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Canada**

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Environmental correlates and energetics of winter flight by bats in Southern Alberta, Canada

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Abstract

Winter activity of bats is common, yet poorly understood. Other studies suggest a relationship between winter activity and ambient temperature, particularly temperature at sunset. We recorded echolocation calls to determine correlates of hourly bat-activity in Dinosaur Provincial Park, Alberta, Canada. We documented bat activity in temperatures as low as -10.4°C . We observed big brown bats (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) flying at colder temperatures than species of *Myotis* bats (genus *Myotis* (Kaup 1829)). We show that temperature and wind are important predictors of winter activity by *E. fuscus* and *Myotis*, and that *Myotis* may also use changes in barometric pressure to cue activity. In the absence of foraging opportunity, we suggest these environmental factors relate to heat loss and thus the energetic cost of flight. To understand the energetic consequences of bat flight in cold temperatures, we estimated energy expenditure during winter flights of *E. fuscus* and *Myotis lucifugus* using species-specific parameters. We estimated that winter flight uses considerable fat stores and that flight thermogenesis could mitigate energetic costs by 20% or more. We also show that temperature-dependent interspecific differences in winter activity likely stem from differences between species in heat loss and potential for activity-thermoregulatory heat substitution.

Key words: bats, big brown bat, echolocation, *Eptesicus fuscus*, energetics, flight, *Myotis*, winter activity

Introduction

During hibernation, metabolic rate (MR) and body temperature (T_b), are decreased for days to weeks (Ruf and Geiser 2015). Hibernating animals save considerable energy and can survive on limited resources (i.e., body fat or cached food) for extended periods, up to months at a time (Humphries et al. 2003). Benefits of hibernation are obvious (Geiser 2004; Geiser and Brigham 2012) but there are associated costs, such as suppressed molecular synthesis (Lillegraven et al. 1987), ceased or delayed reproduction (Racey 1969; Barnes et al. 1986), and immunosuppression (Bouma et al. 2010). For these reasons and likely others, nearly all hibernating mammals arouse periodically (Willis 1982; French 1985), ostensibly to excrete metabolic wastes (Baumber et al. 1971), mount immune responses (Burton and Reichman 1999), mate (Thomas et al. 1979), eat (Humphries et al. 2001), and possibly drink (Thomas and Cloutier 1992; Thomas and Geiser 1997; Ben-Hamo et al. 2013).

Much of what we know about arousals and winter activity of temperate-zone bats comes from research on cavernicolous species. In eastern North America, bats often roost in large groups in sizeable, humid, thermally-stable hibernacula (Webb et al. 1996; Perry 2012). Most activities typical of arousals occur within the hibernacula; caves and mines allow flight within hibernacula and may contain open water sources and hibernating insects that can be consumed (Swanson and Evans 1936; Rysgaard 1942). Opportunistic mating is also possible with mixed-sex groups typically found in cave hibernacula (Thomas et al. 1979).

Bats are also active outside of hibernacula for reasons poorly understood. Early evidence suggested these events were occasional and likely in response to starvation or dehydration (Speakman and Racey 1989; Boratyński et al. 2015). That some bats emerge in winter with low body mass supports the idea that bats emerge to forage (Brigham 1987). More recently, increased

activity outside hibernacula has been associated with white-nose syndrome (WNS)—an invasive fungal disease responsible for the deaths of at least 6 million bats in eastern North America since 2006 (Frick et al. 2015). Interest in winter bat-activity due to WNS has made it apparent that mid-winter flight by bats is common (e.g., Falxa 2007; Schwab and Mabee 2014), even in northern areas with harsh winter climates (Lausen and Barclay 2006).

Winter bat-activity in areas with mild winters is often associated with favourable foraging conditions. In summer, warm calm nights are associated with increased insect abundance (Taylor 1963) and foraging behaviour by bats (e.g., Racey and Swift 1985; Fukui et al. 2006). Likewise, tri-colored bats (*Perimyotis subflavus* (Cuvier, 1832)), little brown myotis (*Myotis lucifugus* (LeConte, 1831)), northern long-eared myotis (*M. septentrionalis* (Trouessart, 1897)), and brown long-eared bats (*Plecotus auritus* (Linnaeus, 1758)) are more active during warmer, calmer winter nights (Hays et al. 1992; Whitaker and Rissler 1992). Bats also use barometric pressure to determine when to forage or move in summer. High activity levels of flying insects and *P. subflavus* occur during periods of low or falling barometric pressure (Paige 1995), and falling barometric pressure cues movement of migratory bat-species (Cryan and Brown 2007; Baerwald and Barclay 2011). Likewise, bat activity increases on warm nights with falling barometric pressure during Austral winters (Turbill 2008), and *M. lucifugus* uses barometric pressure to cue emergence from hibernation (Czenze and Willis 2015).

