

Hibernation phenology of *Myotis lucifugus*

K. J. O. Norquay & C. K. R. Willis

Department of Biology and Centre for Forest Interdisciplinary Research, University of Winnipeg, Winnipeg, MB, Canada

Keywords

hibernation timing; immergence;
emergence; white-nose syndrome.

Correspondence

Craig Willis, Department of Biology and
Centre for Forest Interdisciplinary Research,
University of Winnipeg, 515 Portage Ave,
Winnipeg, MB, Canada R3B 2E9.
Tel: 204 786 9433
Email: c.willis@uwinnipeg.ca

Editor: Nigel Bennett

Received 25 January 2014; revised 24 April
2014; accepted 8 May 2014

doi:10.1111/jzo.12155

Abstract

Hibernating animals must time immergence and emergence carefully to maximize reproductive success and reduce the risk of encountering inclement weather or predators. Few studies of phenology exist for any hibernating species and those that do address species which mate during spring. We used passive transponders (PIT tags) to study hibernation phenology of little brown bats *Myotis lucifugus*, a species that mates prior to hibernation in the fall. We expected that adult females would emerge earliest as early parturition increases juvenile survival. We predicted that females with large fat stores should emerge earliest because of their ability to tolerate inclement spring weather at the maternity roost. We also predicted that adult males would remain active later than females to maximize mating opportunities and compensate for body mass decline during the mating period. We implanted 475 bats with PIT tags and remotely recorded immergence and emergence timing at a hibernaculum in central Canada. As expected, adult males were active significantly later (median immergence date = 16 September 2011) than adult females (11 September 2011) and adult females emerged earlier (median emergence date = 6 May 2012) than both adult males (25 May 2012) and subadults (13 May 2012). Emergence timing was correlated with fall body condition in adult females, with fatter females emerging earlier, but not males. Our results highlight the importance of reproductive timing as an influence on hibernation phenology of mammals.

Introduction

Winter poses an energetic challenge to endotherms that depend on seasonal resources. To meet this challenge, hibernators reduce metabolic rate and body temperature (T_b) dramatically during bouts of torpor, which are interspersed with brief arousals to normothermic T_b (Lyman *et al.*, 1982; Geiser, 2004, 2013). These species can regulate winter energy balance by adjusting 'within-hibernation factors' such as torpor depth, torpor bout duration, and arousal duration (Humphries, Thomas & Kramer, 2003; Jonasson & Willis, 2011, 2012) and 'pre- and post-hibernation factors', such as hibernation phenology (i.e. the timing of immergence and emergence). Adjustments of hibernation phenology could help individuals optimize energy accumulation before hibernation, maximize reproductive opportunities, synchronize reproduction with resource abundance and balance all of these activities against risk of predation (Michener, 1978, 1983; Bieber & Ruf, 2009; Lane *et al.*, 2011). However, despite an abundant literature on phenology of avian migration (e.g. Visser & Both, 2005; Charmanier & Gienapp, 2013), and the potential of hibernation phenology to influence survival and reproductive fitness (Humphries *et al.*, 2003; Lane *et al.*, 2011), the timing of

hibernation immergence and emergence has received relatively little attention.

Studies of hibernation phenology that do exist have focused on a few species of rodents that mate following hibernation (e.g. Michener, 1978, 1979, 1983; Lane *et al.*, 2011). The timing of immergence appears to reflect trade-offs between the need to accumulate pre-hibernation energy stores against risks posed by predation during foraging and decreased mobility from excessive fattening (Michener, 1978, 1979, 1983; Humphries *et al.*, 2003; Bieber & Ruf, 2009). Immergence timing also varies depending on energetic needs of different sex and age classes. In Richardson's ground squirrels *Urocitellus richardsonii*, males and non-reproductive females begin hibernation during mid-summer while reproductive females take more time to store fat after energetically expensive pregnancy and lactation (Michener, 1978, 1979, 1998).

