



Home is where you hang your bat: winter roost selection by prairie-living big brown bats

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Information on the roost requirements of small, temperate-zone hibernating bats, which can spend up to 8 months in hibernation, is crucial to their conservation. We studied male big brown bats (*Eptesicus fuscus*) in southeastern Alberta, Canada, to investigate the physical and microclimate characteristics of hibernacula used by this species in a prairie river valley (Dinosaur Provincial Park, DPP). We monitored roosting behavior and movement, and also compared microclimate conditions (temperature and humidity) within these crevice hibernacula to those of random crevices within the study area, and to conditions inside 4 known cave hibernacula in central and northern Canada. Our results show that male *E. fuscus* in DPP use rock-crevice hibernacula with less variable temperatures than ambient and random crevice temperatures, with evidence of winter roost fidelity within and between years. Bats used only 3 hibernacula and, although mid-winter flight is common in our study area, there was little movement by bats between hibernacula. Rock-crevice hibernacula were warmer and more thermally stable than other available crevices in DPP, and drier but not necessarily colder than known cave hibernacula elsewhere. Our study is the first to examine crevice roost selection by bats during winter, and suggests that specific hibernacula are important for individual bats, despite the fact that numerous crevices are available.

Key words: aridity, bats, crevices, *Eptesicus fuscus*, hibernacula, microclimate, roost selection, winter

Dens, burrows, and roosts play a crucial role in the biology of animals and animals spend a considerable proportion of their time within such structures. These shelters buffer ambient conditions (Buck and Barnes 1999; Solick and Barclay 2006), provide a place to raise young and interact with conspecifics (East et al. 1989; Willis and Brigham 2004), and offer refuge from predators and catastrophic events (Fenton et al. 1994; Stawski et al. 2015). Habitat selection and the roosting, nesting, or denning behaviors of temperate-zone animals are generally well studied during summer (Kalcounis Rüppell et al. 2005; Lesmeister et al. 2008), but less is known about the winter ecology of many species. This represents a considerable knowledge gap about the annual cycle and resource requirements of many animals. Important aspects of winter ecology to investigate are the location and physical characteristics of selected hibernacula, and the microclimate conditions within.

Small mammals can spend up to 8 months hibernating (Davis 1967; Humphrey 1982; Murie and Boag 1984) and environmental conditions impact their overwinter survival (e.g.,

Thomas and Geiser 1997; Boyles and Brack 2009). Reductions in metabolic rate (MR) and body temperature (T_b) conserve considerable energy while torpid (Ruf and Geiser 2015), but all small hibernators spend a disproportionately large amount of energy on periodic arousals (e.g., Thomas et al. 1990; Armitage et al. 2003). The frequency of these arousals and the amount of energy spent defending a torpid T_b set-point are influenced by ambient conditions (Humphries et al. 2003; Geiser 2004). Even small changes in temperature or humidity lead to increased MR, more frequent arousals, and reduced overwinter survival (e.g., Thomas and Geiser 1997; Boyles and Brack 2009). Thus, many hibernators seek out shelter with particular characteristics, often subterranean cavities (e.g., burrows, caves, or mines) with a stable microclimate (i.e., temperature and humidity) to maximize energy savings (Geiser 2004). For example, bats in the eastern United States and Canada are often found roosting in large clusters in hibernacula with stable temperatures a few degrees above freezing and near-saturated humidity (Webb et al. 1996; Perry 2012).

Caves and mines are not ubiquitous across North America, which forces hibernators to either migrate to more suitable winter habitat or use other features as hibernacula, such as rock crevices. Seasonal movements of up to 100s of kilometers are common by many bat species (Fleming and Eby 2003; Norquay et al. 2013), but the big brown bat (*Eptesicus fuscus*) is relatively sedentary and thought to move only 10s of kilometers between summering and wintering grounds (Beer 1955; Goehring 1972; Mills et al. 1975). Although winter habitat requirements likely constrain the range of most temperate-zone bat species (Humphries et al. 2002), *E. fuscus* is one of the most widespread in North America. Roost selection by crevice-roosting *E. fuscus* has been described during both summer (Lausen and Barclay 2002, 2003, 2006a) and autumn (Neubaum et al. 2006), but overwintering behavior is known mainly for bats using buildings (Whitaker and Gummer 1992; Halsall et al. 2012). Documented use of rock-crevice roosts in winter (Lausen and Barclay 2006b) suggests this species may use natural crevice roosts year-round in areas where extensive cavernous systems are absent.

