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ARTICLE

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Seasonal phenology of the little brown bat (*Myotis lucifugus*) at 60° N

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Abstract

To investigate the impact of short summers and long summer solar periods at high latitudes on the behavior of a nocturnal, hibernating mammal, we recorded the phenology of *Myotis lucifugus* (little brown myotis) at 60° N in the Northwest Territories (NWT), Canada. In particular, we assessed the timing of spring emergence from, and autumn entry into, hibernation, reproduction, and seasonal mass fluctuations. We used a combination of acoustic monitoring and capture surveys at two hibernacula and two maternity roosts during 2011 and 2012. *Myotis* spp. were active at the hibernacula from late April to late September/early October, suggesting that the "active" season length is similar to that of populations farther south. At maternity colonies, we detected *M. lucifugus* activity from early May to early October, with peaks during mid-July in both years. Lactation, fledging, and weaning all occurred later in the NWT than at more southern locations, and reproductive rates were significantly lower than rates observed farther south. The average mass of individuals fluctuated throughout the season, with an initial decline immediately following emergence from hibernation likely reflecting increased energy expenditure due to flight and decreased use of torpor, coupled with relatively low prey intake due to low prey abundance associated with cool temperatures. Females did not appear to have lower pre-hibernation masses than those in more southern populations, suggesting that despite the cool spring and autumn temperatures, and short summer nights, bats are able to obtain enough energy for reproduction and mass accumulation for hibernation. However, the lower reproductive rates may indicate that there are limitations to life at the northern limits of the species' range.

KEYWORDS
Chiroptera, hibernation, high latitudes, *Myotis lucifugus*, northern ecology, Northwest Territories, phenology

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INTRODUCTION

In temperate regions, the phenology and reproductive schedule of many organisms is influenced by seasonality, and the year is generally divided into a growing season and a nongrowing season. To balance their energy budget, some mammals hibernate during the nongrowing season, allowing for survival during prolonged periods of low resource abundance (Yahner, 2012). Although hibernation allows individuals to balance their energy budget, it also limits the available "growing" time each year. Hibernating species use the "growing" or "active" season to gather resources for investment into three main activities: (1) current maintenance and growth, (2) future maintenance (fat and/or food storage for the next hibernation period), and (3) reproduction. With a limited "growing" season, individuals must allocate resources to each category optimally to maximize fitness, resolving trade-offs between survival and reproductive success (Stearns, 1992). Annual triggers for when animals invest in each of these activities are often present in the environment. During the growing season, reproductive events can be triggered by changes in available resources (Daan et al., 1988; Hau et al., 2000; Rubenstein & Wikelski, 2003), resulting in the timing of parturition and/or weaning corresponding with high food abundance or quality (Arlettaz et al., 2003; Cumming & Bernard, 1997; Goldizen et al., 1988). The onset of hibernation can be triggered by various cues including photoperiod, ambient temperature, barometric pressure, or changes in food or water abundance (Al-Musfir & Yamaguchi, 2008; Czenze & Willis, 2015; Ware et al., 2012). As latitude and elevation increase, so does the length of the hibernation period, further reducing the duration of the active season (Zervanos et al., 2010).

For nocturnal mammals, such as bats, an increase in latitude is associated with a shorter "active" season as well as shorter nights during summer, which could further reduce the available foraging time on both a nightly and an annual scale. Despite these potential challenges, several species of bats persist in northern environments and have been documented breeding at 68° N–70° N in Europe (*Eptesicus nilssonii*, Rydell et al., 1994) and at 60° N–64° N in North America (*Myotis lucifugus*, Shively & Barboza, 2017; Slough & Jung, 2008; Talerico, 2008). We used seasonal phenology to investigate how bats persist at northern latitudes despite suspected constraints on the active/growing season and foraging period, focusing on *M. lucifugus*, which hibernates in northern Canada at 60° N (Reimer et al., 2014).

M. lucifugus is an insectivorous species that is found across most of North America, from approximately 33° N–69° N latitude (IUCN, 2021). It hibernates in caves and abandoned mines between late September and mid-May in central Alberta (53° N, Schowalter, 1980), with the duration of the active season being longer farther south (Davis & Hitchcock, 1965). Prior to entering hibernation, both male and female *M. lucifugus* congregate at hibernacula for mating (Fenton, 1969). Copulation occurs primarily during a phase known as "swarming" when bats swarm outside and inside the hibernaculum, and ovulation is then delayed until spring when females exit hibernation (Thomas et al., 1979; Wimsatt, 1944). Upon spring emergence, individuals perform small-scale migrations (10–650 km) to relocate to summer roosts (Fenton, 1970; Gifford & Griffin, 1960; Norquay et al., 2013). *M. lucifugus* has been surveyed as far north as 65° N in Alaska during summer (Shively & Barboza, 2017), but the lack of known hibernacula in Alaska and Yukon has led to speculation that little brown bats migrate south to British Columbia or Alberta to overwinter (Parker et al., 1997; Slough & Jung, 2008). The duration of the active season at northern latitudes has traditionally been estimated from the arrival of females at maternity colonies (Slough & Jung, 2008; Talerico, 2008); however, with the known location of two hibernacula near the Northwest Territories–Alberta border (Reimer et al., 2014; SARC, 2017), our study is the first to measure season duration by emergence from, and entrance into, hibernation at known hibernacula near 60° N.

During the active season, the timing of parturition in *M. lucifugus* is affected by weather, with delays corresponding with cooler spring temperatures (Frick et al., 2010; Lewis, 1993) and increasing latitude (Racey, 1982; Schowalter et al., 1979). Given the relatively long life span of little brown bats (up to 34 years; Davis & Hitchcock, 1995), and the higher survival rate of adults than juveniles (Frick et al., 2010), forgoing reproduction when resources are limited due to cool weather, or when inadequate fat stores are present at emergence from hibernation, will typically promote individual performance (Kunz et al., 1998; Wilkinson & South, 2002). Indeed, populations of bats at higher latitudes have lower reproductive rates than those at lower latitudes (Barclay et al., 2004).

To address the question of how the activity and reproductive timing of *M. lucifugus* are adapted to the seasonality and short foraging periods at high latitudes, we assessed (1) the duration of the active season, (2) the timing of reproductive events, (3) reproductive rates of females, and (4) fluctuation of body mass during the season. We hypothesized that the reproduction of bats at northern latitudes is time-constrained due to cool spring and autumn temperatures. We predicted that, compared with more southern populations, bats in the Northwest Territories (NWT) will have: (1) a shorter active season; (2) later reproduction due to later emergence from hibernation and cool spring temperatures; (3) lower female reproductive rates resulting from late emergence and reproduction the previous year; and (4) lower mass of

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reproductive females prior to hibernation due to late parturition, cool autumn temperatures, and thus a brief preparation period. We assessed these predictions with data collected via echolocation recordings and capture surveys at two hibernacula and two maternity colonies that had not previously been studied or monitored.

MATERIALS AND METHODS

Study area

We conducted fieldwork at two hibernacula and two maternity colonies at approximately 60° N latitude in Wood Buffalo National Park, Alberta, and the South Slave and Dehcho regions of the NWT, Canada (Figure 1). The closest municipality to our main study area is Fort Smith, NT (60°01′13″ N, 111°57′43″ W; elevation: 205 m). The surrounding habitat is classified as the taiga plains and mid-boreal ecoregion and is covered by forest (*Populus tremuloides* and *Pinus banksiana*, 96%) and water (lakes and rivers 4%). The average daily temperature during the active bat season (i.e., from emergence from hibernation until entry into hibernation) ranges from −0.4 to 16.5°C and the number of frost-free nights during 2011 and 2012 was 165 and 168 nights (data obtained from Environment Canada; https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). The minimum night length at summer solstice (20 June) is 308 min from sunset to sunrise and only 96 min between evening civil twilight and morning civil twilight (data obtained from http://www.nrc-cnrc.gc.ca/eng/services/sunrise/index.html).

The two hibernacula we studied were caves created by fluvial processes through limestone karst and are accessible through sinkholes. Walk-in Cave is the largest