Similar pressures influence spring emergence timing. In rodents and some marsupials that mate following hibernation, males emerge first to begin spermatogenesis, establish territories and ensure access to females (Michener, 1983; Körtner & Geiser, 1998; Blumstein, 2009). Timing of emergence for females is thought to be shaped by trade-offs between two

opposing influences: the advantage of having young early in the season (Murie & Boag, 1984; Frick, Reynolds & Kunz, 2010a) and the risk posed by encountering inclement spring weather or food scarcity (Michener, 1979; Inouye *et al.*, 2000; Lane *et al.*, 2011).

Hibernating bats provide an interesting contrast to most hibernators because of marked differences in the timing of reproduction. Adult male bats undergo spermatogenesis in summer and store sperm in their cauda epididymis until mating begins at fall swarms immediately before hibernation (Gustafson, 1979; Hosken *et al.*, 1998). Adult females store sperm over the winter and ovulate a few days after spring emergence (Wimsatt & Kallen, 1957; Buchanan, 1987). This decouples spermatogenesis from female reproduction and pairs it, instead, with the period of greatest food abundance (Gustafson, 1979; Hosken *et al.*, 1998; Racey & Entwistle, 2000; Pfeiffer & Mayer, 2012). Male subadults and the majority of female subadults do not reproduce in their first year (Schowalter, Gunson & Harder, 1979; Thomas, Fenton & Barclay, 1979; Frick *et al.*, 2010a). This decoupling of reproductive timing for adult males and females should lead to differences in hibernation phenology between sexes, and differences in phenology compared with other species. Consistent with this hypothesis, several studies have found male-biased sex ratios among captured little brown bats *Myotis lucifugus* in late fall and a female bias in early spring (Davis & Hitchcock, 1965; Humphrey & Cope, 1976). However, none have quantified immersion and emergence timing of individual bats directly.

Data on hibernation phenology of North American bats are also urgently needed from a conservation perspective. White-nose syndrome (WNS) is an emerging disease which has killed millions of bats since its discovery in 2007 (Blehert *et al.*, 2009; Frick *et al.*, 2010b; Langwig *et al.*, 2012). WNS is caused by the cold-tolerant fungus, *Pseudogymnoascus destructans*, which infects exposed skin, causes bats to arouse from hibernation too frequently and emerge prematurely after depleting their fat reserves (Blehert *et al.*, 2009; Lorch *et al.*, 2011; Warnecke *et al.*, 2012). Thus, WNS exerts a direct effect on hibernation phenology. New data on the timing of hibernation in healthy bats are needed to understand consequences of WNS for individuals and populations.

We implanted *M. lucifugus* with passive transponders (PIT tags) to test the hypothesis that fall mating, and the temporal mismatch in reproductive investment between males and females, affects hibernation phenology. This hypothesis predicts that: (1) adult females should emerge first due to selection pressure on them for early parturition and pressure on males and subadults to continue hibernating and reduce predation risk and exposure to unpredictable weather; (2) females with the largest fall fat stores should emerge earliest in spring because of pressure on females to arrive at the maternity roosts early, combined with the ability of fatter females to withstand inclement spring weather; (3) males should remain active longer than females in fall to maximize reproductive interactions and compensate for mass lost during mating.

Materials and methods

Study site and animals

This study was conducted at St. George Bat Cave in central Manitoba, Canada near Fisher River First Nation (14U 613884 5700551). A gated entrance located at the bottom of a sinkhole opens up to the large main chamber of the limestone cave, *c.* 165 m in length (McRitchie & Monson, 2000). The cave has only one entrance and houses over 9000 *M. lucifugus* and northern long-eared bats *M. septentrionalis* mid-winter (J. Dubois & C. Willis, unpublished data). It was negative for WNS at the time of this study.