Although mid-winter foraging is likely in milder winter climates (e.g., Avery 1985; Brigham 1987; Dunbar et al. 2007), bats are active despite a lack of insects in northerly areas with harsher winters (Lausen and Barclay 2006). Without opportunity to supplement fat stores, the energetics of mid-winter flights become particularly important. Cold-weather activity may be especially energetically costly given the small body size of bats; a high body surface area to

volume ratio and large surface area of the wings increase the potential heat loss heat (Phillips and Heath 2001). Conditions that increase thermal exchange during flight, such as high winds and precipitation (Voigt et al. 2011), may negate benefits of leaving the hibernacula.

However, mechanisms to mitigate heat loss in the cold may enable activity through a low range of T_a . Spatial heterothermy in Brazilian free-tailed bats (*Tadarida brasiliensis* (Geoffroy, 1824)) reduces heat loss from their wings while in flight (Reichard et al. 2010). In addition, heat produced through activity is used for thermoregulation in a wide range of animals (Humphries and Careau 2011). Metabolic heat production in cold temperatures is equivalent in perching and foraging black-capped chickadees (*Poecile atricapillus* (Linnaeus, 1766); Cooper and Sonsthagen 2015), and flight metabolic rate is independent of ambient temperature in pigeons (*Columba livia domestica* (Gmelin, 1789); Rothe et al. 1987). Humans (*Homo sapiens* (Linnaeus, 1758)) also maintain steady rates of heat production despite drops in ambient temperature while active (Nielsen and Nielsen 1962). These data suggest that heat produced through movement substitutes for shivering and metabolic thermogenesis typically required to compensate for heat loss in cold conditions. In fact, one reason for nocturnality in bats might be the inability to dissipate heat produced during flight while exposed to solar radiation (Speakman 1991, 1995; Voigt and Lewanzik 2011). Activity-thermoregulatory heat substitution has not been investigated in bats but may mitigate the cost of winter flight.

We investigated correlates of winter bat-activity and estimated the energetic costs of flight by a population of hibernating bats in southern Alberta, Canada. Winter foraging is not possible at this site, yet bats continue to fly. Thus, we hypothesized factors influencing heat loss and the energetic cost of flight (e.g., wind, temperature, and precipitation) predict winter activity outside the hibernacula. Specifically, we predicted that winter bat-activity decreases during conditions of

high wind, low T_a , and precipitation, and increases during warmer, calmer nights. We also proposed that interspecific differences in activity relative to ambient temperature can be explained by body size and associated rates of heat loss. Thus, we predicted that larger-bodied big brown bats (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) fly in colder temperatures than smaller-bodied *Myotis* bat species (genus *Myotis* (Kaup 1829)). Finally, we accounted for activity-thermoregulation heat substitution (heat produced through flight) and estimated species-specific energy expenditure during winter flight. We expected our energetic models to corroborate inter- and intraspecific patterns in activity of bats in relation to ambient temperatures observed at our study site.

Materials and methods

Study area

We monitored bat activity in Dinosaur Provincial Park (DPP), Alberta, Canada from October 2012 through April 2015. The park is located along the Red Deer River in southern Alberta (50°45'09.2"N, 111°31'03.6"W) and represents a mixed landscape of prairie and riparian habitat with an extensive network of creeks and drainages. The semi-arid climate is characterized by hot, dry summers, cold winters, and low overall precipitation (Bailey 1979). At least three species—*E. fuscus*, western small-footed myotis (*M. ciliolabrum* (Merriam, 1886)), and western long-eared myotis (*M. evotis* (Allen, 1864))—over-winter in deep rock crevices in the area (Lausen and Barclay 2006). Dinosaur Provincial Park is the location of the first natural bat hibernation area discovered in Alberta's grasslands natural region. The park provides numerous access points to underground habitat below the frost line, making it a potentially strategically important hibernation site for bats.

Acoustic monitoring

We acoustically monitored bat activity in DPP for three winters, October through April, 2012-2015. We used Anabat (Titley Electronics, Ballina, New South Wales, Australia) and SM2Bat+ (Wildlife Acoustics, Maynard, Massachusetts, USA) detectors set to record every night from an hour before sunset to an hour after sunrise. We calibrated Anabat units (see Larson and Hayes 2000) and deployed one facing out over the Red Deer River and one in an open field at the edge of a stand of cottonwood trees (*Populus deltoids* (Bartram ex Marshall)). We deployed one SM2Bat+ detector on the bank of the Little Sandhill Creek, the only permanent creek in the park. The creek is the only location where bats can be reliably captured in mist nets during winter despite being frozen. We housed Anabat detectors in custom waterproof boxes mounted on wooden stands approximately 1.5 m above ground, with microphones shielded and pointed parallel to the ground. We housed the SM2Bat+ in a plastic bin and mounted the microphone on a 1.5 m pole with a small plastic hood located 10 cm above to shield it from precipitation. We powered each detector with a 12 V, 12 Ah sealed lead acid battery coupled with a 10 W solar panel.