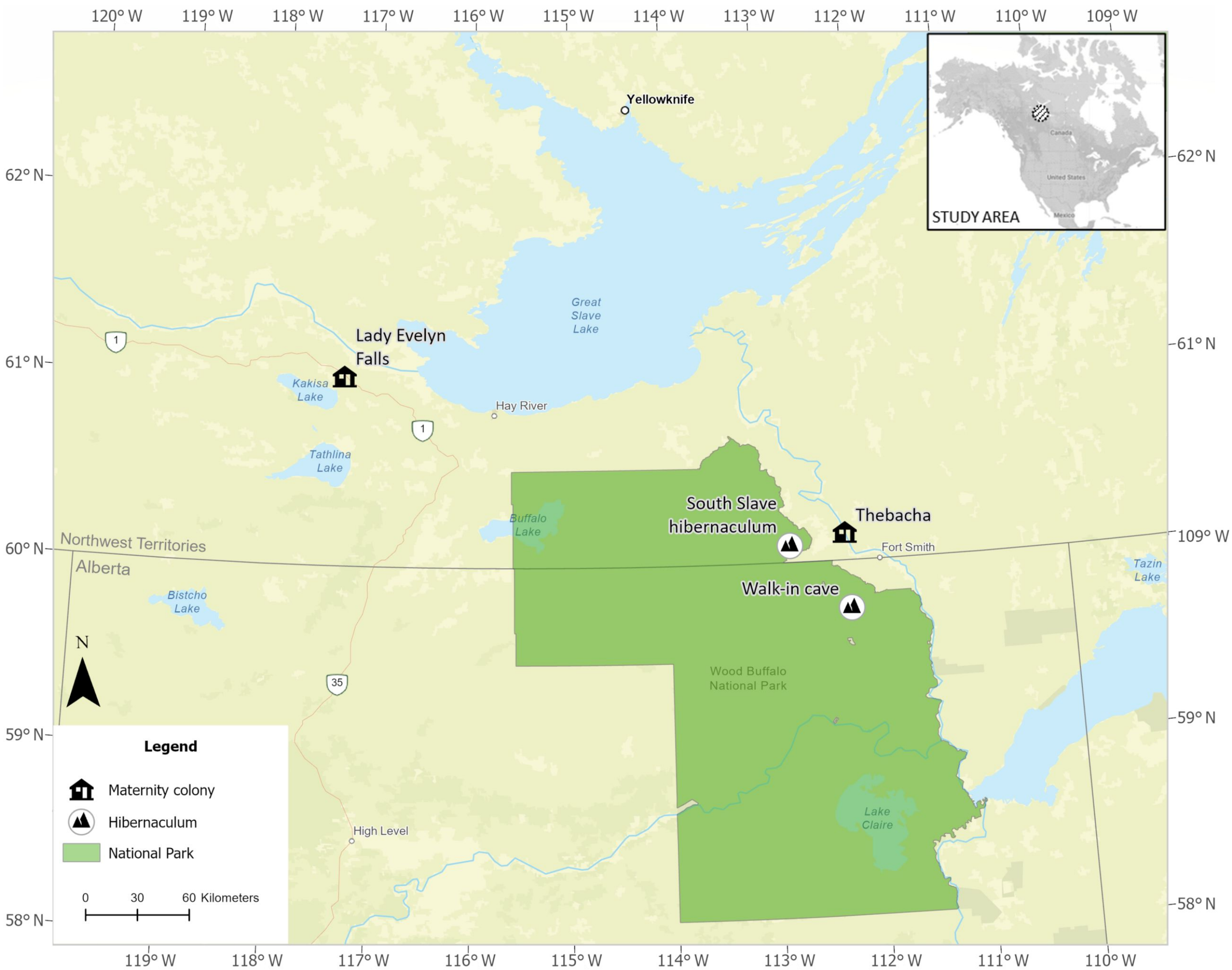

FIGURE 1 Study area for *Myotis lucifugus* seasonal phenology study in the South Slave region, Northwest Territories, Canada, 2011–2012.

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cave yet discovered in Wood Buffalo National Park with an entrance approximately 12 m wide and 4 m high, and a depth of approximately 400 m (Lewis, 1974–1975). Four chambers house *M. lucifugus*, *Myotis septentrionalis*, and *Eptesicus fuscus* during winter. Winter population sizes of *M. lucifugus* fluctuate from year to year and have been reported to be at least 35–75 bats (Reimer et al., 2014). The South Slave hibernaculum (SSR-1) is the largest cave yet discovered in the NWT. It has an entrance approximately 4 m wide and 1 m tall and is approximately 500 m long. Winter populations total approximately 3000 bats, including *M. lucifugus* and presumably *M. septentrionalis* and *E. fuscus* (Allicia Kelly, Government of the Northwest Territories, Fort Smith, NT, personal communication, December 2020).

The two *M. lucifugus* maternity colonies we studied were in seasonally occupied buildings. The Thebacha maternity colony included approximately 400 adult females before parturition, roosting in a network of cabins. The Lady Evelyn Falls maternity colony included approximately 100 females before parturition, roosting in two buildings. Neither of these colonies had been monitored prior to this study.

Acoustic recordings

To assess seasonal bat activity, we recorded echolocation calls using AnaBat II ultrasonic detectors with CF-ZCAIMs set to a division ratio of 16 (Titley Electronics, Ballina, Australia) at five sites including both hibernacula, one beaver pond within 3 km of each hibernaculum, and at the Thebacha maternity colony (Table 1).

At Walk-in Cave, we placed the detector in a weatherproof box, 3 m from the entrance with the microphone pointed away from the entrance to prevent recording bats flying within the cave. Two detectors were installed in weatherproof boxes at the South Slave hibernaculum by the Government of the Northwest Territories, approximately 10 m from the cave entrance with the microphones positioned toward the cave entrance, but the restricted cave opening prevented recording of bat activity inside the cave. At the Thebacha maternity colony, we mounted the detector directly along a bat flight path outside the main building used by the colony, 3 m off the ground and 5 m from the bat exit.

Acoustic analysis

We reviewed all AnaBat files using AnaLookW version 3.2.15. We used a filter to extract *Myotis* spp. calls, identified by a minimum frequency ≥30 kHz, and counted files recorded per night. Bats with lower frequency echolocation calls (primarily *E. fuscus*) were omitted from the data. Call characteristics of *M. lucifugus* and *M. septentrionalis* overlap (Fenton & Bell, 1981), often making them indistinguishable with AnaBat II detectors; therefore, we did not attempt to remove *M. septentrionalis* calls from the data. The composition of *Myotis* captures (via mist-netting) at these sites averaged 86% *M. lucifugus* and 14% *M. septentrionalis* (https://doi.org/10.25338/B8KH19); therefore, we assume that the *Myotis* echolocation passes in our data were largely *M. lucifugus*.

Capture surveys

We used mist nets (Avinet Inc., Dryden, New York), to capture bats adjacent to the two maternity colonies (Thebacha and Lady Evelyn Falls), and various foraging sites around the South Slave region, during 2011 (35 nights; May–September) and 2012 (23 nights; June–September). At maternity colonies, we captured bats during emergence, before they had an opportunity to feed, and at all sites, we held bats in a cloth bag for ≥0.5 h to allow defecation prior to weighing. We identified individuals to species, sex, age (adult or juvenile), and reproductive condition, weighed them with a portable balance, measured forearm with calipers, fitted them

TABLE 1 Acoustic survey effort at monitoring sites throughout the South Slave region, NT, during 2011 and 2012.

		2011		2012	
Site type	Site name	Start	End	Start	End
Hibernaculum	Walk-in Cave	21 Apr	22 Sep	20 Apr	26 Oct
Hibernaculum	South Slave hibernaculum	…	…	30 Mar	26 Oct
Beaver pond	WBBP	16 May	9 Oct	…	…
Beaver pond	NTBP	21 May	5 Oct[a]	…	…
Maternity colony	Thebacha	3 May	11 Oct	25 May	31 Oct

Note: Ellipses indicate "no data collected."

[a]Detector deployed intermittently for a total of 66 nights.

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with a unique band (2.9 mm; Porzana Ltd., East Sussex, United Kingdom) for future identification, and released them at their point of capture. We classified adult females into three categories: (1) pregnant: swollen abdomen, detection of fetus via palpation of abdomen, nonenlarged nipples; (2) lactating: enlarged, calloused nipples, milk expressed with gentle massage of mammary glands; (3) post lactating: enlarged keratinized nipples with no milk expression (Racey, 2009). Females captured prior to 1 June were not included when calculating reproductive rates as nonreproductive and early pregnancy females were indistinguishable by external examination. All volant juveniles were identified by evenly tapered phalangeal–metacarpal joints and unfused epiphyseal plates observed by back-illuminating the wing (Brunet-Rossinni & Wilkinson, 2009). During November 2011, after hibernation was well underway, we entered both hibernacula and recorded sex, mass, and forearm length for 45 bats captured from the cave walls (Walk-in Cave: $n = 5$; South Slave hibernaculum: $n = 40$). All captures followed American Society of Mammalogists guidelines (Sikes et al., 2016) and were compliant with the University of Calgary Animal Care and Use Committee protocols (Animal Care Certificate BI09R-01).

Solar and weather data collection

We obtained photoperiod data (including sunset, sunrise, and civil twilight) for Fort Smith, NT, using the sunrise/sunset calculator developed by the National Research Council of Canada (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/index.html), and hourly weather data (temperature, wind speed, relative humidity, and sky cover) for the Fort Smith Airport weather station from the Environment Canada National Climate Data and Information Archive (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). "Maximum nightly temperature" was calculated as the highest temperature value recorded between sunset and sunrise for each night and site. "Average nightly temperature" was calculated as the mean temperature value recorded between sunset and sunrise for each night and site. The Fort Smith Airport is 17 km from the Thebacha maternity colony and approximately 30 km from each hibernaculum.

RESULTS

Weather

The temperature recorded at the Fort Smith, NT, airport weather station during the active bat season ranged from −15 to 26°C and the mean monthly temperature was not significantly different from Climate Normals reported by Environment Canada for 1981–2010 (linear regression, $F_{1,34} = 0.06$, $p = 0.81$). During the 2011 season, the maximum nightly temperature was consistently above 0°C between 25 April and 24 October. The dates of last spring frost and first autumn frost were 5 June and 12 September. During the 2012 season, maximum nightly temperature was consistently above 0°C between 25 April and 10 October. The dates of the last spring frost and the first autumn frost were 14 May and 15 September.

Active season

We recorded the echolocation calls of *Myotis* spp. at the two hibernacula from late April to late September in 2011 (Walk-in Cave; Figure 2) and late April to early October in 2012 (Walk-in Cave and SSR-1; Figure 3). During 2011, *Myotis* passes were recorded at Walk-in Cave on both the first (21 April) and last (22 September) nights of deployment, suggesting that bats may have emerged earlier and/or later than our survey period. The reduced activity recorded at the nearby beaver pond (WBBP) suggests that bats were not very active away from the hibernaculum through September (Figure 2). High activity levels were recorded during August and September, suggesting swarming had commenced.

During 2012, *Myotis* activity was similar at both hibernacula, with activity beginning in mid-April and with higher activity levels recorded from mid-July through early September indicating swarming activity (Figure 3). Activity levels were greatly reduced by mid-September through early October, suggesting that bats had entered hibernation. Similarly, activity at a beaver pond (NTBP) 3 km from the South Slave hibernaculum was low from 30 August to 1 September (range: 0–3; mean: 1 ± 2.3 passes/night), with no activity recorded during the final deployment period from 8 September through 5 October.

