–1102. doi:10.1644/05-MAMM-A-254R3.1.
- Elliott, W.R., and Clawson, R.L. 2001. Temperature data logging in Missouri bat caves. In *1999 National Cave and Karst Management Symposium*. Edited by G.T. Rea. Southeastern Cave Conservancy Inc., Chattanooga, Tenn. pp. 52–57.
- Fleming, T.H., and Eby, P. 2003. Ecology of bat migration. In *Bat ecology*. Edited by T.H. Kunz and M.B. Fenton. University of Chicago Press, Chicago, Ill. pp. 157–208.
- Flory, A.R., Kumar, S., Stohlgren, T.J., and Cryan, P.M. 2012. Environmental conditions associated with bat white-nose syndrome mortality in the north-eastern United States. *J. Appl. Ecol.* **49**: 680–689. doi:10.1111/j.1365-2664.2012.02129.x.
- Frost, S.W. 1962. Winter insect light-trapping at the Archbold Biological Station, Florida. *Fla. Entomol.* **45**: 175–190. doi:10.2307/3492400.
- Geiger, R., Aron, R.H., and Todhunter, P. 2003. The microclimate of caves. In *The climate near the ground*. Rowman and Littlefield Publishers Inc., Lanham, Md. pp. 418–424.
- Gore, J.A., Lazure, L., and Ludlow, M.E. 2012. Decline in the winter population of gray bats (*Myotis grisescens*) in Florida. *Southeast. Nat.* **11**: 89–98. doi:10.1656/058.011.0108.
- Hall, L.S. 1982. The effect of cave microclimate on winter roosting behaviour in the bat, *Miniopterus schreibersii blepotis*. *Austral Ecol.* **7**: 129–136. doi:10.1111/j.1442-9993.1982.tb01586.x.
- Harris, J.A. 1970. Bat-guano cave environment. *Science*, **169**: 1342–1343. PMID:5454150.
- Hattingh, J. 1972. A comparative study of transepidermal water loss through the skin of various animals. *Comp. Biochem. Physiol.* **43A**: 715–718. doi:10.1016/0300-9629(72)90139-9.
- Hayes, M.A., Schorr, R.A., and Navo, K.W. 2011. Hibernacula Selection by Townsend's big-eared bat in southwestern Colorado. *J. Wildl. Manage.* **75**: 137–143. doi:10.1002/jwmg.6.
- Hays, G.C., Speakman, J.R., and Webb, P.I. 1992. Why do brown long-eared bats (*Plecotus auritus*) fly in winter? *Physiol. Zool.* **65**: 554–567.
- Heath, D.R., Saugey, D.A., and Heidt, G.A. 1986. Abandoned mine fauna of the Ouachita Mountains, Arkansas: vertebrate taxa. *Proc. Ark. Acad. Sci.* **40**: 33–36. Available from <http://libinfo.uark.edu/aas/issues/1986v40/v40a10.pdf>.
- Henshaw, R.E., and Folk, G.E., Jr. 1966. Relation of thermoregulation to seasonally changing microclimate in two species of bats (*Myotis lucifugus* and *M. sodalis*). *Physiol. Zool.* **39**: 223–236.
- Herman, J.R., and Goldberg, R.A. 1978. Sun, weather, and climate. National Aeronautics and Space Administration, Scientific and Technical Information Branch SP-426, Washington, D.C.
- Hill, C.A. 1987. Geology of Carlsbad Cavern and other caves in the Guadalupe Mountains, New Mexico and Texas. New Mexico Bureau of Mines and Mineral Resources, Bulletin 117, Socorro, N.M. Available from <http://geoinfo.nmt.edu/publications/bulletins/downloads/117/Bulletin117.pdf>.
- Hock, R.J. 1951. The metabolic rates and body temperatures of bats. *Biol. Bull.* **101**: 289–299. doi:10.2307/1538547.
- Howarth, F.G. 1980. The zoogeography of specialized cave animals: a bioclimatic model. *Evolution*, **34**: 394–406. doi:10.2307/2407402.
- Humphrey, S.R. 1978. Status, winter habitat, and management of the endangered Indiana bat, *Myotis sodalis*. *Fla. Scientist*, **41**: 65–76.
- Humphries, M.M., Thomas, D.W., and Speakman, J.R. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature*, **418**: 313–316. doi:10.1038/nature00828.
- Humphries, M.M., Thomas, D.W., and Kramer, D.L. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiol. Biochem. Zool.* **76**: 165–179. doi:10.1086/367950.