Summer roosts of *E. fuscus* occur mostly in trees, buildings, and sometimes in rock crevices (Kurta and Baker 1990). Trees may be used as hibernacula in locations with milder climates (Burler et al. 2014) but are unlikely to buffer bats from ambient conditions in areas with harsh winters. *Eptesicus fuscus* is one of few bat species known to use buildings as hibernacula (Whitaker and Gummer 1992; Halsall et al. 2012) but a reliance on heated anthropogenic structures would suggest a limited historical range for this species. Few studies have investigated use of rock crevices by hibernating *E. fuscus* (Lausen and Barclay 2006b; Neubaum et al. 2006). If rock crevices meet the requirements of this species, their importance as naturally occurring, non-cavernous hibernacula may have been underestimated. The prairies have extensive networks of river valleys that likely house a considerable number of bats during the winter (Lausen and Barclay 2006b), and rock-crevice hibernacula may also be used by other temperate-zone bat species with similar roosting ecology and limited evidence of seasonal movements.

We explored multiple aspects of the hibernation ecology of male *E. fuscus* in a non-cavernous, prairie landscape, specifically addressing: 1) physical and microclimate characteristics of hibernacula within the study area; 2) microclimate of multiple hibernacula across a wide, heterogeneous landscape; and 3) winter movements and roost fidelity of bats in our study area. We hypothesized that *E. fuscus* choose hibernacula based on microclimate, specifically that rock crevices used as hibernacula would be warmer and more humid than other available (i.e., randomly selected) crevices. We also hypothesized that microclimates of rock-crevice hibernacula would differ from that of known cavernous hibernacula elsewhere, specifically that rock-crevice hibernacula would be drier, colder, and less thermally stable than known cave hibernacula in central and northern Canada. Lastly, we hypothesized that the thermal variability, small size, and potentially large number of available rock-crevice hibernacula at our study site would affect mid-winter movements of bats. Specifically, we predicted that bats

overwintering in the prairies would hibernate alone or in small groups and occasionally switch roosts to sites with more suitable microclimates as the weather varied.

MATERIALS AND METHODS

Study site and captures.—We monitored the roosting behavior and movement by individuals from a population of *E. fuscus* in Dinosaur Provincial Park (DPP), Alberta, Canada (50°45′09.2″N, 111°31′03.6″W) during the winters (November–March) of 2012–2015. The park is comprised of prairie and riparian areas with an extensive network of creeks and drainages. It has a semiarid climate with winters characterized by low temperatures and precipitation (mean January temperature = −19°C, winter precipitation ~105 mm—Campbell 1987). At least 3 species—*E. fuscus*, the western small-footed myotis (*Myotis ciliolabrum*), and the long-eared myotis (*M. evotis*)—overwinter in deep (ca. 1–2 m) rock crevices within the park and are active during the winter when the weather is favorable (Lausen and Barclay 2006b; Klüg-Baerwald et al. 2016). DPP is more than 300 km east of known cavernous sites in the Rocky Mountains and the only known hibernation area in the grasslands region of Alberta. The landscape contains no large subterranean features (i.e., caves or mines) but crevices provide access to underground habitat below the frost line (Lausen and Barclay 2006b).

We captured bats in mist nets set across the Little Sandhill creek, a tributary to the Red Deer River. Although typically frozen during winter, the creek and river are the only non-ephemeral water features within the study area. We took morphometric measurements (e.g., forearm length and mass) of all captured *E. fuscus* and permanently marked individuals with a 0.1-g passive integrated transponder (PIT) tag (Trovan ID100 nano-transponders; EIDAP Inc., Sherwood Park, Alberta, Canada) injected under the skin of the lower back. After tagging, we used tissue adhesive (Vetbond; 3M Canada, London, Ontario, Canada) to close the injection site and then monitored each bat during the next hour for signs of distress or injury and to ensure proper insertion of the PIT tag. For a subset of individuals, we also affixed radiotransmitters (Lotek Ag392 1.2-g temperature-sensitive radiotransmitters; Lotek Wireless Inc., Newmarket, Ontario, Canada) to the interscapular region using latex adhesive (Perma-Type; The Perma-Type Company Inc., Plainville, Connecticut). The combined mass of a transmitter and PIT tag was approximately 5% of mean winter body mass of *E. fuscus* captured during our study (23.5 g—Klüg-Baerwald et al. 2016) and we expected negligible adverse effects on behavior and survival (Aldridge and Brigham 1988; Neubaum et al. 2005; Wimsatt et al. 2005). We released all bats at the site of capture within 1.5 h of processing.

The University of Regina President's Committee on Animal Care approved all methods and procedures (Animal Use Protocol #12-12), which conformed to the guidelines for animal care and use outlined by the American Society of Mammalogists (Sikes et al. 2016). We performed field-work under research and collection permits issued by Alberta

Sustainable Resource Development and Alberta Tourism, Parks and Recreation Division.