Maternity colony activity and timing of reproductive events

At the Thebacha maternity colony, we detected *Myotis* activity from early May to late September (2011) and early October (2012), with peaks during mid-July in both years (Figure 4). Activity decreased through the end of July and was relatively low through August and September for both years. Activity during August and September may have involved bats flying in the general vicinity, rather than using the maternity roost. The last

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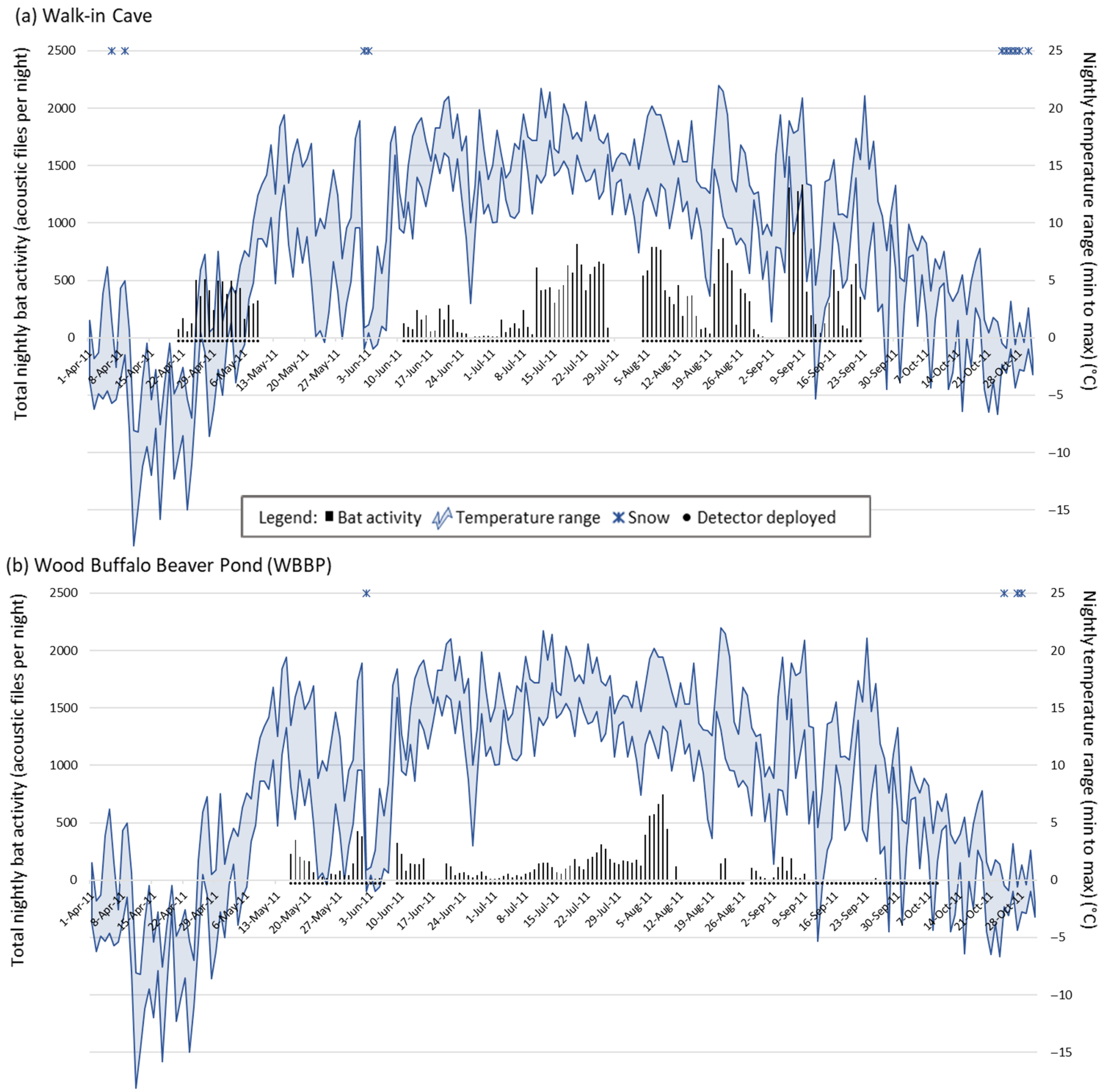

FIGURE 2 Total number of *Myotis* files recorded with Anabat detectors during 2011 at (a) Walk-in Cave hibernaculum in northern Alberta and (b) a beaver pond 3 km from the hibernaculum (WBBP). The temperature values depict the range between minimum and maximum degrees Celsius recorded at the Fort Smith Airport (Environment Canada) between sunset and sunrise for each given date. In this and subsequent figures, the black dots below the acoustic bars represent the period when the Anabat detector was functioning correctly.

Myotis calls were detected on 27 September 2011 and 15 October 2012.

We captured female *M. lucifugus* at the Thebacha and Lady Evelyn Falls maternity colonies, and nearby locations (within 5 km of maternity colonies) between 13 May and 6 September 2011 ($n = 35$ nights, 90 individuals), and 6 June to 16 August 2012 ($n = 23$ nights, 172 individuals). Lactating females were first captured on 6 July 2011 and 27 June 2012 (Figure 5). Most of the lactating females were captured from 6 July to 6 August 2011 and 3 July to 7 August 2012. Volant young-of-the-year were first captured on 19 July 2011 and 8 July 2012, and post-lactating females were first captured on 6 August 2011 and 18 July 2012. Most post-lactating females were captured after 10 August 2011 and 6 August 2012. Average nightly temperature during gestation (1 May until the first lactating female

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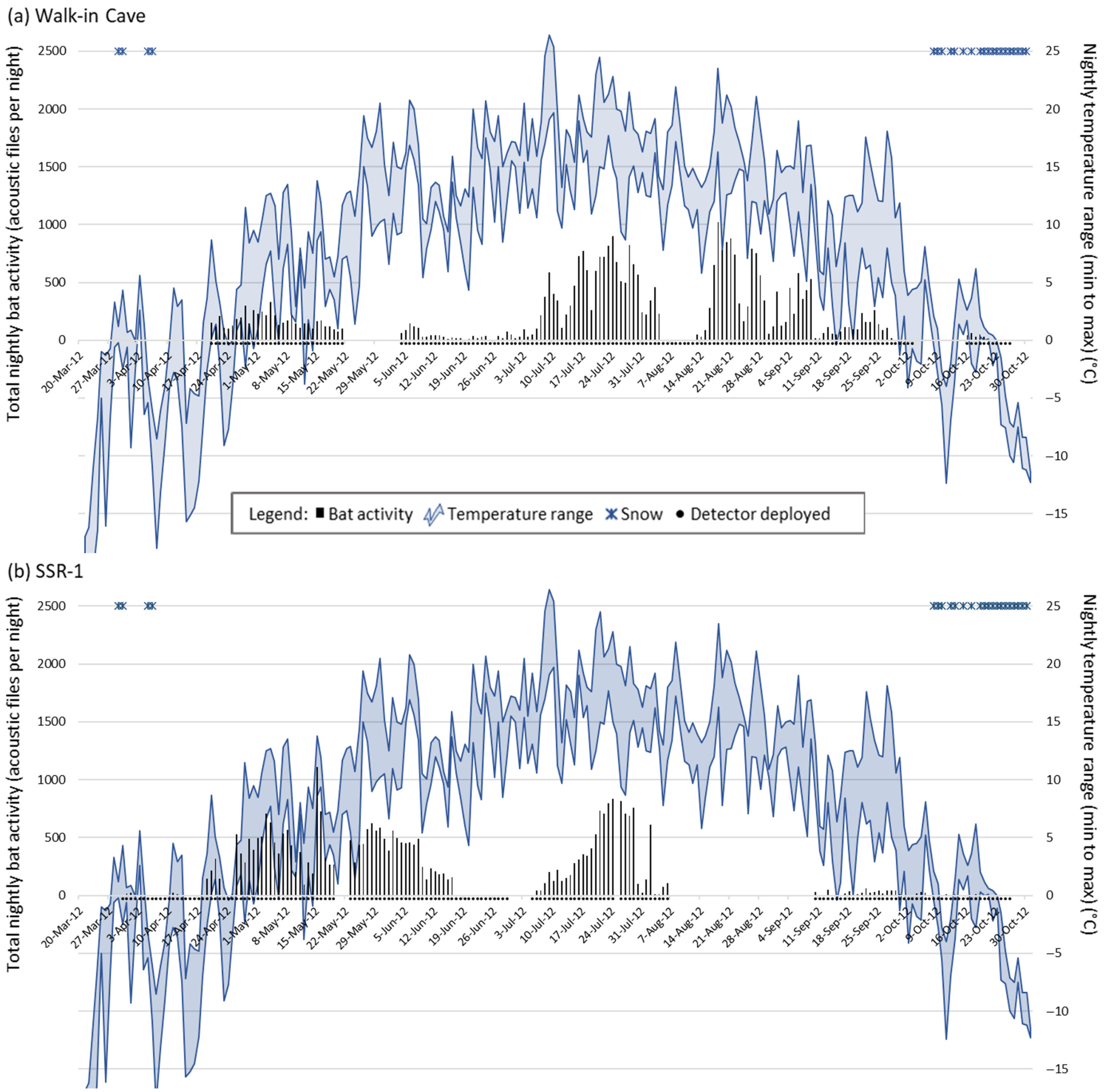

FIGURE 3 *Myotis* files recorded with Anabat detectors during 2012 at (a) Walk-in Cave hibernaculum in northern Alberta and (b) South Slave hibernaculum (SSR-1), Northwest Territories. The temperature values depict the range between minimum and maximum degrees Celsius recorded at the Fort Smith Airport (Environment Canada) between sunset and sunrise for each given date.

was observed) was $9.9 \pm 5.4°C$ ($\bar{x} \pm SD$) in 2011 and $10.1 \pm 4.5°C$ in 2012 (range: −2.2 to 19.4°C).