- Humphries, M.M., Umbanhowar, J., and McCann, K.S. 2004. Bioenergetic prediction of climate change impacts on northern mammals. *Integr. Comp. Biol.* **44**: 452–462. doi:10.1093/icb/44.2.152.
- Humphries, M.M., Speakman, J.R., and Thomas, D.W. 2005. Temperature, hibernation energetics, and the cave and continental distributions of little brown myotis. In *Functional and Evolutionary Ecology of Bats*. Edited by A. Zubaid, G.F. McCracken, and T.H. Kunz. Oxford Press, Oxford, UK. pp. 23–37.
- Ingersoll, T.E., Navo, K.W., and de Valpine, P. 2010. Microhabitat preferences during swarming and hibernation in the Townsend's big-eared bat, *Corynorhinus townsendii*. *J. Mammal.* **91**: 1242–1250. doi:10.1644/09-MAMM-A-288.1.
- Kryštufek, B. 2007. Bat hibernacula in a cave-rich landscape of the northern Dinaric Karst, Slovenia. *Hystrix*, **18**: 195–204. doi:10.4404/hystrix-18.2-4403.
- Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H., and Kilpatrick, A.M. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecol. Letters*, **15**: 1050–1057.
- Lausen, C.L., and Barclay, R.M.R. 2006. Winter bat activity in the Canadian prairies. *Can. J. Zool.* **84**: 1079–1086. doi:10.1139/Z06-093.
- Lewis, T.J., and Wang, K. 1998. Geothermal evidence for deforestation induced

- warming: Implications for the climate impact of land development. *Geophys. Res. Lett.* **25**: 535–538. doi:10.1029/98GL00181.
- Lewis, W.C. 1991. Atmospheric pressure changes and cave airflow: A review. *Nat. Speleol. Soc. Bull.* **53**: 1–12.
- Licht, P., and Leitner, P. 1967. Physiological responses to high environmental temperatures in three species of microchiropteran bats. *Comp. Biochem. Physiol.* **22**: 371–387. doi:10.1016/0010-406X(67)90601-9.
- Luetscher, M., and Jeannin, P. 2004a. Temperature distribution in karst systems: the role of air and water fluxes. *Terra Nova*, **16**: 344–350. doi:10.1111/j.1365-3121.2004.00572.x.
- Luetscher, M., and Jeannin, P. 2004b. The role of winter air circulations for the presence of subsurface ice accumulations: an example from Monlési ice cave (Switzerland). *Theor. Appl. Karstology*, **17**: 19–25.
- Luetscher, M., Lismonde, B., and Jeannin, P. 2008. Heat exchanges in the heterothermic zone of a karst system: Monlési cave, Switzerland. *J. Geophys. Res.* **113**: F02025. doi:10.1029/2007JF000892.
- McLean, J.S. 1971. The microclimate of Carlsbad Caverns, New Mexico. U.S. Geological Survey, Open File Report 76-171, Albuquerque, N.M. Available from <http://pubs.usgs.gov/of/1971/0198/report.pdf>.
- McNab, B.K. 1974. The behavior of temperate cave bats in a subtropical environment. *Ecology*, **55**: 943–958. doi:10.2307/1940347.
- Moore, G.W., and Sullivan, N. 1997. *Speleology: caves and the cave environment*. Cave Books, St. Louis, Mo.
- Nagel, A., and Nagel, R. 1991. How do bats choose optimal temperatures for hibernation? *Comp. Biochem. Physiol.* **99A**: 323–326. doi:10.1016/0300-9629(91)90008-Z.
- Nagy, Z.L., and Postawa, T. 2011. Seasonal and geographical distribution of cave-dwelling bats in Romania: implications for conservation. *Anim. Conserv.* **14**: 74–86. doi:10.1111/j.1469-1795.2010.00392.x.
- Pearson, E.W. 1962. Bats hibernating in silica mines in southern Illinois. *J. Mammal.* **43**: 27–33. doi:10.2307/1376877.
- Perry, R.W. 2012. Fire effects on bats and bat habitat in the eastern oaks region: a review. In: Proceedings of the 4th Fire in Eastern Oak Forests Conference. Edited by D.C. Dey, M.C. Stambaugh, S.L. Clark, and C.J. Schweitzer. USDA For. Serv. Gen. Tech. Rep. NRS-P-102. pp. 170–191.