We implanted PIT tags (11.5 × 2.1 mm, 0.1 g, Trovan Ltd ID 100-01, Douglas, UK) subdermally between the scapulae in 475 bats in September 2008 (*n* = 189) and September 2011 (*n* = 286). The majority of bats (*n* = 450) were captured at swarms using harp traps and the remainder (*n* = 25) were removed from the walls and ceilings of the hibernaculum. All bats were sexed and aged as either adult or subadult (<1 year). Subadults were identified based on the presence of unfused third digit metapalangeal joints, small testes, undistended epididymis and dark tunica vaginalis in males, or small nipples without a surrounding bare patch in females (Davis & Hitchcock, 1965; Racey, 1974). Bats were weighed to the nearest 0.01 g (*n* = 462 of 475 due to battery failure of our electronic balance) and forearm length for all individuals were measured to the nearest 0.05 mm. Body condition index (BCI) was defined as mass/forearm (Pearce, O'Shea & Wunder, 2008; Reynolds, Sullivan & Kunz, 2009).

A 475 × 400 × 40 mm panel antenna (ANT-612 Large Panel Antenna, Trovan Ltd) was installed in the centre of the cave entrance to detect arrival and departure of PIT-tagged bats. The panel antenna had a detection range of *c.* 35 cm on both sides, exceeding the diameter of the cave. The antenna and a corresponding decoder/data logger (LID 650, Trovan Ltd) were powered by four 12-V, deep-cycle batteries in a weather-proof box and charged via a 64-W solar panel. The PIT tag system operated continuously from 2 September 2011 to 25 November 2012, and from 17 March 2012 to mid-July 2012.

All procedures were approved by the University of Winnipeg Animal Care Committee and conducted under Manitoba Conservation Wildlife Scientific Permits. We closely followed United States Fish and Wildlife Service guidelines for decontamination of *P. destructans* during fieldwork (United States Fish and Wildlife Service (USFWS), 2011).

Analysis

We only analysed hibernation duration and emergence timing for bats which we could confirm 'entered' the hibernaculum in fall and emerged in spring. Bats often remained near the hibernaculum entrance for several minutes resulting in multiple detections by the reader and the inability to determine flight direction. To account for this, each time a bat flew over the plate we coded the pass as an entry or exit. The first time the bat was detected was coded as entry, the second as exit,

the third as entry, and so on. Instances where bats were detected continuously (i.e. >once per second) were counted as one pass. We validated this method using bats detected entering in fall 2011 and emerging in April and May 2012 and were able to correctly classify the fall detection as immersion in 92% (94/102) of cases. We considered the first detection of a bat in spring, prior to 30 June 2012, to represent emergence as bats began visiting the area for 'fall' swarming as early as the first week of July (K. Norquay, unpublished data). In their study of *M. lucifugus* from Vermont, Davis & Hitchcock (1965) reported <3% of bats emerging in June and none in July.

We examined fall activity of bats detected in September and October 2011 which had been tagged prior to 1 September 2011. We assumed that the last date a bat was detected was the last date that individual was active. Data were non-normally distributed so we used a Kruskal–Wallis test with post hoc Mann–Whitney *U*-tests (Bonferroni corrected) to test for differences in fall activity and emergence date between age/sex classes. We used Levene's test for equality of variances to test for differences in variability of emergence dates between the adult sexes. We also tested for an effect of BCI on emergence date of males and females using least squares regression. We only included individuals captured and measured on 17 September 2011 in this analysis, as this date was close to the average immersion date for the study while providing a large enough sample size of recaptured bats ($n = 23$). We excluded immersion date from the analysis as most of these bats immersed within two nights of capture. We tested for effects of age/sex class on hibernation duration using analysis of variance (ANOVA) with Tukey's test for pairwise comparisons and for differences in hibernation duration between males and females using analysis of covariance (ANCOVA) with BCI and emergence date as covariates.