Reproductive rates at maternity colonies

At Thebacha, 78.9% (2011, $n = 90$) and 75.0% (2012, $n = 172$) of adult females captured in mist nets were reproductive. At the Lady Evelyn Falls maternity colony, 78.6% (2011, $n = 70$) and 49.1% (2012, $n = 116$) of females captured in mist nets were reproductive. Most banded females captured in 2011 and 2012 (with identifiable reproductive status) were reproductive in both years (Table 2).

Seasonal fluctuations in body size

Body size varied between sexes and throughout the season. Mean forearm length was significantly greater for adult females (39.2 ± 1.2 mm, $n = 517$; $\bar{x} \pm SD$) than adult males

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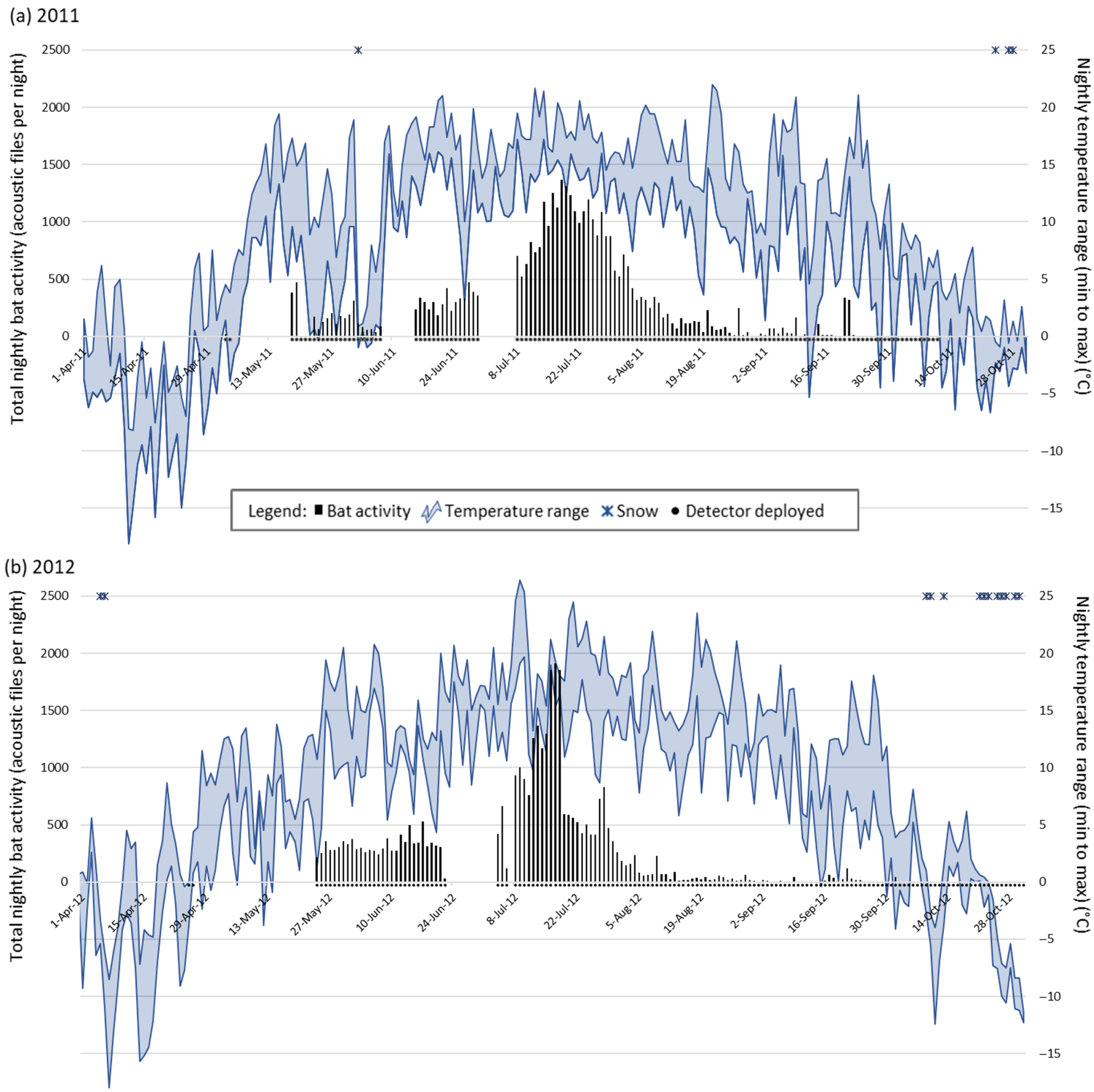

FIGURE 4 Nightly echolocation activity of *Myotis* at the Thebacha maternity colony, Northwest Territories, recorded with an Anabat detector from (a) 3 May to 10 October 2011 and (b) 24 May to 31 October 2012. The temperature values depict the range between minimum and maximum degrees Celsius recorded at the Fort Smith Airport (Environment Canada) between sunset and sunrise for each given date.

(38.3 ± 1.3 mm, $n = 284$; $t_{534} = 9.60$, $p < 0.001$). Mean mass was significantly greater for nonpregnant females (9.1 ± 1.1 g, $n = 347$) than for males (8.9 ± 1.5 g, $n = 282$; $t_{500} = 2.34$, $p = 0.02$). There was a decline in mass for both female and male *M. lucifugus* during May as bats emerged from hibernation (Figure 6). Female mass increased as pregnancy progressed from early June to early July and decreased again at parturition from early July to early August. Post-parturition mass was significantly greater for reproductive females than for nonreproductive females ($t_{333} = -5.96$, $p < 0.01$). The mass of both females and males increased to a maximum in early September, with no significant difference between sexes (female: 11.0 ± 0.8 g, $n = 6$; male: 10.3 ± 0.8 g, $n = 24$; $t_8 = 1.8$, $p = 0.113$). The mass of both males and females was lower in November following a month in hibernation, with no significant difference between sexes (female: 9.0 ± 0.7 g, $n = 6$; male: 9.3 ± 0.8 g, $n = 39$; $t_7 = -0.63$, $p = 0.550$).

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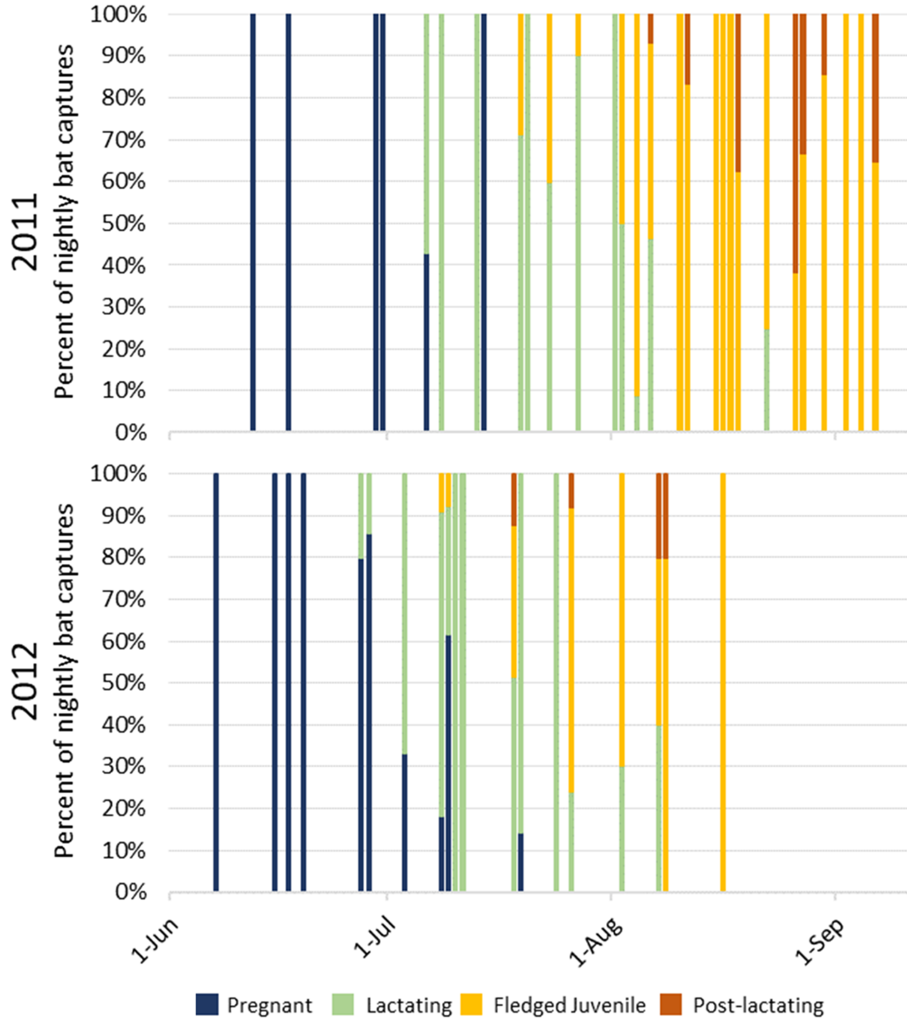

FIGURE 5 Reproductive state of female *Myotis lucifugus* captured in mist nets at the Thebacha and Lady Evelyn Falls maternity colonies, Northwest Territories, and surrounding area during 2011 and 2012.

TABLE 2 Interannual reproduction rates for adult female (older than one year) and yearling (banded as pups and recaptured the following year) *M. lucifugus* banded during 2011 and recaptured during 2012 at Thebacha and Lady Evelyn Falls maternity colonies, Northwest Territories.