We analyzed echolocation calls in zero-crossing format using AnalookW software (version 3.9c; C. Corben, Columbia, Missouri, USA). We used a custom filter to separate background noise (e.g., insects and wind) from identifiable calls (see Lausen et al. 2014 for details). We then manually identified bat calls to species using a combination of call characteristics, such as minimum frequency (F-min) and call duration, slope, and shape (Corben 2002; Lausen et al. 2014). Overlap occurs in call characteristics between sympatric silver-haired bats (*Lasionycteris noctivagans* (Le Conte 1831)) and *E. fuscus* (Barclay 1999), but we attributed all low-frequency

(i.e., F-min between 20 and 23 kHz) calls recorded between October and April to *E. fuscus* given that *L. noctivagans* is migratory and does not occur in the area during winter. We attributed all high-frequency calls (i.e., F-min > 35 kHz) to *Myotis* but did not differentiate between *M. ciliolabrum*, *M. evotis*, or *M. lucifugus*. We used the presence of “feeding buzzes”, segments of quickly repeating pulses characteristic of an individual locating and closing in on prey to identify foraging by bats (Fenton 2003).

We recorded hourly ambient temperature (T_a ; °C) with a HOBO data logger (U23 Pro v2; Onset Computer Corporation, Bourne, Massachusetts, USA) shielded by a solar radiation shield (RS3; Onset Computer Corporation, Bourne, Massachusetts, USA) and located next to the SM2Bat+ detector on the bank of the Little Sandhill Creek. We gathered all other hourly environmental data (wind speed (m/s) 2 m above ground, precipitation (mm), and barometric pressure (kPa)) from the Alberta Agriculture and Forestry weather station (AgroClimatic Information Service 2015) located in Patricia, Alberta, 15 km from the study site.

Statistical analyses

We used bat passes per hour (passes/hour) across all detectors to quantify bat-activity. We defined a bat pass as a sequence of ≥ 2 echolocation calls (Vonhof 2006). Hourly bat-activity data was not normally distributed due to overdispersion, which precluded the use of parametric tests for analyses. Instead, we used negative-binomial regression analyses to model hourly bat-activity as a function of temperature (Temp), wind speed (Wind), precipitation (Precip), and 24-hour change in barometric pressure (BPDiff). We used an information theoretic approach (i.e., Akaike information criterion (AIC)) to construct and compare *a priori* models (Hosmer and Lemeshow 1989; Anderson et al. 2000).

We analyzed data separately for *E. fuscus* and *Myotis* activity. Before model construction, we ran correlation analyses to eliminate highly correlated ($r > 0.70$) predictor variables. We constructed 14 candidate models containing the variables of interest for each group and ranked them according to their quasi-likelihood modified AIC_c values (QAIC_c) and weights (w_i). The AIC_c value considers sample size, the QAIC_c value accounts for overdispersion of the data, and w_i is a normalized value reflecting the probability the given model is correct given the entire subset of candidate models (Burnham and Anderson 2002). The best model has the lowest QAIC_c and highest w_i . However, we considered all models with a QAIC_c value within 2 of the best model ($\Delta\text{QAIC}_c < 2$) to have empirical support (Burnham and Anderson 2002). To determine the probability of detecting bats in relation to ambient temperature based on our data, we ran binomial logistic regressions of hourly activity of *E. fuscus* and *Myotis* as functions of temperature.

To exclude late-stage summer and swarming activity and ensure we examined winter activity only, we defined the start of hibernation as the first day of the season with a daytime high $T_a \leq 0^\circ\text{C}$ (23 October 2012, 28 October 2013, 9 November 2014). We also excluded data beyond the last day of the season with a daytime high $T_a < 0^\circ\text{C}$ (24 March 2013, 1 April 2014, 4 March 2015). We used analyses of variance (ANOVA) with Tukey's post-hoc adjustments to test for interannual differences in weather patterns. We conducted all statistical analyses using R (R Development Core Team 2016) and present all data as means with standard deviation ($\bar{X} \pm SD$).