- Pflitsch, A., and Piasecki, J. 2003. Detection of an airflow system in Niedzwiedzia (Bear) Cave, Kletno, Poland. *J. Cave Karst Stud.* **65**: 160–173.
- Pflitsch, A., Wiles, M., Horrocks, R., Piasecki, J., and Ringeis, J. 2010. Dynamic climatologic processes of barometric cave systems using the example of Jewel Cave and Wind Cave in South Dakota, U.S.A. *Acta Carsologica*, **39**: 449–462.
- Plummer, B. 1962. A note on cave breathing. *Speleo Digest*, **1962**: 101–107.
- Poulson, T.L., and White, W.B. 1969. The cave environment. *Science*, **165**: 971–981. doi:10.1126/science.165.3897.971.
- Prather, J.W., and Briggler, J.T. 2002. Use of small caves by the Ozark big-eared bat (*Corynorhinus townsendii ingens*) in Arkansas. *Am. Midl. Nat.* **148**: 193–197. doi:10.1674/0003-0031(2002)148[0193:UOSCB0]2.0.CO;2.
- Press, F., and Siever, R. 1978. *Earth*. Second edition. W.H. Freeman and Company, San Francisco, Calif.
- Raesy, R.L., and Gates, J.E. 1987. Winter habitat selection by north temperate cave bats. *Am. Midl. Nat.* **118**: 15–31. doi:10.2307/2425624.
- Reeder, D.M., Frank, C.L., Turner, G.G., Meteyer, C.U., Kurta, A., Britzke, E.R., Vozzak, M.E., Darling, S.R., Stihler, C.W., Hicks, A.C., Jacob, R., Grieneisen, L.E., Brownlee, S.A., Muller, L.K., and Blehert, D.S. 2012. Frequent arousals from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *Plos One*, **7**: e38920. doi:10.1371/journal.pone.0038920.
- Řehák, Z. 2006. Areal and altitudinal distribution of bats in the Czech part of the Carpathians (Chiroptera). *Lynx (Praha)*, **37**: 179–205.
- Richards, J.M. 2001. Lechuguilla Cave culvert replacement project (abstract). Proceedings of the 2001 National Cave and Karst Management Symposium. Tucson, Ariz. Available from <http://www.nckms.org/pdf/RICHARDS.pdf>.
- Richter, A.R., Humphrey, S.R., Cope, J.B., and Brack, V., Jr. 1993. Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana Bats (*Myotis sodalis*). *Conserv. Biol.* **7**: 407–415. doi:10.1046/j.1523-1739.1993.07020407.x.
- Roy, R.F., Blackwell, D.D., and Decker, E.R. 1972. Continental heat flow. In *The nature of the solid Earth*. Edited by E.C. Robertson. McGraw Hill, New York, NY. pp. 506–544.
- Rygalov, V.Y., Fowler, P.A., Wheeler, R.M., and Bucklin, R.A. 2004. Water cycle and its management for plant habitats at reduced pressures. *Habitation*, **10**: 49–59. doi:10.3727/154296604774808865.
- Saugy, D.A., Heidt, G.A., Heath, D.R., and McDaniel, V.R. 1990. Hibernating Indiana bats (*Myotis sodalis*) from the Ouachita Mountains of southeastern Oklahoma. *Southwest. Nat.* **35**: 341–342. doi:10.2307/3671951.
- Siivonen, Y., and Wermundsen, T. 2008. Characteristics of winter roosts of bat species in southern Finland. *Mammalia*, **72**: 50–56. doi:10.1515/MAMM.2008.003.
- Smithson, P.A. 1991. Inter-relationship between cave and outside air temperatures. *Theor. Appl. Climatol.* **44**: 65–73. doi:10.1007/BF00865553.
- Smithson, P.A. 1993. Vertical temperature structure in a cave environment. *Geoarchaeology*, **8**: 229–240. doi:10.1002/gea.3340080305.
- Speakman, J.R., and Racey, P.A. 1989. Hibernation ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. *J. Anim. Ecol.* **58**: 797–813. doi:10.2307/5125.
- Speakman, J.R., and Thomas, D.W. 2003. Physiological ecology and energetics of bats. In *Bat biology*. Edited by T.H. Kunz and M.B. Fenton. University of Chicago Press, Chicago, Ill. pp. 430–490.
- Stoer, A., and Maglova, P. 1993. Influence des facteurs biologiques sur le microclimat en conditions karstiques tropicales. *Bulletin de la Société géographique de Liège*, **29**: 119–124.