Microclimate, microhabitat, and landscape measurement.—We tracked bats to hibernacula and recorded microclimate, microhabitat, and landscape variables at each site. We inserted the probes of microclimate dataloggers (HOBO U23 Pro v2; Onset Computer Corp., Bourne, Massachusetts) as far into the hibernacula as possible (up to 1.8 m) to record hibernacula temperature (T_{hib} ; accuracy: $\pm 0.21^\circ\text{C}$, resolution: 0.02°C) and relative humidity (RH_{hib} ; accuracy: $\pm 2.5\%$, resolution: 0.03%) every 3 h; we used the mean of these recordings in our analyses. Bats continued to occupy the roosts despite presence of the probes. We concurrently measured ambient temperature (T_a) and relative humidity (RH_a). Given the limitation of using RH_a as a means of assessing the rate at which evaporative water loss would occur (Kurta 2014), we converted all RH measurements to absolute water vapor pressure (WVP_{abs} ; kPa—Brice and Hall, 2016) for analyses. For microhabitat and landscape, we measured the area, aspect, and orientation of the crevice opening; crevice depth (i.e., depth of the microclimate datalogger probe); roost material (e.g., sandstone); distance to water, calculated using GPS points (eTrex Legend HCx; Garmin Canada, Olathe, Kansas); and distance from crevice opening to level ground below, calculated using GPS points and clinometer measurements.

In the winters of 2013–2015, we paired each hibernaculum with a randomly selected rock and tree crevices, and used the same type of datalogger (HOBO U23 Pro v2; Onset Computer Corp.) to record microclimate inside (T_{rock} , WVP_{rock} , T_{tree} , and WVP_{tree}). To locate random crevices, we first moved to a point on the map within park boundaries in a random direction (0 – 359°) and at a random distance (500–2,500 m) from each hibernaculum that was outside the immediate area surrounding the hibernaculum but within a reasonable winter flight range based on previous radiotracking efforts from our study area (Lausen and Barclay 2006b). We then found the nearest rock or tree crevice with an opening of sufficient size to allow big brown bats to enter (entrance at least 2×2 cm—Greenhall 1982) and room enough for at least 1 bat. All random tree crevices were located in eastern cottonwoods (*Populus deltoides*).

In the winter of 2013–2014, we also recorded microclimate at 4 known cave hibernacula across central and northern Canada. Cadomin cave (CA), a large sandstone cave located in the Rocky Mountains near Cadomin, Alberta (53.0325°N , 117.3265°W); Walk-In cave (WI), a limestone cave located in the boreal forest of northern Alberta near Fort Smith, Northwest Territories (60.0055°N , 111.8849°W); Abyss cave (AB), part of a series of limestone caves located in the boreal forest near Grand Rapids, Manitoba (53.1842°N , 99.2679°W); and Richard Lake mine (RL), an abandoned mine located in the boreal forest near Kenora, Ontario (49.7670°N , 94.4894°W). We deployed microclimate dataloggers (HOBO U23 Pro v2 in CA, WI, and AB; HOBO H21-002 micro station in RL; Onset Computer Corp.) to measure temperature (T_{hib}) and relative humidity (RH_{hib}) in a chamber where bats are known to hibernate. All sites are known to have overwintering populations of little brown myotis

(*M. lucifugus*) and northern myotis (*M. septentrionalis*—Olson et al. 2011; Reimer et al. 2014; C. K. R. Willis, pers. obs.), and CA also houses hibernating long-legged myotis (*M. volans*—Olson et al. 2011). However, *E. fuscus* occurs only in WI, RL, and DPP during winter (Reimer et al. 2014; C. K. R. Willis pers. obs.).

Movement and group size.—To estimate group size and determine frequency of roost switching by bats overwintering in DPP, we continuously monitored locations and movements of marked individuals. In all 3 winters, we used receiver dataloggers (SRX400A; Lotek Wireless Inc.) with 5-element yagi antennas placed at the base of each hibernaculum to monitor the location of radiotagged bats. We programmed receivers to scan for the presence of radiotagged individuals every 15 min. In 2013–2015, we also mounted PIT-tag readers (Trovan LID650; EIDAP Inc.) with custom flexible antennas around the entrance of each of the 3 rock-crevice hibernacula to log activity of PIT-tagged bats. We defined an “emergence” as an event when: 1) the signal for a radiotagged bat was lost for 2 or more scans following arousal; or 2) when paired bouts of activity (i.e., exit and return) of PIT-tagged bats were recorded at the entrance of the hibernacula. We assumed a bat did not leave the hibernaculum if only a single PIT-triggered event was recorded (i.e., no clear exit and return) and the bat was recorded in the same hibernaculum at a later date.