	Adults >1 year old			Yearlings		
Maternity colony	Non-repro both years	Reproductive one year	Reproductive both years	Non-repro	Reproductive	*n*
Thebacha	0	4	12	0	1	17
Lady Evelyn	2	4	9	3	0	18
Total	2 (6.5%)	8 (25.8%)	21 (67.8%)	3 (75%)	1 (25%)	35

DISCUSSION

Active season length

In the South Slave study area, *Myotis* spp. were active from late April to late September with an active season duration of approximately five months. Following spring emergence, and prior to fall entrance to hibernation, nightly temperatures regularly fell below freezing. Contrary to our predictions, despite the relatively cool ambient temperature, the "active" season for *M. lucifugus* was similar in duration to that observed for numerous populations a further south (Table 3). However, many of the published studies we reviewed

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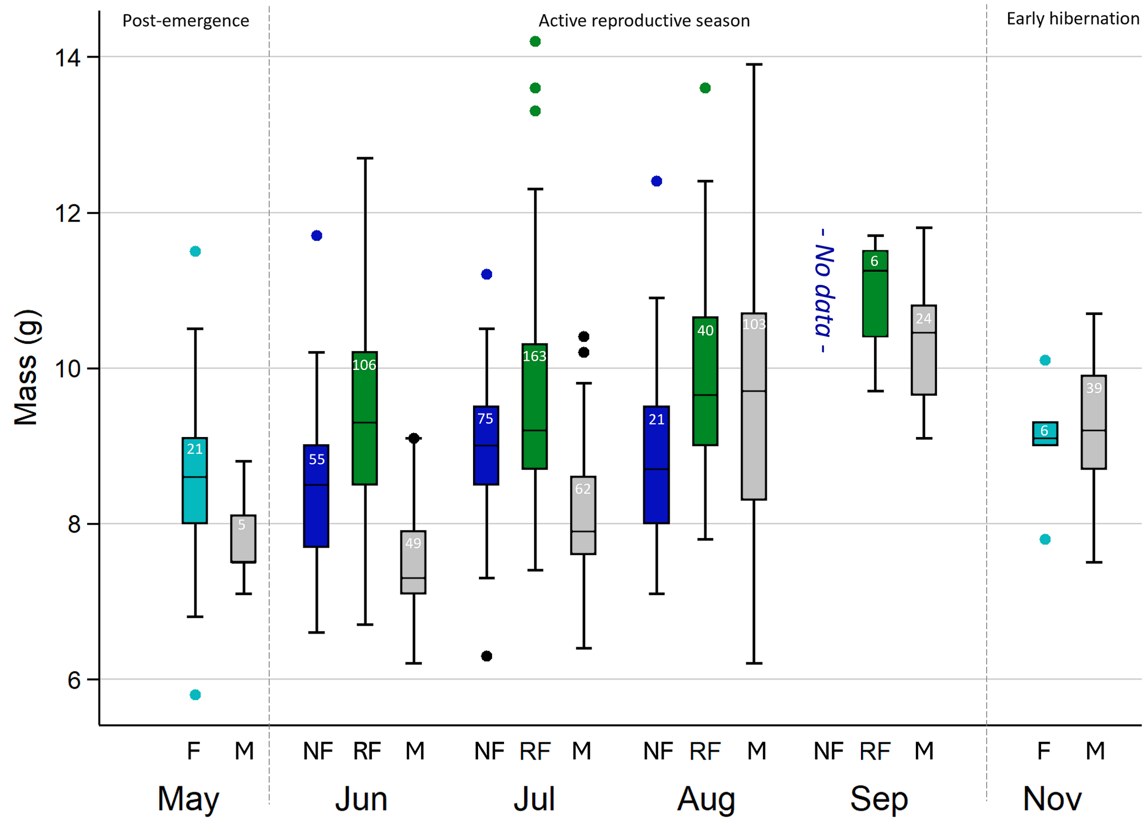

FIGURE 6 Seasonal fluctuations in adult female (F) and male (M) *Myotis lucifugus* mass as determined from captures in the South Slave region, Northwest Territories, during 2011 and 2012. Data were grouped by sex (F, teal; M, gray) during early spring (May) and post-hibernation (November) as reproductive status could not be determined. Females were grouped into reproductive females (RF; green) and nonreproductive females (NF; blue) during the active reproductive period. The box limits represent the range of the central 50% of the data, the whiskers represent the remaining data, the midline marks the median value, and the dots beyond the whiskers represent data outliers. Boxes are labeled with sample sizes. There were no captures in October.

TABLE 3 Dates for emergence and immergence of *Myotis lucifugus* at winter hibernacula throughout their range, organized on the order of earliest emergence.

Location	Latitude	Emergence	Immergence	Site type	Citation
Indiana, USA	40°	Mar	Nov	Mine	Whitaker and Rissler (1992)
Indiana, USA	38°–41°	Late Mar–mid-Apr	Nov	Cave	Humphrey (1971)
Vermont, USA	43°	Early Apr–mid-May	Sept–Oct	Cave	Davis and Hitchcock (1965)
Wisconsin, USA	43°	10 Apr–20 Apr	14 Oct–11 Nov	Cave	Meyer et al. (2016)
Wisconsin, USA	43°	Mid-Apr	Late Nov	Mine	Rupprecht (1980)
Alberta, Wood Buffalo NP, Canada	**60°**	**<21 Apr**	**Late Sep to mid-Oct**	**Cave**	Reimer et al. (2014); **This study**
Northwest Territories, Canada	**60°**	**Late Apr**	**Late Oct**	**Cave**	**This study**
New England, USA	42°–44°	Apr–May	9 Oct–12 Oct	Cave	Griffin (1940)
Manitoba, Canada	51°	6 May	11 Sep–16 Sep	Cave	Norquay and Willis (2014); Czenze and Willis (2015)
Alberta, Canada	53°		20 Sep/late Sep	Cave	Schowalter (1980)

Note: Bold emphasis indicates "this study."

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for comparison were carried out more than three decades ago and the population may now experience shorter hibernation periods than originally reported (Boyles et al., 2024).

For reproductive females, spring emergence initiates the onset of gestation (Wimsatt, 1944), and moving from the cooler hibernacula into warmer maternity roosts allows females to take advantage of passive warming, further promoting fetal development (Geiser & Drury, 2003). In principle, a female *Myotis* that leaves hibernation earlier can begin gestation sooner and cycle through the stages of reproduction, leaving more time post-lactation for both her and her offspring to acquire resources for hibernation. However, bat activity is limited by food availability (Richards, 1989; Rydell, 1989), and the increased energetic cost of activity must be met with increased energetic gain from foraging. We expected that primary foods such as aquatic emergent insects are absent at the cool emergence temperatures present in April and May; however, recent results from our field site (Kaupas & Barclay, 2017) in Yukon (Talerico, 2008) and in Alaska (Boyles et al., 2016; Shively et al., 2018) identified spiders in the diet of *M. lucifugus* during spring and autumn when primary food sources (flying insects) were unavailable. By diversifying their diet, females may be able to extend their growing season and function on a schedule similar to that of populations farther south, despite the cooler spring and autumn temperatures.

An overall increase in bat activity at the hibernacula occurred during mid to late July, suggesting the arrival of males to the caves. A second increase in activity at the NWT hibernaculum (SSR-1) occurred in late August/early September, approximately two weeks after females left the Thebacha maternity colony. This may reflect the arrival of females at the hibernaculum for swarming. This second "swarming" peak is commonly observed at a similar timing in Pennsylvania (late August to early September; Hall & Brenner, 1968) and slightly later in Ontario (early September to early October; Fenton, 1969; Thomas et al., 1979); however, given the age of these previous studies, swarming may now be occurring earlier at more southern sites. Activity at the two hibernacula we studied declined drastically by mid-September, in association with reduced activity at nearby ponds. Average nightly temperatures began dropping below 0°C in early October and no bat activity was recorded after mid-October, suggesting that all bats were hibernating. This early to mid-October timing is consistent with both the onset of nightly freeze at the hibernacula and with the timing of hibernation of *Myotis* at sites farther south (Table 3).

Reproductive timing and rate

Female *M. lucifugus* began arriving at the Thebacha maternity colony in early May, which is in the middle of the spectrum compared with populations farther south (Table 4). While females were active at the maternity colony by early May, parturition was not observed until early July in 2011 and late June in 2012, which is later than in populations farther south (Table 5). The typical duration of gestation for *M. lucifugus* is 50–60 days (Wimsatt, 1945); therefore, based on the emergence timing at the hibernacula (early April), we would have expected to start observing lactating females by late May or early June. The later timing (late June/mid-July) may reflect cool spring temperatures and low insect abundance (Frick et al., 2010; Linton & Macdonald, 2017; Racey, 1982) and suggests an increased use of torpor by pregnant females in southern NWT, thereby prolonging gestation (Dietz & Kalko, 2006; Racey, 1973). Parturition is similarly delayed in Yukon and northern Alberta (Table 5).

We suggest two alternative explanations for delayed parturition at the South Slave sites. First, as resident bats experience a large change in night duration during the active season (approx. range: 300–700 min; Reimer, 2013), females may use torpor to delay parturition until after solstice to align lactation with increasing night length (i.e., increasing foraging time). Other bat species align lactation with periods of high resource abundance (Arlettaz et al., 2003), and if we consider time as a resource at these high latitudes, *M. lucifugus* may also delay parturition to capitalize on increased foraging time at these northern sites. Second, females may experience delayed parturition as they are investing more time and resources into fetal development. This behavior may result in larger pups and thereby increase juvenile survival (Frick et al., 2010). *Eptesicus nilssoni* at 57° N and 65° N in Sweden do not give birth until after solstice (Rydell, 1993, 2009), but whether natal mass varies has not been assessed.

Reproductive rates differed between the two maternity colonies during 2012, with lower rates at Lady Evelyn Falls (located 295 km to the northwest of Thebacha). As predicted, rates at both colonies were significantly lower than rates observed elsewhere (Table 5), which is consistent with a study that found that bat populations at higher latitudes have lower reproductive rates (Barclay et al., 2004). However, recaptures of banded females included individuals that reproduced during both years and one juvenile that reproduced as a one-year-old. Thus, some females obtain enough resources during the active season to support both current reproduction and winter survival, with sufficient reserves to reproduce the following year.

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TABLE 4 Dates for the arrival and departure of *Myotis lucifugus* at summer maternity roosts throughout their range, organized on the order of earliest arrival.