Energetic modelling

To estimate energy expenditure by resting euthermic bats (E_{rest}) in temperatures below the thermoneutral zone, we used the equation of Humphries et al. (2006):

$$E_{rest} = \text{BMR} + (T_{lc} - T_a)C_{eu},$$

which accounts for basal metabolic rate (BMR) and metabolic heat needed to compensate for convective heat loss (H_c , represented by $(T_{lc} - T_a)C_{eu}$). In this equation, T_{lc} is the lower critical temperature, T_a is the mean ambient temperature of known hibernacula in Dinosaur Provincial Park during our study (1.1°C; B. Klüg-Baerwald, unpublished data), and C_{eu} is wet thermal conductance ($\text{mW g}^{-1} \text{ } ^\circ\text{C}^{-1}$) at euthermic T_b . We used published values of BMR (6.31 mW g^{-1}) and T_{lc} (26.7°C) reported for *E. fuscus* by (Willis et al. 2005). However, Willis et al. reported C_{eu} for *E. fuscus* measured in summer when conductance of fur is higher than in winter (Shump and Shump 1980). Thus, we estimated C_{eu} for *E. fuscus* during winter ($1.41 \text{ mW g}^{-1} \text{ } ^\circ\text{C}^{-1}$) as that of *M. lucifugus* measured in winter ($1.47 \text{ mW g}^{-1} \text{ } ^\circ\text{C}^{-1}$; Stones and Wiebers 1967) and corrected for the 4.6% higher insulative value of *E. fuscus* fur (Shump and Shump 1980). We used published values of BMR (14.53 mW g^{-1}) and T_{lc} (33°C) reported for *M. lucifugus* by (Stones and Wiebers 1967). For whole animal estimates, we used the mean masses of *E. fuscus* captured during winter in DPP (21.7 g; B. Klüg-Baerwald, unpublished data) and *M. lucifugus* captured during early hibernation at a site located in Manitoba, Canada (10.1 g; Jonasson and Willis 2012).

To estimate net energy expenditure by active bats flying in cold conditions (E_{flight}), we modified the heat balance equation of Schmidt-Nielsen (1997) to include the energetic costs of flight (P_{flight}) and temperature-dependent rates of heat loss via forced convection (H_c) and long-wave radiation (H_r), as well as the energetic offset of flight thermogenesis:

$$E_{flight} = 0.2P_{flight} + H_c + H_r.$$

We assumed 20% muscle efficiency during flight (Speakman and Thomas 2003), with the remaining 80% of P_{flight} contributing to activity-thermoregulation heat substitution (Humphries

and Careau 2011). If exercise thermogenesis exceeds total heat loss, then $E_{flight} < P_{flight}$; in such cases, we considered P_{flight} as the total cost of activity.

To calculate P_{flight} , we used the equation of Speakman and Racey (1991):

$$\log_{10}P_{flight} = -0.638 + 0.808 \log_{10}m,$$

where m is the mass reported above for each species. Given that this equation was extrapolated from measurements of bats flying in mild thermal conditions (room-temperature air; Speakman and Racey 1991), we assumed it does not include added thermoregulatory costs (i.e., heat produced during flight compensated completely for heat lost) and could thus be used to estimate the energetic cost of flight only.

We calculated H_c of body and wings using the equation of Schmidt-Nielsen (1997):

$$H_c = (T_{sk} - T_a)C_f.$$

For wings, we assumed skin temperature (T_{sk}) to approximate T_a but not drop below 1°C to avoid freezing, and used the convective coefficient of wing tissue during flight (C_f ; W m⁻² °C⁻¹) reported for *T. brasiliensis* (Reichard et al. 2010). For body calculations, we used euthermic T_{sk} for *E. fuscus* (35.8°C; Willis et al. 2005) and *M. lucifugus* (35°C; Stones and Wiebers 1965) to calculate temperature-dependent rates of heat loss via forced convection from skin surface through fur. We accounted for forced convection experienced in flight by using the equation for wind-dependent thermal conductance of fur (K_{fur} ; W m⁻² °C⁻¹) of Bakken (1991):

$$K_{fur} = a + bu^c.$$

In this non-linear equation, a is the thermal conductance of fur in the absence of wind (3.969 W m⁻² °C⁻¹ and 4.154 W m⁻² °C⁻¹ for *E. fuscus* and *M. lucifugus*, respectively; Shump and Shump 1980), u is wind speed (m/s), which we set as the reported minimum-power flight-speed of *E. fuscus* (3.8 m s⁻¹; Brigham and Fenton 1991) and *M. lucifugus* (3.7 m s⁻¹; Patterson and Hardin

1969), and b and c are constants. Given that no such data exist for bats, we set b at 1.3, a value reported for a small rodent in winter (Boyles and Bakken 2007), and used a common exponent of 1 (Campbell et al. 1980).