Statistical analyses.—We used an information theoretic approach (i.e., Akaike Information Criterion, AIC) to compare logistic regression models differentiating microhabitat and landscape characteristics of hibernacula from those of random crevices. Before constructing models for AIC analysis, we eliminated highly correlated variables ($r > 0.70$) and performed an initial logistic regression with an arbitrarily high α -value ($P = 0.35$) to reduce the number of variables but retain those that may be biologically important (Hosmer and Lemeshow 1989). We constructed 4 candidate binomial models containing the remaining variables—crevice depth (Depth) and distance to level ground below (DistGB)—and ranked them according to their AIC_c values (AIC value corrected for small sample size) and weights (w_i —Burnham and Anderson 2002).

We confirmed all microclimate data met assumptions of normality with Kolmogorov–Smirnov goodness-of-fit tests and used quantile–quantile (Q–Q) plots to visually compare data against normal distributions. To compare microclimate data between roost types in DPP during the winters of 2013–2015, we used linear mixed models (LMMs) with mean temperature and humidity (recorded across crevice types every 3 h) as response variables, roost type (hibernaculum, random rock crevice, and random tree crevice) and T_a as predictor variables, and month and year as crossed random effects for the temperature model only; we removed these random effects from the humidity model because estimates of the variance explained by these effects were indistinguishable from zero. We also used a LMM to compare temperature of DPP hibernacula to that of known cavernous hibernacula (i.e., CA, WI, AB, and RL) across Canada, with T_h as a response variable, site as a predictor, and month as a random effect. The random effect of month

was indistinguishable from zero in the mixed model for humidity data, so we used a linear model (LM) to compare humidity data between sites, with WVP_{abs-h} as a response variable and site as a predictor. We used analysis of deviance (type II Wald chi-square tests) to derive P -values for predictors in each mixed model, and set statistical significance at $\alpha < 0.05$. We conducted analyses using R (R Development Core Team 2016) and present all data as means with SD ($\bar{X} \pm SD$).

RESULTS

Hibernacula microhabitat.—We PIT-tagged 75 *E. fuscus* (23 females and 52 males) and attached radiotransmitters to a subset of 36 individuals (3 females and 33 males). We did not re-locate any of the females after initial capture, and typically did not re-locate males caught earlier in the season (before 1 November). We successfully tracked 25 males to 3 hibernacula in DPP. Hibernacula were situated high ($\bar{X} = 10 \pm 2.5$ m) above the ground in south-facing ($\bar{X} = 160 \pm 32.8^\circ$), vertically oriented, sandstone crevices (Table 1). The highest-ranked model, with w_i of 0.68, suggested crevice depth (Depth) was a key variable differentiating hibernacula from randomly selected crevices (Table 2). Hibernacula were deeper ($\bar{X} = 150 \pm 26.5$ cm) than random rock ($\bar{X} = 112 \pm 27.7$ cm) and tree crevices ($\bar{X} = 34 \pm 9.1$ cm). The high (> 2) ΔAIC_c values of subsequently ranked models suggested good empirical support for the top-ranked model (Burnham and Anderson 2002).

In the winters of 2013–2015, T_a in DPP ranged from -40.8°C to 19.4°C ($\bar{X} = -8.2 \pm 9.97^\circ\text{C}$), but mean temperature of rock-crevice hibernacula was less variable (Fig. 1). Mean temperature within DPP crevices differed with T_a ($\chi^2_1 = 6,265.2$, $P < 0.001$) and crevice type ($\chi^2_2 = 4,839.1$, $P < 0.001$; Fig. 2). Rock-crevice hibernacula were warmer and more thermally stable than other available crevices in DPP (random rock and tree crevices), but less humid. Mean hibernacula temperature (T_h) was $0.8 \pm 0.87^\circ\text{C}$ ($N = 3$), ranged from -1.6°C to 2.7°C , and was higher and more stable than mean temperatures of random rock ($\bar{X} = -4.9 \pm 5.86^\circ\text{C}$) and tree crevices ($\bar{X} = -7.6 \pm 8.70^\circ\text{C}$), which ranged from -18.0°C to 9.0°C and -36.7°C to 16.9°C , respectively. Mean T_h fell below freezing for at most 10.5 days, which occurred 23 February–5 March

2013; during this time, mean T_h was -0.6°C with a minimum T_h of -1.2°C , compared to a concurrent mean and minimum T_a of -20.5°C and -36.7°C , respectively. Humidity also varied with WVP_{abs-a} ($\chi^2_1 = 11,447.2$, $P < 0.001$) and crevice type ($\chi^2_2 = 99.6$, $P < 0.001$; Fig. 2). Mean WVP_{abs} of hibernacula ranged from 0.12 to 0.58 kPa ($\bar{X} = 0.35 \pm 0.10$ kPa). Hibernacula had less variable but lower humidity than random rock crevices ($\bar{X} = 0.38 \pm 0.18$ kPa), and less variable but similar humidity to random tree crevices ($\bar{X} = 0.36 \pm 0.22$ kPa). Mean WVP_{abs} ranged from 0.11 to 1.02 kPa in random rock crevices and 0.02 to 1.41 kPa in random tree crevices. Ambient WVP_{abs} ranged from 0.01 to 1.03 kPa ($\bar{X} = 0.32 \pm 0.20$ kPa).