All values are presented as the mean \pm SD and we assessed significance at $\alpha = 0.05$ except where we used Bonferroni-adjusted alpha levels. Statistical analyses were performed using SYSTAT 11 (Systat Software Inc., Point Richmond, CA, USA) with the exception of Levene's test for equality of variances, which was performed in MS Excel 2010.

Results

During September and October 2012, we detected 37% (186/475) of the bats we captured and tagged at the cave. Based on their patterns of activity at the cave entrance, we concluded that 171 of these individuals entered the cave to hibernate (Table 1, Fig. 1). We also detected two bats entering hibernation which were PIT tagged at maternity colonies in 2011 as part of another study. Unfortunately, water damage to the antenna sustained during winter reduced its detection sensitivity in spring to a distance of 10 cm and tags could be detected on only 75% of the plate. This meant we failed to record some of the emerging bats and were not able to calculate survival estimates. However, we were still able to detect 94 bats exiting hibernation between 18 March and 25 June 2012 (Table 1). Adult ($n = 48$, range = 100 days) and subadult males ($n = 15$, range = 77 days) began emerging in late March

Table 1 Sample sizes for each age/sex class detected immersing and emerging from hibernation at St. George Bat Cave

Age/sex class	Immersion	Emergence
AF	43	21
AM	79	48
SF	19	10
SM	30	15
Total	171	94

AF = adult female; AM = adult male; SF = subadult female; SM = subadult male.

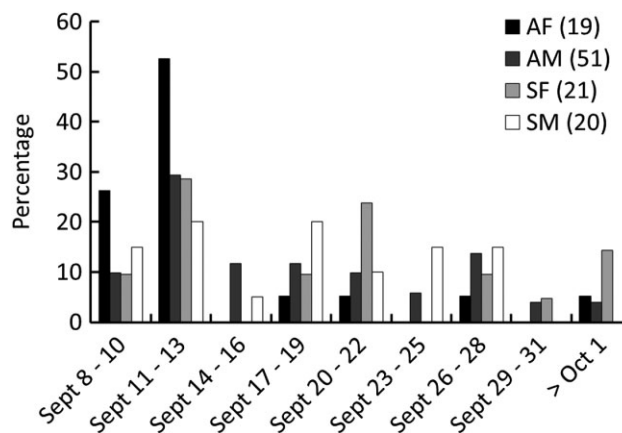


Figure 1 Difference between age and sex classes for the last date of fall activity in 2011 at St. George Bat Cave. 1 October represents the 95th percentile of the distribution so the dates of fall activity recorded in October are combined into one bin for clarity. AF = adult female, AM = adult male, SF = subadult female, SM = subadult male. Numbers in brackets indicate sample size.

and their emergence continued well into June, while adult ($n = 21$, range = 25 days) and subadult females ($n = 10$, range = 35 days) had much shorter ranges of emergence dates with both beginning emergence in late April. Adult females finished emergence by 18 May 2012, while the last subadult female was detected emerging on 3 June 2012 (Table 2, Fig. 2). Adult females exhibited significantly less variability in emergence dates than adult males ($F_{1,67} = 3.98$, $P = 0.005$). There was also a significant effect of age/sex class on emergence date ($H = 259$, $n = 94$, $P = 0.005$). Adult females emerged earlier than both adult males (Bonferroni-adjusted $\alpha = 0.0083$, $U = 259$, $P = 0.001$) and subadult females ($U = 41.5$, $P = 0.007$, Table 3). Emergence was positively correlated with BCI for adult females ($n = 11$, $r^2 = 0.42$, $P = 0.031$, Fig. 3a), but not for adult males ($n = 12$, $r^2 = 0.11$, $P = 0.29$, Fig. 3b).