To estimate thermal radiation exchange between bat and night sky, we used the equation of Schmidt-Nielsen (1997):

$$H_r = \sigma \epsilon_{bat} \epsilon_{sky} (T_s^4 - T_{sky}^4) A,$$

where σ is Stefan-Boltzmann's constant ($5 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), ϵ_{bat} is emissivity of the bat (0.98; Monteith and Unsworth 1990), and ϵ_{sky} is emissivity of the sky calculated using the equation of Swinbank (1963):

$$\epsilon_{sky} = 0.398 \times 10^{-5} \times (T_a + 273.15)^{2.148}.$$

To calculate the radiative temperature of the night sky (T_{sky}), we used the equation of Gates (1980):

$$T_{sky} = T_a - 20.4 + 0.22 T_a.$$

Rates of heat loss depend on the temperature differential between environment and the surface of an object (T_s ; Schmidt-Nielsen 1997). Little data exist on flight temperatures of bats while in flight, so we assumed T_s of the body to approximate the lowest surface temperature measured during flight in *T. brasiliensis* ($\sim 18^\circ\text{C}$; Reichard et al. 2010) and calculated T_s of the wings as described above for H_c . We calculated surface area (A) of the body to be that of a cylinder (Chappell 1980) with dimensions based on the morphometrics of each species (van Zyll de Jong 1985; Nagorsen and Brigham 1993) and used surface areas reported in the literature for the wings (Farney and Fleharty 1969).

For our estimates, we assumed that bats fly at minimum-power speed (i.e., they maximize flight time with a given amount of energy; Thomas 1975), and that there is no influence of wind

beyond that experienced via flight speed. We also assumed heat loss as a consequence of convection and radiation only. Heat is lost from a warm body to a colder environment through conduction, evaporation, radiation, and convection (Schmidt-Nielsen 1997). However, we excluded conduction given that bats are not in contact with any solid surface during flight, and evaporative heat loss is negligible in temperatures below thermoneutral. Finally, we assumed peripheral cooling minimizes heat loss from the wings during flight (Reichard et al. 2010) and did not consider effects of piloerection and vascular adjustments.

Results

General patterns in weather and bat activity

We recorded 1 310 bat passes over 405 nights ($\bar{X} = 3.2 \pm 7.41$ passes/night) of monitoring during the winters of 2012-13, 2013-14, and 2014-15 (Table 1). Activity occurred during every month (October through April) in each year of the study. We detected bat-activity on 34.1% (138 of 405) of the nights sampled, when temperatures were as low as -10.4°C . Over the three winters of this study, mean temperature at sunset was $-7.3 \pm 8.20^{\circ}\text{C}$ and mean nightly low was $-14.0 \pm 13.34^{\circ}\text{C}$. Nightly low ambient temperature varied among winters ($F_{2,402} = 5.85$, $P = 0.003$); in particular 2013-14 was colder ($\bar{X} = -16.9 \pm 19.66^{\circ}\text{C}$) than 2012-13 ($\bar{X} = -11.3 \pm 6.94^{\circ}\text{C}$; $P = 0.003$). Mean nightly wind speed also varied among winters ($F_{2,402} = 18.58$, $P < 0.001$); 2014-15 ($\bar{X} = 3.5 \pm 1.72$ m/s) was windier than 2012-13 ($\bar{X} = 2.5 \pm 1.42$ m/s; $F_{2,402} = 5.85$, $P = 0.003$) and 2013-14 ($\bar{X} = 2.5 \pm 1.46$ m/s; $F_{2,402} = 5.85$, $P = 0.003$). Total nighttime precipitation during the winter hibernation periods was 32.6 mm in 2012-13, 24.7 mm in 2013-14, and 27.9 mm in 2014-15.

Nearly all calls (97.9%, $N = 1\,283$) occurred creekside, with only 17 (1.3%) passes at the riverbank detector and 10 (0.8%) at the Cottonwood flats detector. We identified 91.3% ($N = 1\,196$) of calls as belonging to *E. fuscus* and 8.7% ($N = 114$) to *Myotis* bat species. We did not detect any other phonic group of bats during the hibernation period. For both groups, the majority of activity occurred within 4–5 hours of sunset, but activity continued during all hours of the night with a notable peak in *Myotis* activity in the final few hours of the night (Figs. 1a, 1b). We did not observe any feeding buzzes in recordings made within the hibernation period in any of the years.

Influence of weather and environment on bat activity

After initial correlation, we included four variables in candidate models: ambient temperature (Temp), wind speed (Wind), precipitation (Precip), and 24-hr change in barometric pressure (BPDiff). For both species groups, the highest-ranked model with the lowest QAIC_c value and highest AIC weight (w_i) contained an interaction between the variables Temp and Wind (Tables 2, 3). For *E. fuscus*, there was no support for any other candidate model (Table 2). The second best model for *Myotis* had $\Delta\text{QAIC}_c < 2$ and a relatively low evidence ratio (w_1/w_2 ; Table 3), which suggests it could also explain considerable variation in the model (Burnham and Anderson 2002).