During the winter of 2013–2014, rock-crevice hibernacula in DPP were drier but not colder compared to known cave hibernacula in central and northern Canada. Temperatures varied with site ($\chi^2_4 = 28,969$, $P < 0.001$; Fig. 3), and temperatures of DPP hibernacula ($\bar{X} = 0.6 \pm 0.91^\circ\text{C}$) were higher than those in WI cave ($\bar{X} = 0.0 \pm 0.63^\circ\text{C}$) but lower than those of all other sites. Temperatures were similar between CA ($\bar{X} = 2.0 \pm 0.01^\circ\text{C}$) and RL mine ($\bar{X} = 2.1 \pm 1.88^\circ\text{C}$). Humidity also varied with site ($\chi^2_4 = 19,308$, $P < 0.001$; Fig. 4). In particular, WVP_{abs} of DPP hibernacula ($\bar{X} = 0.33 \pm 0.09$ kPa) was lower than that of all other sites.

Movement and group size.—We collected 622 days of radiotelemetry data from 13 male *E. fuscus* (mean 48 ± 18.5 days/bat, range 15–85 days) during the 3 winters of our study. We also continuously recorded PIT-tag activity at the hibernacula entrances for 112 days in 2013–2014 and 146 days in 2014–2015. We detected 48% of the captured and uniquely identified (i.e., 52 PIT-tagged, 33 of which were also radiotagged) male *E. fuscus* in at least 1 of the 3 rock-crevice hibernacula during at least 1 winter. Bats roosted in small groups (< 7 individuals) and 5 of 7 returning individuals used the same hibernaculum each year. Despite 107 recorded emergences (46 in 2013–2014 and 61 in 2014–2015), bats rarely moved between hibernacula mid-winter; the majority of monitored individuals (22/25) returned to the same hibernaculum after mid-winter flights. Bats that moved between hibernacula mid-winter ($n = 3$) did so multiple (3–7) times, and 2 of those individuals also changed roosts between winters.

Table 1.—Mean microclimate, microhabitat, and landscape characteristics ($\bar{X} \pm SD$) of 3 rock-crevice hibernacula used by *Eptesicus fuscus*, 3 random rock crevices, and 3 random tree crevices in Dinosaur Provincial Park, Alberta.

Variable	Hibernacula	Random rock crevice	Random tree crevice
Microclimate			
Temperature ($^\circ\text{C}$)	0.8 ± 0.87	-4.9 ± 5.86	-7.6 ± 8.70
Humidity (WVP_{abs} ; kPa)	0.35 ± 0.10	0.38 ± 0.18	0.36 ± 0.22
Microhabitat			
Area of opening (cm^2)	235 ± 281.1	302 ± 157.3	377 ± 242.7
Aspect of opening ($^\circ$)	160 ± 32.8	165 ± 44.5	305 ± 39.8
Depth of crevice (cm)	150 ± 26.5	112 ± 27.7	34 ± 9.1
Material	Sandstone	Sandstone	Wood
Landscape			
Distance to ground above (m)	19 ± 3.1	2.6 ± 3.38	N/A
Distance to ground below (m)	10 ± 2.5	5.5 ± 5.01	2.2 ± 1.02
Distance to water (m)	78 ± 35.7	$1,876 \pm 664.2$	153 ± 210.1

Table 2.—Ranking of logistic regression models comparing microhabitat and landscape characteristics used in hibernacula selection by *Eptesicus fuscus* in Dinosaur Provincial Park, Alberta. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set; w_i = Akaike model weight; w_1/w_i is the evidence ratio; k = number of estimable parameters; and deviance = measure of model fit. Model covariates include crevice depth (Depth) and distance to level ground below (DistGB).