Location	Latitude	Arrival	Departure	Citation
Indiana, USA	40°	Late Mar	Early Aug	Whitaker and Rissler (1992)
Illinois, USA	38°	1 Apr	Sep–Nov	Cagle and Cockrum (1943)
Indiana, USA	38°–41°	Early–mid-Apr	Late Sep–early Oct	Humphrey (1971)
Ohio, USA	41°	10 Apr–26 Apr	22 Sep–17 Oct	Smith (1954)
Alberta, Canada[a]	50°–52°	14 Apr	6 Oct	Micalizzi (2022)
New York, USA	42°	Mid-Apr	Late Oct	Buchler (1980)
Yukon, Canada	60°–62°	Mid–late Apr	29 Aug–18 Sep	Slough and Jung (2008, 2020); Talerico (2008)
Vermont, USA	43°	22 Apr	Late Jul–mid-Sep	Davis and Hitchcock (1965)
Ontario, Canada	44°	Late Apr	Early Aug	Barclay (1982)
New Hampshire, USA	43°	Late Apr/early May	Mid–late Aug	Anthony et al. (1981)
New Mexico, USA	36°	Late Apr/early May	Sep	O'Farrell and Studier (1975)
Northwest Territories, Canada	**60°**	**Early May**	**Late Sep**	**This study**
Iowa, USA	42°	2 May–30 May	19 Sep–16 Oct	Sherman (1929) *in* Griffin (1940)
New England, USA	42°–44°	11 May–20 May	Mid-Aug–late-Sep	Griffin (1940)
Vermont, USA	44°	19 May–23 May		Osgood *in* Griffin (1940)
Iowa, USA[a]	41°–43°	14 May	16 Oct	Benedict et al. (2020)

Note: Bold emphasis indicates "this study."
[a]Not a known maternity roost.

This high body condition may be associated with individuals that gave birth early the previous year and thus had sufficient time to rebuild their body condition before hibernation (Frick et al., 2010). There was no obvious explanation for the lower reproductive rate at Lady Evelyn Falls in 2012. Long-term mark–recapture data may provide insight into individual fitness at northern latitudes.

Seasonal fluctuations in body mass

Female *M. lucifugus* were heavier and had longer forearms than males, which is consistent with sexual dimorphism observed in other studies of this species (Kalcounis & Brigham, 1995; Kurta & Kunz, 1988; Williams & Findley, 1979). Average mass fluctuated throughout the season with an initial decline immediately following emergence from hibernation. A similar initial mass decline is seen in male ground squirrels associated with increased energy expenditure during spring mating (*Spermophilus parryii*; Buck & Barnes, 1999; *Spermophilus saturates*; Boswell et al., 1994). Little brown bats, however, mate during autumn, prior to hibernation, and to a lesser degree, during hibernation (Fenton, 1969; Thomas et al., 1979); we would therefore expect to see a steady increase in body mass post emergence, as bats begin to forage and replenish depleted fat reserves (Encarnação et al., 2004). The decline in body mass for both males and females after emergence from hibernation at our site may reflect increased energy expenditure due to flight and decreased use of torpor, coupled with relatively low prey intake due to low prey abundance associated with cool temperatures. This leads to the question: If energetic output is greater than energetic input, why not delay emergence until temperatures and prey abundance increase (i.e., energetic consumption exceeds energetic cost)? If the minimum time required for successful reproduction and spermatogenesis is an issue in the north, then the reproductive benefit of emerging early in the season may outweigh the energetic cost, and females that emerge from hibernation with fat reserves may benefit from using their reserves to begin ovulation and gestation despite there being limited resources available on the landscape. In addition, there are other nonenergetic costs to hibernation such as predation, freezing, and decreased immune function that may encourage earlier emergence when possible (Boyles et al., 2020).

The average body mass of both females and males increased during late August/early September, as has been observed elsewhere (Balzer et al., 2022; Kunz et al., 1998; Schowalter, 1980), and reflects preparation for

TABLE 5 Dates of parturition and juvenile fledging for *Myotis lucifugus* at summer sites throughout their range, organized on the order of earliest parturition.

Location	Latitude	Parturition	Fledging	Repro rates	Citation
Illinois, USA[a]	38°	Early May–early/ mid-Jun		91%	Layne (1958)
Illinois, USA	38°	17 May–12 Jul	14 Jun	97%	Cagle and Cockrum (1943)
Kentucky, USA	38°	21 May–21 Jun			Davis et al. (1965)
New York, USA	43°	23 May–14 Jul			Stegeman (1954) *in* Benton and Scharoun (1958)
Iowa, USA[a]	41°–43°	Early Jun	Mid-Jun		Benedict et al. (2020)
Indiana, USA	39°–41°	5 Jun–13 Jul	29 Jun–10 Jul	97%–100%	Humphrey (1971)
Vermont, USA	43°	7 Jun–10 Jul	Mid-Jul		Davis and Hitchcock (1965)
Ontario, Canada	44°	7 Jun–early Jul		100%	Barclay (1982)
Ontario, Canada	45°	7 Jun–29 Jun	25 Jun	97%	Fenton (1966) *in* Humphrey (1971)
New Hampshire, USA	43°	8 Jun	1 Jul		Veilleux et al. (2008)
Ohio, USA	41°	10 Jun–17 Jul		99%	Smith (1954)
New England, USA	42°–44°	13 Jun–14 Jul	Early Jul		Griffin (1940)
New York, USA	42°	14 Jun	Early Jul		Buchler (1980)
Quebec, Canada	47°	15 Jun–15 Jul			Henry et al. (2002)
Wyoming, USA	45°	17 Jun–28 Aug			Johnson et al. (2019)
New York, USA	42°	22 Jun–5 Jul			Wimsatt (1945)
New Hampshire, USA	43°	Late Jun	Mid-Jul		Anthony et al. (1981)
Northwest Territories, Canada	**60°**	**Late Jun–early Jul**	**8–19 Jul**	**49%–79%**	**This study**
British Columbia, Canada	53°	Late Jun–early Jul	20 Jul	73%	Burles et al. (2009)
New Hampshire, USA	43°	Late Jun–mid-Jul		92%–99%	Frick et al. (2010)
New Mexico, USA	36°	Late Jun–early Aug	Mid-Jul		O'Farrell and Studier (1975)
Alberta, Canada[a]	51°	26 Jun–8 Jul	10 Jul–1 Aug	43%–73%	Coleman and Barclay (2011)
Alberta, Canada	55°	5 Jul–early Jul			Olson and Barclay (2013)
Yukon, Canada	60°–62°	Late Jun–mid-Jul	6 Jul–early Aug	87%	Slough and Jung (2008, 2020)
Yukon, Canada	60°	14 Jul–early Aug	Early Aug	32%–74%	Talerico (2008)
Alberta, Canada[a]	50°–52°	22 Jul	5 Aug	0%–75%	Micalizzi (2022)

Note: Bold emphasis indicates "this study."
[a]Not a known maternity roost.

hibernation (Speakman & Rowland, 1999; Thomas et al., 1990). Contrary to our predictions, however, females did not appear to have lower pre-hibernation masses (11.0 ± 0.8 g) than more southern populations (e.g., range: 7.2–9.7 g, Balzer et al., 2022; 9.2 ± 0.2 g, Kunz et al., 1998; 12.2 ± 0.1 g, Schowalter, 1980). Thus, despite having later parturition and weaning, females were able to obtain enough energy to acquire sufficient mass for hibernation. Given the foraging constraints of short nights, these results suggest that feeding rates are higher (as confirmed in Reimer, 2013), prey may be energetically richer at the South Slave sites than at more southern locations

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(e.g., foraging on spiders; Boyles et al., 2016; Kaupas & Barclay, 2017; Shively et al., 2018), and/or bats may use increased torpor to build fat stores (McGuire et al., 2016). Furthermore, reproductive females were heavier post-parturition than nonreproductive females, suggesting that females with lower body condition may forgo reproduction in a given year.

In summary, contrary to our predictions, *M. lucifugus* in the South Slave region did not have a shorter active season than bats farther south; however, reproductive timing was delayed, perhaps due to cool spring temperatures, low insect abundance, and torpor use. Alternatively, delaying parturition could synchronize the energetic expense of lactation with lengthening nights after the solstice and increasing resource abundance. Early emergence from hibernation may allow females to begin gestation and perhaps invest more in fetal development, resulting in larger pups, thereby increasing juvenile survival. Pre-hibernation mass was similar to that in southern populations, suggesting that despite delayed timing of parturition, fledging, and weaning, bats still had adequate time during the active season to gather resources for maintenance/growth, reproduction, and fat deposition for winter survival. However, the long-term effect of these time restrictions on female body condition may contribute to lower reproductive rates.

AUTHOR CONTRIBUTIONS

Jesika P. Reimer contributed equally to the conceptualization and methodology, took the lead in formal analysis and investigation, led the writing of the original draft, and contributed equally to writing, review, and editing. Additionally, she provided supporting contributions to funding acquisition. Robert M. R. Barclay contributed equally to conceptualization and methodology, took the lead in providing resources, and played a lead role in project administration, supervision, and funding acquisition. He provided supporting contributions to formal analysis and the writing of the original draft, as well as equal contributions to writing, review, and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Reimer & Barclay, 2023) are available from Dryad: https://doi.org/10.25338/B8KH19.

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REFERENCES

Al-Musfir, H. M., and N. Yamaguchi. 2008. "Timings of Hibernation and Breeding of Ethiopian Hedgehogs, *Paraechinus aethiopicus*, in Qatar." *Zoology in the Middle East* 45: 3–10.

Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. "Night Roosting and the Nocturnal Time Budget of the Little Brown Bat, *Myotis lucifugus*: Effects of Reproductive Status, Prey Density, and Environmental Conditions." *Oecologia* 51: 151–56.

Arlettaz, R., P. Christe, A. Lugon, N. Perrin, and P. Vogel. 2003. "Food Availability Dictates the Timing of Parturition in Insectivorous Mouse-Eared Bats." *Oikos* 95: 105–111.