The two variables present in the top-ranked models for both species are temperature and wind, which suggests these variables are key predictors of hourly bat-activity. Temperature was positively correlated with bat activity (Tables 4a, 4b) with an estimated increase of 1.75 *E. fuscus* calls and 1.72 *Myotis* calls detected for every 1°C increase. Wind was negatively correlated with bat activity (Tables 4a, 4b), with an estimated decrease of 0.78 *E. fuscus* calls

and 0.73 *Myotis* calls detected for every 1 m/s increase. However, the intercepts of each model (1.54 for *E. fuscus* and 0.17 for *Myotis*) and probability of detection in relation to ambient temperature (Fig. 2) suggest a lower temperature threshold for activity by *E. fuscus*. Most importantly, the inclusion of the interaction between temperature and wind produced a better model fit for both species, suggesting the effects of temperature and wind speed on bat activity are interdependent. Bats were more active when temperatures were high, but this was influenced by wind such that even in warmer conditions, bats were not active if it was windy.

Energetic estimates of flight

To maintain euthermic T_b in a crevice hibernaculum with a T_a of 1.1°C, we estimated energy expenditure of 0.92 W for a 21.7 g *E. fuscus* and 0.61 W for a 10.1 g *M. lucifugus*. Based on these body masses, we estimated the cost of flight for bats to be 2.77 W for *E. fuscus* and 1.49 W for *M. lucifugus*. Estimated rates of heat loss via convection and radiation during flight differed with species, body region, and T_a (Table 5). When we included convective and radiative heat loss, the temperature below which heat loss exceeded metabolic heat production during flight was 5°C in *M. lucifugus* and 1°C in *E. fuscus* (Fig. 3). Flight activity was more energetically costly per gram body-mass for *M. lucifugus* than *E. fuscus* at all T_a (Fig. 3), and the rate of increase in the energetic cost of flight as T_a drops (i.e., slope) was higher for *M. lucifugus*. When converted to fat usage, we estimate *E. fuscus* and *M. lucifugus* spend an extra 0.19–0.87 g and 0.13–0.51 g of fat, respectively, per hour of flight in T_a ranging from 0°C–10°C compared to that used per hour during euthermic rest within the hibernacula (0.08 g and 0.06 g, respectively). At 20% muscle efficiency (Speakman and Thomas 2003), we calculated 2.22 W and 1.19 W is available for activity-thermoregulatory heat substitution for *E. fuscus* and *M.*

lucifugus, respectively. By our estimates, in T_a ranging from -10°C – 0°C , flight thermogenesis could offset heat loss by 23–89% in *E. fuscus* and 20–70% in *M. lucifugus*.

Discussion

We recorded bat activity in Dinosaur Provincial Park throughout the entire winter each year of our study, which is consistent with other studies on winter bat-activity. Bat activity appears tied to foraging opportunity in areas with mild winter climates temperatures. For example, *L. noctivagans* and California myotis (*M. californicus* (Audubon and Bachman 1842)) foraged all winter in Washington State (mean sunset temperature = 9.1°C ; Falxa 2007). Likewise, eastern red bats (*Lasiurus borealis* (Müller 1776)), *L. noctivagans*, and *E. fuscus* captured during winter in Missouri at sunset temperatures of 4 – 12°C showed evidence of feeding (Dunbar et al. 2007). In stark contrast, winters at our site in the Canadian prairies are colder (mean temperature at sunset = -7.3°C). No insects occur at our site during winter (Lausen and Barclay 2006) and no feeding buzzes have been detected (this study). Few other studies have reported mid-winter flight without evidence of insects or feeding (Whitaker and Rissler 1992, 1993; Schwab and Mabee 2014). These data suggest winter foraging is opportunistic and not the impetus for flight. Bats may instead be to find water (Speakman and Racey 1989; Hays et al. 1992; Thomas and Geiser 1997), switch roosts for more favourable microclimates (Whitaker and Gummer 1992; Whitaker and Rissler 1992; Boyles et al. 2006), or excrete built-up waste and metabolites outside hibernacula (Baumber et al. 1971).

Regardless of the reasons for mid-winter flight, our data support the hypothesis that weather conditions, particularly temperature and wind, influence bat-activity. Warmer temperatures and calmer winds led to higher activity in both *E. fuscus* and *Myotis*. Our results are

consistent with other studies, but given the lack of insects at our site, such conditions likely reflect the energetic costs of flight rather than the possibility to forage. The rate of heat transfer is proportional to the temperature gradient between bat and environment (Bakken and Kunz 1988). Wind exacerbates convective heat loss by disturbing the insulative layer of air within fur (Bakken 1991) and also increases the power needed for flight. Although tailwinds can benefit airborne animals, power required for flight typically increase under conditions of headwinds or crosswinds (Tucker and Schmidt-Koenig 1971; Liechti et al. 1994). Avoidance of colder, windier conditions minimizes energetic costs of mid-winter flights and conserves fat stores, which likely improves body condition and chance of survival upon emergence in the spring (Humphries et al. 2003).