- Szewczak, J.M., Szewczak, S.M., Morrison, M.L., and Hall, L.S. 1998. Bats of the White and Inyo Mountains of California-Nevada. *Great Basin Nat.* **58**: 66–75.
- Thomas, D.W., and Cloutier, D. 1992. Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. *Physiol. Zool.* **65**: 443–456.
- Thomas, D.W., and Geiser, F. 1997. Periodic arousals in hibernating mammals: is evaporative water loss involved? *Funct. Ecol.* **11**: 585–591. doi:10.1046/j.1365-2435.1997.00129.x.
- Thomas, D.W., Dorais, M., and Bergeron, J.M. 1990. Winter energy budgets and the cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *J. Mammal.* **71**: 475–479.
- Tinkle, D.W., and Patterson, I.G. 1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. *J. Mammal.* **46**: 612–633. doi:10.2307/1377932.
- Toomey, R.S., III. 2009. Geological monitoring of caves and associated landscapes. In *Geological monitoring*. Edited by R. Young and L. Noby. Geological Society of America, Boulder, Colo. pp. 27–46.
- Tuttle, M.D. 1977. Gating as a means of protecting cave-dwelling bats. In 1976 National Cave Management Symposium Proceedings. Edited by T. Aley and D. Rhodes. Speleobooks, Albuquerque, N.M. pp. 77–82.
- Tuttle, M.D., and Kennedy, J. 2002. Thermal requirements during hibernation. In *The Indiana bat: biology and management of an endangered species*. Edited by A. Kurta and J. Kennedy. Bat Conservation International, Austin, Tex. pp. 68–78.
- Tuttle, M.D., and Stevenson, D.E. 1978. Variations in the cave environment and its biological implications. In *National Cave Management Proceedings, 3–7 October 1977*, Big Sky, Mont. Edited by R. Zuber, J. Chester, S. Gilbert, and D. Rhodes. Speleobooks, Albuquerque, N.M. pp. 180–121. Available from <http://www.batcon.org/pdfs/workshops/AZ11BCM.pdf#page=24>.
- Tuttle, M.D., and Taylor, D.A.R. 1998. Bats and mines. *Bat Conservation International, Inc. Resource Publication No. 3*. Austin, Tex. Available from http://www.batcon.org/pdfs/batsmines/batsmines_01-08.pdf.
- Twente, J.W., Jr. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology*, **36**: 706–732. doi:10.2307/1931308.
- Twente, J.W., Jr. 1960. Environmental problems involving the hibernating bats in Utah. *Proc. Utah Acad. Sci., Arts and Letters*, **37**: 67–71.
- Twente, J.W., Twente, J., and Brack, V., Jr. 1985. The duration of the period of hibernation of three species of vespertilionid bats. II. Laboratory studies. *Can. J. Zool.* **63**: 2955–2961. doi:10.1139/z85-443.
- U.S. Fish and Wildlife Service (USFWS). 2012. North American bat death toll exceeds 5.5 million from white-nose syndrome. USFWS Press Release. Available from http://www.fws.gov/whitenosesyndrome/pdf/WNS_Mortality_2012_NR_FINAL.pdf [accessed 30 April 2012].
- Verant, M.L., Boyles, J.G., Waldrep, W., Jr., Wibbelt, G., and Blehert, D.S. 2012. Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. *Plos One*, **7**: 46280. doi:10.1371/journal.pone.0046280.
- Webb, P.I., Speakman, J.R., and 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.
- Wigley, T.M.L. 1969. Cave microclimate: a note on moisture. *Helictite*, **7**: 43–49.
- Wigley, T.M.L., and Brown, M.C. 1971. Geophysical applications of heat and mass transfer in turbulent pipe flow. *Bound.-Lay. Meteorol.* **1**: 300–320. doi:10.1007/BF02186034.
- Wigley, T.M.L., and Brown, M.C. 1976. The physics of caves. In *The science of speleology*. Edited by T.D. Ford and C.H.D. Cullingford. Academic Press, New York, N.Y. pp. 329–358.
- Williams, P.W. 1983. The role of the subcutaneous zone in karst hydrology. *J. Hydrol.* **61**: 45–67. doi:10.1016/0022-1694(83)90234-2.
- Willis, C.K.R., Menzies, A.K., Boyles, J.G., and Wojciechowski, M.S. 2011. Evaporative water loss is a plausible explanation for mortality of bats from white-nose syndrome. *Integrat. Comp. Biol.* **51**: 364–373. doi:10.1093/icb/ict076.