Balzer, E. W., A. D. Grottoli, L. E. Burns, and H. G. Broders. 2022. "Active Season Body Mass Patterns of Little Brown and Northern Myotis Bats." *Ecology and Evolution* 12(8): e9230. https://doi.org/10.1002/ece3.9230.

Barclay, R. M. R. 1982. "Night Roosting Behavior of the Little Brown Bat, *Myotis lucifugus*." *Journal of Mammalogy* 63(3): 464–474. https://doi.org/10.2307/1380444.

Barclay, R. M. R., J. Ulmer, C. J. A. MacKenzie, M. S. Thompson, L. Olson, J. McCool, E. Cropley, and G. Poll. 2004. "Variation in the Reproductive Rate of Bats." *Canadian Journal of Zoology* 82: 688–693.

Benedict, R. A., A. Chipps, R. Heatwole, D. Howell, D. A. Mandi, A. Oblander, J. Riebkes Clough, and S. Roush. 2020. "Geographic Distribution, Reproduction, and Seasonal Activity of Bats in Iowa." *Western North American Naturalist* 80(3): 292–315. https://doi.org/10.3398/064.080.0302.

Benton, A. H., and J. Scharoun. 1958. "Notes on a Breeding Volony of Myotis." *Journal of Mammalogy* 39: 293–95.

Boswell, T., S. C. Woods, and G. J. Kenagy. 1994. "Seasonal Changes in Body Mass, Insulin, and Glucocorticoids of Free-Living Golden-Mantled Ground Squirrels." *General and Comparative Endocrinology* 96(3): 339–346.

Boyles, J. G., V. Brack, Jr., K. E. Marshall, and D. Brack. 2024. "Shifts in Population Density Centers of a Hibernating Mammal Driven by Conflicting Effects of Climate Change and Disease." *Global Change Biology.* 30: e17035. https://doi.org/10.1111/gcb.17035.

Boyles, J. G., J. S. Johnson, A. Blomberg, and T. M. Lilley. 2020. "Optimal Hibernation Theory." *Mammal Review* 50: 1–120.

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Boyles, J. G., L. P. McGuire, E. Boyles, J. P. Reimer, C. A. Brooks, R. W. Rutherford, T. A. Rutherford, J. O. Whitaker, Jr., and G. F. McCracken. 2016. "Physiological and Behavioral Adaptations in Bats Living at High Latitudes." *Physiology & Behavior* 165: 322–27.

Brunet-Rossinni, A. K., and G. S. Wilkinson. 2009. "Chapter 15: Methods for Age Estimation and the Study of Senescence in Bats." In *Ecological and Behavioral Methods for the Study of Bats*, 2nd ed., edited by T. H. Kunz and S. Parsons, 315–325. Baltimore, MD: The John Hopkins University Press.

Buchler, E. R. 1980. "The Development of Flight, Foraging, and Echolocation in the Little Brown Bat (*Myotis lucifugus*)." *Behavioral Ecology and Sociobiology* 6: 211–18.

Buck, C. L., and B. M. Barnes. 1999. "Annual Cycle of Body Composition and Hibernation in Free-Living Arctic Ground Squirrels." *Journal of Mammalogy* 80: 430–442.

Burles, D. W., R. M. Brigham, R. A. Ring, and T. E. Reimchen. 2009. "Influence of Weather on Two Insectivorous Bats in a Temperate Pacific Northwest Rainforest." *Canadian Journal of Zoology* 87(2): 132–38. https://doi.org/10.1139/Z08-14.

Cagle, F. R., and L. Cockrum. 1943. "Notes on a Summer Colony of *Myotis lucifugus lucifugus*." *Journal of Mammalogy* 24: 474–492.

Coleman, J. L., and R. M. R. Barclay. 2011. "Influence of Urbanization on Demography of Little Brown Bats (*Myotis lucifugus*) in the Prairies of North America." *PLoS One* 6(5): e20483. https://doi.org/10.1371/journal.pone.0020483.

Cumming, G. S., and R. T. F. Bernard. 1997. "Rainfall, Food Abundance and Timing of Parturition in African Bats." *Oecologia* 111: 309–317.

Czenze, Z. J., and C. K. R. Willis. 2015. "Warming Up and Shipping Out: Arousal and Emergence Timing in Hibernating Little Brown Bats (*Myotis lucifugus*)." *Journal of Comparative Physiology B* 185: 575–586.

Daan, S., C. Dijkstra, R. Drent, and T. Meijer. 1988. "Food Supply and the Annual Timing of Avian Reproduction." *Proceedings of the International Ornithological Congress* 19: 392–407.

Davis, W. H., M. D. Hassell, and M. J. Harvey. 1965. "Maternity Colonies of the Bat Myotis *I. lucifugus* in Kentucky." *The American Midland Naturalist* 73(1): 161–65.

Davis, W. H., and H. B. Hitchcock. 1965. "Biology and Migration of the Bat, *Myotis lucifugus*, in New England." *Journal of Mammalogy* 46: 296–313.

Davis, W. H., and H. B. Hitchcock. 1995. "A New Longevity Record for the Bat *Myotis lucifugus*." *Bat Research News* 36: 6.

Dietz, M., and E. K. V. Kalko. 2006. "Seasonal Changes in Daily Torpor Patterns of Free-Ranging Female and Male Daubenton's Bats (*Mytois daubentonii*)." *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 176: 223–231.

Encarnação, J. A., M. Dietz, U. Kierdorf, and V. Wolters. 2004. "Body Mass Changes in Male Daubenton's Bats *Myotis daubentonii* (Chiroptera, Vespertilionidae) during the Seasonal Activity Period." *Mammalia* 68: 291–97.

Fenton, M. B. 1969. "Summer Activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at Hibernacula in Ontario and Quebec." *Canadian Journal of Zoology* 47: 597–602.

Fenton, M. B. 1970. "A Technique for Monitoring Bat Activity with Results Obtained from Different Environments in Southern Ontario." *Canadian Journal of Zoology* 48: 847–851.

Fenton, M. B., and G. P. Bell. 1981. "Recognition of Species of Insectivorous Bats by Their Echolocation Calls." *Journal of Mammalogy* 62: 233–243.

Frick, W. F., D. S. Reynolds, and T. H. Kunz. 2010. "Influence of Climate and Reproductive Timing on Demography of Little Brown Myotis *Myotis lucifugus*." *Journal of Animal Ecology* 79: 128–136.

Geiser, F., and R. L. Drury. 2003. "Radiant Heat Affects Thermoregulation and Energy Expenditure during Rewarming from Torpor." *Journal of Comparative Physiology B* 173: 55–60.

Gifford, C. E., and D. R. Griffin. 1960. "Notes on Homing and Migratory Behavior of Bats." *Ecology* 41: 378–381.

Goldizen, A. W., J. Terborgh, F. Cornejo, D. T. Porras, and R. Evans. 1988. "Seasonal Food Shortage, Weight Loss, and the Timing of Births in Saddle-Back Tamarins (*Saguinus fuscicollis*)." *Journal of Animal Ecology* 57: 893–901.

Griffin, D. R. 1940. "Notes on the Life Histories of New England Cave Bats." *Journal of Mammalogy* 21: 181–87.

Hall, J. S., and F. J. Brenner. 1968. "Summer Netting of Bats at a Cave in Pennsylvania." *Journal of Mammalogy* 49: 779–781.

Hau, M., M. Wikelski, and J. C. Wingfield. 2000. "Visual and Nutritional Food Cues Fine-Tine Timing of Reproduction in a Neotropical Rainforest Bird." *Journal of Experimental Zoology* 286: 494–504.

Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. "Foraging Distances and Home Range of Pregnant and Lactating Little Brown Bats (*Myotis lucifugus*)." *Journal of Mammalogy* 83(3): 767–774.

Humphrey, S. R. 1971. "Population Ecology of the Little Brown Bat *Myotis lucifugus*, in Indiana and North-Central Kentucky." PhD diss., Oklahoma State University.

International Union for Conservation of Nature (IUCN). 2021. "*Myotis lucifugus*." The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org.

Johnson, J. S., J. T. Treanor, A. C. Slusher, and M. J. Lacki. 2019. "Buildings Provide Vital Habitat for Little Brown Myotis (*Myotis lucifugus*) in a High-Elevation Landscape." *Ecosphere* 10(11): e02925. https://doi.org/10.1002/ecs2.2925.

Kalcounis, M. C., and R. M. Brigham. 1995. "Intraspecific Variation in Wing Loading Affects Habitat Use by Little Brown Bats (*Myotis lucifugus*)." *Canadian Journal of Zoology* 73: 89–95.

Kaupas, L. A., and R. M. R. Barclay. 2017. "Temperature-Dependent Consumption of Spiders by Little Brown Bats (*Myotis lucifugus*), but Not Northern Long-Eared Bats (*Myotis septentrionalis*), in Northern Canada." *Canadian Journal of Zoology* 96: 261–68.

Kunz, T. H., J. A. Wrazen, and C. D. Burnett. 1998. "Changes in Body Mass and Fat Reserves in Pre-Hibernating Little Brown Bats (*Myotis lucifugus*)." *Ecoscience* 5: 8–17.

Kurta, A., and T. H. Kunz. 1988. "Roosting Metabolic Rate and Body Temperature of Male Little Brown Bats (*Myotis lucifugus*) in Summer." *Journal of Mammalogy* 69: 645–651.

Layne, J. N. 1958. "Notes on Mammals of Southern Illinois." *The American Midland Naturalist* 60(1): 219–254.

Lewis, R. 1974–1975. "Cave Report." Unpublished Report to Parks Canada. 6 pp.

Lewis, S. 1993. "Effect of Climatic Variation on Reproduction by Pallid Bats (*Antrozous pallidus*)." *Canadian Journal of Zoology* 71: 1429–33.

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Linton, D. M., and D. W. Macdonald. 2017. “Spring Weather Conditions Influence Breeding Phenology and Reproductive Success in Sympatric Bat Populations.” *Journal of Animal Ecology* 87: 1080–90.