Model	ΔAIC_c	w_i	w_1/w_i	k	Deviance
Depth		0.68		2	4.80
DistGB	2.07	0.24	2.83	2	5.87
Depth + DistGB	4.94	0.06	11.33	3	9.23
Null (no covariates)	7.57	0.02	34.00	1	11.46

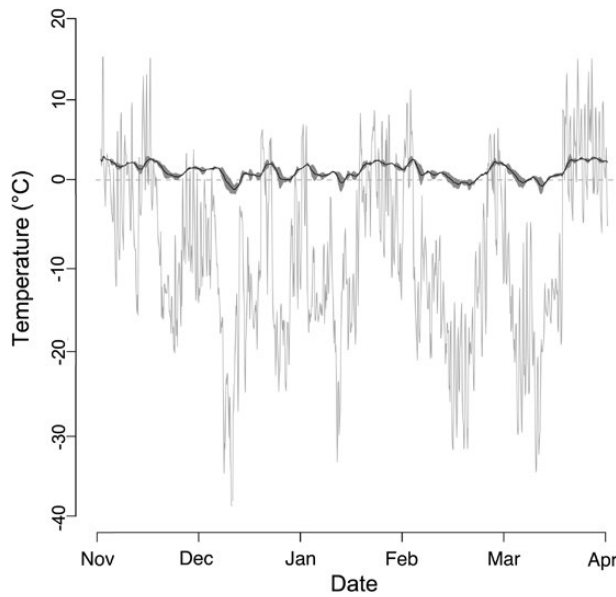


Fig. 1.—Ambient temperature (light gray line) and mean temperature inside 3 rock-crevice hibernacula (black line) with 95% CI (dark gray shade) in Dinosaur Provincial Park, Alberta, Canada during the winter (November–March) of 2013–2014. Light gray dashed line represents 0°C.

DISCUSSION

Documented use of rock crevices by hibernating bats is rare (Lausen and Barclay 2006b; Neubaum et al. 2006; Perry et al. 2010) and our study is the first to examine crevice roost selection during winter. Our results show that male *E. fuscus* in DPP use specific rock-crevice hibernacula with particular microclimate and microhabitat characteristics, with evidence of winter roost fidelity within and between years. Bats we captured used only 3 rock crevices during hibernation, despite numerous crevices being potentially available. Our data also show that mid-winter flight is common in our study area, yet there was little movement by *E. fuscus* between hibernacula. We also show that crevice hibernacula in our study area were less humid than cave hibernacula in other parts of Canada.

As predicted, despite the small sample size of roosts, our binomial models of physical characteristics suggested that rock-crevice hibernacula in DPP were deeper, warmer, and less thermally variable than random rock or tree crevices.

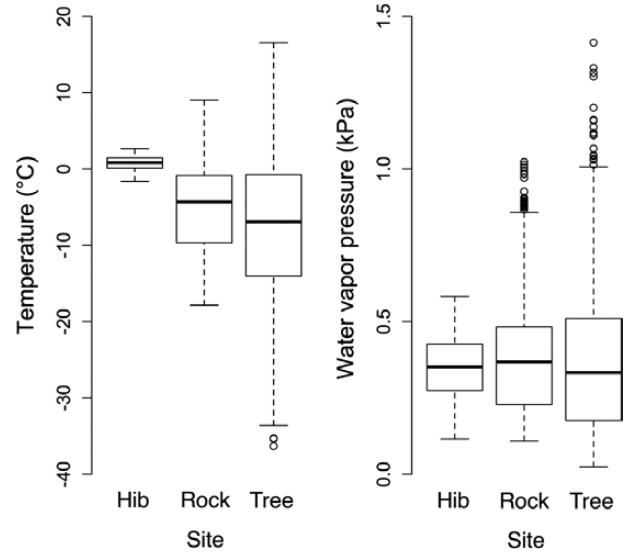


Fig. 2.—Boxplot of mean temperature and absolute water vapor pressure recorded inside 3 rock-crevice hibernacula (Hib), 3 random rock crevices (Rock), and 3 random tree crevices (Tree) in Dinosaur Provincial Park, Alberta, Canada during the winters (November–March) of 2013–2015. Bold bars represent the median. Upper and lower box limits are the 75th and 25th quartiles, respectively. Whiskers extend to the minimum and maximum values of each stage. Open circles represent possible outliers.

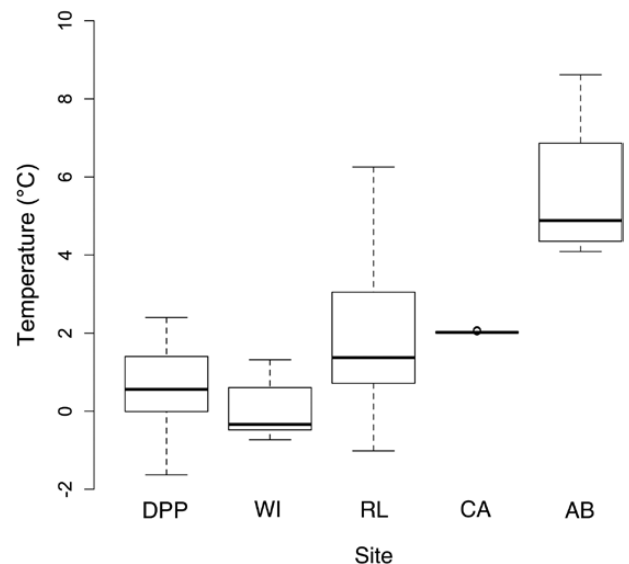


Fig. 3.—Boxplot of mean temperature recorded inside rock-crevice hibernacula in Dinosaur Provincial Park (DPP), Alberta and known cave hibernacula across northern and central Canada—Walk In (WI), Richard Lake (RL), Cadomin (CA), and Abyss (AB)—during the winter (November–March) of 2013–2014. Bold bars represent the median. Upper and lower box limits are the 75th and 25th quartiles, respectively. Whiskers extend to the minimum and maximum values of each stage. Open circles represent possible outliers.