The interaction between temperature and wind may be particularly important in describing trends in bat activity recorded in our study area. Similarly to other studies (e.g., O'Farrell et al. 1967; Schwab and Mabee 2014), we recorded most calls during the warmer, early-evening period 4–5 hours after sunset. However, some activity persisted through all hours of the night with a slight increase in *Myotis* activity just prior to sunrise. Mild winter temperatures in southern Alberta are sometimes the consequence of “chinooks”—warm, westerly winds that can quickly and drastically increase ambient temperatures. Chinook winds often arrive during the night but die down by morning, leaving warm temperatures to persist through morning. Based on our data, it appears as though bats remain in the hibernacula despite warm temperatures due to high winds during chinooks and emerge later in the night, after winds have subsided.

Our data also suggest interspecific differences in the variables that influence activity. *Eptesicus fuscus* activity is predominantly influenced by temperature and wind, while *Myotis* activity is also influenced by changes in barometric pressure. *Eptesicus fuscus* roost close to

hibernacula entrances (Rysgaard 1942), which may allow them to detect changes in ambient temperature. Conversely, *Myotis* roost deep in caves or crevices where temperature is relatively stable; detecting changes in barometric pressure to track approaching storm fronts (Paige 1995; Turbill 2008) reduces the risk of emerging during inclement weather. In addition, larger-bodied *E. fuscus* were more active at all temperatures and had a lower thermal threshold for activity than small-bodied *Myotis*. We recorded *E. fuscus* at temperatures as low as -10.4°C and *Myotis* as low as -5.1°C and there was a distinct difference between groups in the probability of activity relative to temperature. *Eptesicus fuscus* likely tolerate lower temperatures than smaller-bodied *Myotis* given that *Myotis* have higher surface area to volume ratios and lose more heat per unit of metabolically active mass (Kleiber 1947), and that *Myotis* fur has a lower insulation value than *E. fuscus* (Shump and Shump 1980).

We suggested that differences in net energetic costs of flight underlie disparities observed between species in winter activity. Based on the metrics of body size, fur insulation, and metabolic rates during flight and rest that we included in our calculations, our energetic estimates suggest that smaller-bodied *M. lucifugus* spend more net energy per gram body mass in flight than larger-bodied *E. fuscus*. We estimated the temperature below which convective heat loss exceeds metabolic heat production via activity to be 5°C for *M. lucifugus* and 1°C for *E. fuscus*, which corroborates that larger-bodied *E. fuscus* energetically tolerate flight in colder temperatures than *Myotis*. Although mid-winter flight is energetically expensive, we estimated that activity-thermoregulatory heat substitution could mitigate costs by at least 20% and as much as 89% in milder temperatures. This phenomenon is especially important in areas devoid of prey where non-energetic benefits of flight may be attainable only with such reductions in net energetic cost. Interestingly, the mean mass of *E. fuscus* entering hibernation in October at our

study site (23.6 g; Klüg-Baerwald, unpublished data) appears higher than that reported in Ontario (21.6 g; Fenton 1972) where winter foraging is possible (Brigham 1987), but masses observed in March-April post-hibernation are similar (16.8 g and 16.4 g, respectively); extra fat reserves may go toward fuelling mid-winter flight.

Our study presents data on the winter activity and energetics of mid-winter flight of bats in an environment where foraging is unlikely. We show that temperature and wind are important predictors of *E. fuscus* and *Myotis* winter activity, and that *Myotis* may also use changes in barometric pressure to cue activity. We suggest these environmental factors relate to minimizing the energetic cost of flight. That bats take part in the behaviour of mid-winter flight without the opportunity to forage suggests other causal reasons and emphasizes the importance of winter energy budgets in hibernating animals. Our energetic estimates suggest that exercise thermogenesis partly mitigates energetic cost of flights in the cold, and that differences in winter activity between species likely stem from differences in rates of heat loss and potential for activity-thermoregulatory heat substitution. Winter activity of bats has been poorly studied to date, but as interest in studying the winter behaviours of bats increases, it is becoming apparent that activity following arousal is not an abnormal behaviour (Boyles et al. 2006). Given that bats can spend over half their lives in hibernation and that mid-winter flight ostensibly consumes a substantial amount of energy during this time of energetic constraint, it is important that we increase our understanding of this phenomenon.

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Table 1. Summary of nightly low ambient temperatures and acoustic bat-activity recorded in three locations (see Method for details) at Dinosaur Provincial Park over three hibernation seasons: 23 October 2012 through 24 March 2013, 10 November 2013 through 1 April 2014, and 9 November 2014 through 4 March 2015. Means are presented with standard deviation.