McGuire, L. P., K. A. Muise, A. Shrivastav, and C. K. R. Willis. 2016. “No Evidence of Hyperphagia during Prehibernation in a Northern Population of Little Brown Bats (*Myotis lucifugus*).” *Canadian Journal of Zoology* 94: 821–27. https://doi.org/10.1139/cjz-2016-0110.

Meyer, G. A., J. A. Senulis, and J. A. Reinartz. 2016. “Effects of Temperature and Availability of Insect Prey on Bat Emergence from Hibernation in Spring.” *Journal of Mammalogy* 97(6): 1623–33. https://doi.org/10.1093/jmammal/gyw126.

Micalizzi, E. 2022. “Roosting Behaviour of Little Brown Bats (*Myotis lucifugus*) in the Canadian Rocky Mountains.” MSc thesis, University of Calgary. https://prism.ucalgary.ca. http://hdl.handle.net/1880/114656.

Norquay, K. J. O., F. Martinez-Nuñez, J. E. Dubois, K. M. Monson, and C. K. R. Willis. 2013. “Long-Distance Movements of Little Brown Bats (*Myotis lucifugus*).” *Journal of Mammalogy* 94(2): 506–515. https://doi.org/10.1644/12-MAMM-A-065.1.

Norquay, K. J. O., and C. K. R. Willis. 2014. “Hibernation Phenology of *Myotis lucifugus*.” *Journal of Zoology* 294: 85–92.

O’Farrell, M. J., and E. H. Studier. 1975. “Population Structure and Emergence Activity Patterns in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) in Northeastern New Mexico.” *The American Midland Naturalist* 93(2): 368–376. https://doi.org/10.2307/2424169.

Olson, C. R., and R. M. R. Barclay. 2013. “Concurrent Changes in Group Size and Roost Use by Reproductive Female Little Brown Bats, *Myotis lucifugus*.” *Canadian Journal of Zoology* 91: 149–155.

Parker, D. I., B. E. Lawhead, and J. A. Cook. 1997. “Distributional Limits of Bats in Alaska.” *Arctic* 50: 256–265.

Racey, P. A. 1973. “Environmental Factors Affecting the Length of Gestation in Heterothermic Bats.” *Journal of Reproduction and Fertility. Supplement* 19: 175–189.

Racey, P. A. 1982. “Chapter 2: Ecology of Bat Reproduction.” In *Ecology of Bats*, edited by T. H. Kunz, 57–104. New York: Plenum Press.

Racey, P. A. 2009. “Chapter 12: Reproductive Assessment of Bats.” In *Ecological and Behavioral Methods for the Study of Bats*, 2nd ed., edited by T. H. Kunz and S. Parsons, 249–264. Baltimore, MD: The John Hopkins University Press.

Reimer, J., and R. Barclay. 2023. “Data from: Seasonal Phenology of the Little Brown Bat (*Myotis lucifugus*) at 60° N.” Dataset. Dryad. https://doi.org/10.25338/B8KH19.

Reimer, J. P. 2013. “Nocturnality under the Midnight Sun: Behavioural Adaptations of the Little Brown Bat (*Myotis lucifugus*) at 60° N Latitude.” MSc thesis, University of Calgary.

Reimer, J. P., C. L. Lausen, R. M. R. Barclay, S. Irwin, and M. K. Vassal. 2014. “Bat Activity and Use of Hibernacula in Wood Buffalo National Park, Alberta.” *Northwestern Naturalist* 95(3): 277–288.

Richards, G. C. 1989. “Nocturnal Activity of Insectivorous Bats Relative to Temperature and Prey Availability in Tropical Queensland.” *Wildlife Research* 16: 151–58.

Rubenstein, D. R., and M. Wikelski. 2003. “Seasonal Changes in Food Quality: A Proximate Cue for Reproductive Timing in Marine Iguanas.” *Ecology* 84: 3013–23.

Rupprecht, C. 1980. “Seasonal Activity Patterns in the Bat Community at Neda Mine.” *Field Station Bulletin* 13(2): 1–7.

Rydell, J. 1989. “Feeding Activity of the Northern Bat *Eptesicus nilssoni* during Pregnancy and Lactation.” *Oecologia* 80: 562–65.

Rydell, J. 1993. “Variation in Foraging Activity of an Aerial Insectivorous Bat during Reproduction.” *Journal of Mammalogy* 74: 503–9.

Rydell, J. 2009. “Occurrence of Bats in Northernmost Sweden (65° N) and Their Feeding Ecology in Summer.” *Journal of Zoology* 227: 517–529.

Rydell, J., K. B. Strann, and J. R. Speakman. 1994. “First Record of Breeding Bats above the Arctic Circle: Northern Bats at 68–70° N in Norway.” *Journal of Zoology* 233: 335–39.

Schowalter, D. B. 1980. “Swarming, Reproduction, and Early Hibernation of *Myotis lucifugus* and *M. volans* in Alberta, Canada.” *Journal of Mammalogy* 61: 350–54.

Schowalter, D. B., J. R. Gunson, and L. D. Harder. 1979. “Life History Characteristics of Little Brown Bats (*Myotis lucifugus*) in Alberta.” *Canadian Field-Naturalist* 93: 243–251.

Shively, R., and P. Barboza. 2017. “Range and Roosting Ecology of the Little Brown Bat, *Myotis lucifugus*, in Interior and Northern Alaska.” *Northwestern Naturalist* 98: 122–131.

Shively, R., P. Barboza, P. Doak, and T. S. Jung. 2018. “Increased Diet Breadth of Little Brown Bats (*Myotis lucifugus*) at Their Northern Range Limit: A Multimethod Approach.” *Canadian Journal of Zoology* 96: 31–38.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. “2016 Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research and Education.” *Journal of Mammalogy* 97: 663–688.

Slough, B. G., and T. S. Jung. 2008. “Observations on the Natural History of Bats in the Yukon.” *The Northern Review* 29: 127–150.

Slough, B. G., and T. S. Jung. 2020. “Little Brown Bats Utilize Multiple Maternity Roosts within Foraging Areas: Implications for Identifying Summer Habitat.” *Journal of Fish and Wildlife Management* 11(1): 311–320. https://doi.org/10.3996/052019-JFWM-039.

Smith, E. 1954. “Studies on the Life History of Non-Cave-Dwelling Bats in Northwestern Ohio.” *Ohio Journal of Sciences* 54: 1–12.

Speakman, J. R., and A. Rowland. 1999. “Preparing for Inactivity: How Insectivorous Bats Deposit a Fat Store for Hibernation.” *Proceedings of the Nutrition Society* 58: 123–132.

Species at Risk Committee. 2017. *Species Status Report for Big Brown Bat, Little Brown Myotis, Northern Myotis, Long-Eared Myotis, and Long-Legged Myotis (Eptesicus fuscus, Myotis lucifugus, Myotis septentrionalis, Myotis evotis, and Myotis volans) in the Northwest Territories*. Yellowknife, NT: Species at Risk Committee. https://www.nwtspeciesatrisk.ca/sites/enr-species-at-risk/files/bat_status_report_and_assessment_final_apr617.pdf.

Stearns, S. C. 1992. “Chapter 4: Trade-Offs.” In *The Evolution of Life Histories* 72–89. New York: Oxford University Press.

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Stegeman, L. C. 1954. "Notes on the Development of the Little Brown Bat *Myotis lucifugus lucifugus*." *Journal of Mammalogy* 35: 432–33.

Talerico, J. 2008. "The Behaviour, Diet and Morphology of Little Brown Bats (*Myotis lucifugus*) near the Northern Extent of its Range in Yukon, Canada." MSc thesis, University of Calgary.

Thomas, D. W., M. Dorais, and J. Bergeron. 1990. "Winter Energy Budgets and Cost of Arousals for Hibernating Little Brown Bats, *Myotis lucifugus*." *Journal of Mammalogy* 71: 475–79.

Thomas, D. W., M. B. Fenton, and R. M. R. Barclay. 1979. "Social Behavior of the Little Brown Bat, *Myotis lucifugus*." *Behavioral Ecology and Sociobiology* 6: 129–136.

Veilleux, J. P., T. H. Howard, and P. R. Moosman. 2008. "Bats of Pisgah State Park, New Hampshire." *Northeastern Naturalist* 15(1): 25–34.

Ware, J. V., O. L. Nelson, C. T. Robbins, and H. T. Jansen. 2012. "Temporal Organization of Activity in the Brown Bear (*Ursus arctos*): Roles of Circadian Rhythms, Light, and Food Entrainment." *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 303: R890–R902.

Whitaker, J. O., Jr., and L. J. Rissler. 1992. "Winter Activity of Bats at a Mine Entrance in Vermillion County, Indiana." *The American Midland Naturalist* 127(1): 52–59.

Wilkinson, G. S., and J. M. South. 2002. "Life History, Ecology and Longevity in Bats." *Aging Cell* 1: 124–131.

Williams, D. F., and J. S. Findley. 1979. "Sexual Size Dimorphism in Vespertilionid Bats." *American Midland Naturalist* 102: 113–126.

Wimsatt, W. A. 1944. "Growth of the Ovarian Follicle and Ovulation in *Myotis lucifugus lucifugus*." *American Journal of Anatomy* 74: 129–173.

Wimsatt, W. A. 1945. "Notes on Breeding Behavior, Pregnancy, and Parturition in Some Vespertilionid Bats of the Eastern United States." *American Society of Mammalogists* B26: 23–33.

Yahner, R. H. 2012. "Winter Strategies." In *Wildlife Behavior and Conservation* 139–143. New York: Springer. https://doi.org/10.1007/978-1-4614-1518-3_16.

Zervanos, S. M., C. R. Maher, J. A. Waldvogel, and G. L. Florant. 2010. "Latitudinal Differences in the Hibernation Characteristics of Woodchucks (*Marmota monax*)." *Physiological and Biochemical Zoology* 83: 135–141.

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