Deep hibernacula buffer hibernating animals from ambient conditions and freezing temperatures can be avoided at depths beyond the limit of frost penetration in our study area (~2 m—Crawford 1955). Temperature is crucial to overwinter survival in hibernators and most species avoid hibernacula with

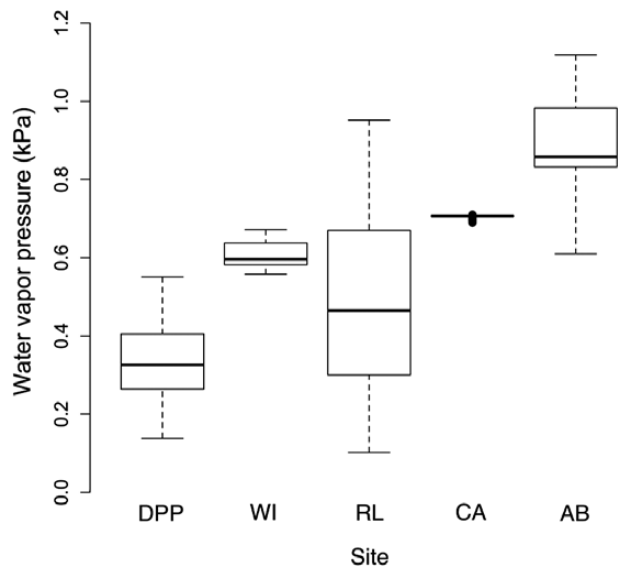


Fig. 4.—Boxplot of mean absolute water vapor pressure recorded inside rock-crevice hibernacula in Dinosaur Provincial Park (DPP), Alberta and known cave hibernacula across central Canada—Walk In (WI), Richard Lake (RL), Cadomin (CA), and Abyss (AB)—during the winter (November–March) of 2013–2014. Bold bars represent the median. Upper and lower box limits are the 75th and 25th quartiles, respectively. Whiskers extend to the minimum and maximum values of each stage. Open circles represent possible outliers.

subfreezing temperatures (Geiser 2004). Therefore, we were surprised to record subzero temperatures within hibernacula. In DPP, bats may roost deeper than we could monitor, although we did observe bats roosting close to the probes, which reached to depths of 1.8 m. The temperature inside WI also dropped below freezing at times (as low as -0.7°C). *Eptesicus fuscus* is commonly observed using cooler, drier areas of hibernation sites than other species (Beer and Richards 1956; Davis 1970; Fenton 1970), and has been recorded hibernating in freezing temperatures elsewhere (Fenton 1970). The 3 sites used by overwintering *E. fuscus* in this study were the driest and coldest of the hibernacula we examined, with temperatures lower than the average reported for bat hibernacula in North America (6°C —Webb et al. 1996), further suggesting the relative cold-hardiness of this species.

Contrary to our predictions, randomly selected rock and tree crevices had higher mean humidity than hibernacula. WVP is a function of temperature, with higher levels of saturation in warmer air (Campbell and Norman 1998) and the higher levels of humidity we recorded in random crevices occurred mainly during periods with higher temperatures. For bats we studied to have benefitted from higher humidity in hibernacula, they would have also needed to tolerate higher, more variable temperatures. Instead, *E. fuscus* appeared to favor thermal stability over high humidity during hibernation, highlighting the importance of hibernaculum temperature for this species (see also Beer and Richards 1956). Likewise, hibernating *E. fuscus* in Colorado prefer more thermally stable rock crevices over warmer buildings with more extreme thermal maxima and minima (Neubaum et al. 2006). Most hibernators respond

negatively to decreases in humidity (e.g., Speakman and Racey 1989; Thomas and Cloutier 1992; Thomas and Geiser 1997; Ben-Hamo et al. 2013) with reduced overwinter survival in dry conditions (Willis et al. 2011). The ability of *E. fuscus* to hibernate in more stable but colder, drier conditions, such as those found in rock-crevice hibernacula in DPP, may depend on adaptation or acclimatization to arid conditions (Klüg-Baerwald and Brigham 2017).