Winter Season	Mean Night				
	Mean Nightly Low T_a (°C)	Wind Speed (m/s)	Detector Nights	Number of Passes	Mean Passes/Night
2012-13	-11.3 ± 6.94	2.5 ± 1.42	146	574	3.9 ± 7.76
2013-14	-16.9 ± 19.66	2.5 ± 1.46	143	470	3.3 ± 8.56
2014-15	-13.2 ± 8.52	3.5 ± 1.72	116	266	2.3 ± 4.97

Table 2. The top 5 models used to test the influence of weather and environmental variables on hourly activity (calls/hour) of *Eptesicus fuscus* activity during winter in Dinosaur Provincial Park. Models are ranked according to QAIC_c scores, with the lowest score indicating the top ranked model. ΔQAIC_c is the difference in QAIC_c scores between model *i* and the top ranked model. The probability of each being the best model, given the entire subset of models, is indicated by AIC weight (*w_i*).

Model	QAIC _c	ΔQAIC _c	<i>w_i</i>	<i>w₁/w_i</i>
Temp + Wind + Temp*Wind	3760.239		1.0000	
Temp + BPDiff + Temp*BPDiff	3815.315	55.076	0.0000	>1000
Temp + Wind + Precip	3816.247	56.008	0.0000	>1000
Global model (all variables)	3817.704	57.465	0.0000	>1000
Temp + Wind + BPDiff	3819.297	59.058	0.0000	>1000

Note: A complete description of each variable is given in materials and methods.

Table 3. The top 5 models used to test the influence of weather and environmental variables on hourly activity (calls/hour) of *Myotis* bats during winter in Dinosaur Provincial Park. Models are ranked according to QAIC_c scores, with the lowest score indicating the top ranked model. Δ QAIC_c is the difference in QAIC_c scores between model *i* and the top ranked model. The probability of each being the best model, given the entire subset of models, is indicated by AIC weight (w_i).

Model	QAIC _c	Δ QAIC _c	w_i	w_1/w_i
Temp + Wind + Temp*Wind	731.998		0.4876	
Temp + BPDiff	732.894	0.896	0.3116	1.57
Temp + Wind + BPDiff	735.119	3.121	0.1024	4.76
Temp + Precip + BPDiff	736.643	4.645	0.0478	10.20
Temp	739.052	7.054	0.0143	34.01

Note: A complete description of each variable is given in materials and methods.

Table 4. Top-ranked model based on negative binomial regression used to explain the influence of environmental conditions on hourly activity (passes/hour) of **a) *Eptesicus fuscus*** and **b) *Myotis*** bats in Dinosaur Provincial Park.

a) *E. fuscus*

Model term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Intercept	0.4335	0.0143	3.03	0.003
Temp	0.5607	0.0288	19.46	<0.001
Wind	-0.2438	0.0323	-7.55	<0.001
Temp*Wind	-0.0567	0.0053	-10.69	<0.001

b) *Myotis* bats

Model term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Intercept	-1.7578	0.3580	-4.91	<0.001
Temp	0.5393	0.0735	7.34	<0.001
Wind	-0.3173	0.0863	-3.68	<0.001
Temp*Wind	-0.0611	0.0137	-4.46	<0.001

Table 5. Surfaces areas and estimated rates of heat transfer via convection (H_c) and radiation (H_r) from big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*). Rates of thermal radiation depend on ambient temperature (T_a) and are presented as ranges calculated for T_a 15°C--10°C.

		Heat transfer (W m ⁻² °C ⁻¹)	
Species and region	Surface area (m ²)	H _c	H _r
<i>Eptesicus fuscus</i>			
Body	0.00491	8.91	66.8-118.0
Wings	0.01517*	44.27 [†]	50.0-70.8
<i>Myotis lucifugus</i>			
Body	0.00314	8.96	66.8-118.0
Wings	0.00860*	44.27 [†]	51.1-70.8

*Farney and Fleharty 1969

[†]Reichard et al. 2010

Figure Captions

Fig. 1. Hourly distribution relative to sunset of a) 1 196 *Eptesicus fuscus* calls and b) 114 *Myotis* calls recorded by three acoustic detectors over 405 winter nights in Dinosaur Provincial Park, Alberta from 23 October 2012 to 4 March 2015.

Fig. 2. Cumulative probability plot showing the probability of detecting winter activity by *Eptesicus fuscus* (dashed line) and *Myotis* (solid line) in relation to ambient temperature in Dinosaur Provincial Park.

Fig. 3. Estimated cost of flight (black lines) in relation to external ambient temperature for *Eptesicus fuscus* (solid lines) and *Myotis lucifugus* (dashed lines). Estimates for energy use during rest (grey lines) in a crevice hibernaculum with an internal temperature of 1.1°C are given for reference.

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1481x1481mm (72 x 72 DPI)

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1881x1881mm (72 x 72 DPI)