Nearly all small hibernators arouse periodically during hibernation (Willis 1982) and roosting ecology likely influences the motivation for and frequency of these arousals. Bats that hibernate in large, mixed-sex groups in humid caves that may contain open water and insects likely arouse less frequently (e.g., Ben-Hamo et al. 2013) and have opportunities to mate, drink, and forage during arousals. Rock-crevice hibernacula in DPP were drier and less thermally stable than known cave hibernacula, which may increase evaporative water loss and arousal frequency, and require that bats overwintering in the prairies exit the hibernacula to drink (Thomas and Cloutier 1992; Thomas and Geiser 1997) or mate. Bats in some areas may forage during arousals (Brigham 1987) but insect prey are not available during winter in our study area (Lausen and Barclay 2006b), which adds to the energetic constraint and importance of fat stores for bats in the prairies. In support of this, mean mass of *E. fuscus* entering hibernation in DPP (23.6 g—Klüg-Baerwald et al. 2016) is higher than that reported for a population of cave-hibernating *E. fuscus* in Ontario (21.6 g—Fenton 1972) where winter foraging may be possible (Brigham 1987), but spring emergence masses are similar (16.8 and 16.4 g, respectively). Extra fat stores of bats hibernating in DPP may compensate for the effect of their roosting ecology on winter energetics.

Roost fidelity is thought to be low among bats that roost in ubiquitous, ephemeral structures (e.g., tree foliage and crevices—Lewis 1995; but see Willis et al. 2003; Klüg et al. 2012). We thus predicted the large number of rock crevices across the landscape and variable microclimate within would prompt *E. fuscus* in DPP to use multiple winter roosts and switch between them often. However, our data suggest that *E. fuscus* rarely move during winter and that winter roosts with suitable microclimate are not ubiquitous in our study area. We also documented between-year fidelity to rock-crevice hibernacula, supporting the hypothesis that suitable roosts in the area are limited, much like that documented for cavernicolous populations (Glover and Altringham 2008). The need to exit the hibernaculum to switch roosts may contribute to the rarity of roost switching during winter flights in our study area. Outdoor winter flights are energetically costly (Klüg-Baerwald et al. 2016) and could increase predation risk (Thomas and Jacobs 2013). That bats still occasionally fly outside of the hibernacula despite such costs suggests that these flights are necessary and beneficial for reasons not related to roost switching. The impetus for winter flight may be associated with the need to drink or exercise flight muscles, and future work aimed at testing hypotheses about winter flight is warranted.

Limited space within rock-crevice hibernacula undoubtedly constrains the number of bats able to roost inside a given

crevice and limits potential for social thermoregulation. Bats may occasionally arouse together to save energy during arousals (Boyles et al. 2008) and may even cluster to reduce evaporative water loss (Boratyński et al. 2015). Although group size and thus associated benefits are likely reduced in narrow crevice hibernacula, roosting in tight quarters may still be beneficial from a heat loss perspective if the surrounding substrate insulates bats during arousals or reduces surface area exposed to cold, open air in the hibernaculum, thereby reducing convective heat loss. Previous studies have investigated heat conductance of summer roosts (Lausen and Barclay 2002) but none have evaluated the influence of substrate conditions on energetics and water balance during hibernation.

This information gathered from this study is important in the context of bats persisting on the prairies in the face of climate change and white-nose syndrome (WNS)—an invasive fungal disease that kills bats during hibernation (Frick et al. 2016). Use of non-cavernous hibernacula increases the amount of winter habitat available to sedentary species, and rising temperatures may expand suitable overwintering habitat at the northern edge of a species range (Humphries et al. 2002, 2004). However, temperatures inside rock-crevice hibernacula generally reflect external temperatures (Fig. 1) and the consequences for existing overwintering sites are uncertain. Warming temperatures are associated with decreased survival in many hibernators (e.g., Geiser and Kenagy 1988; Geiser and Broome 1993; Turbill and Prior 2016) and existing hibernacula may become too warm for some species, particularly those like *E. fuscus* that appear cold-adapted. Use of small, dry, cold hibernacula may benefit some bat populations as WNS continues to spread across North America (Frick et al. 2016). The fungus grows best in high humidity at 12–16°C (Verant et al. 2012) and is spread mainly through bat-to-bat contact (Lorch et al. 2011; Langwig et al. 2012). If conditions and behaviors of bats in the prairies are not conducive to the growth and spread of the fungus, the prairies may act as a barrier to the spread of WNS (Hallam and Federico 2012). Our data suggest that male *E. fuscus* hibernate in small clusters and use cold, dry hibernacula, and thus may be less impacted by the disease. Mortality may also be low for other prairie-living bat species detected in this area (e.g., *M. ciliolabrum* and *M. evotis*—Lausen and Barclay 2006b) if their overwintering behaviors are similar.

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