There was a significant difference in hibernation duration between age/sex classes ($H = 9.7$, $n = 94$, $P = 0.021$) with adult males ($n = 48$) hibernating longer than adult females ($n = 21$; Bonferroni-adjusted $\alpha = 0.0083$, $P = 0.003$, Tables 2 and 3). No other pairwise comparisons were significant for hibernation duration after Bonferroni correction (Table 3). There was

Table 2 Median, minimum, maximum, and range for emergence dates and hibernation duration of each age/sex class of bats detected emerging from St. George Bat Cave in spring 2012

Demographic	<i>n</i>	Median	Minimum	Maximum	Range (days)	Duration (mean ± SD)
AF	21	6 May	22 April	May 18	25	232.35 ± 10.37
AM	48	25 May	17 March	June 25	100	241.61 ± 23.35
SF	10	13 May	29 April	June 3	35	236.52 ± 12.50
SM	15	21 May	22 March	June 7	77	235.96 ± 25.67

AF = adult female; AM = adult male; SF = subadult female; SM = subadult male.

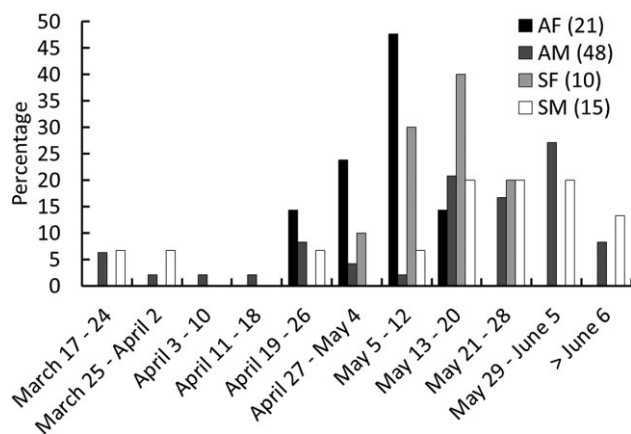


Figure 2 Difference between age and sex classes for spring emergence in 2012 at St. George Bat Cave. 6 June represents the 95th percentile of the distribution so emergence events recorded after 6 June are combined into one bin for clarity. AF = adult female, AM = adult male, SF = subadult female, SM = subadult male. Numbers in brackets indicate sample size.

no significant influence of sex on hibernation duration for the subset of bats we caught, weighed and tagged on 17 September 2011 after controlling for BCI and emergence date ($P > 0.05$).

There was a significant effect of age/sex class on fall activity ($H = 9.5$, $n = 111$, $P = 0.02$), with adult males ($n = 51$) active significantly later than adult females ($n = 19$; $U = 271.5$, Bonferroni-adjusted $\alpha = 0.0083$, $P = 0.005$, Fig. 1), while no other pairwise comparisons were significant (Table 3).

Discussion

As we predicted, fall mating and desynchronization of reproductive investment for adult males and females was reflected in the hibernation phenology of *M. lucifugus*. We found that, in contrast to hibernators that mate in spring, adult females emerged earlier than both adult males and subadult females. Also consistent with our predictions, females with the largest fall fat stores emerged earliest and adult males were active significantly later than adult females.

Emergence patterns of adult bats reversed patterns typically seen in other hibernators with adult females emerging earlier than males. Davis & Hitchcock (1965) found a similar pattern for banded bats from Aeolus Cave in Southwestern

Vermont (UTMs = 18T 659240 4789400) although timing of female emergence was *c.* 2 weeks later at our northern study site. The benefits of arriving early at maternity colonies, and having young as early as possible, are potentially large since early parturition dates increase the chance of offspring survival. Embryonic growth rates are influenced by ambient temperature (T_a) in bats so exploiting warm spring days, and opportunities for passive heating in maternity roosts, may advance parturition and save energy for mother bats (Geiser & Drury, 2003; Lausen & Barclay, 2006; Warnecke & Geiser, 2010). Although T_a in maternity roosts will be more variable and less predictable than in hibernacula, on warm days maternity roosts can reach temperatures exceeding 35°C, and are often >8°C warmer than T_a (Brittingham & Williams, 2000; Lausen & Barclay, 2006; Willis & Brigham, 2007). For the other demographics, remaining in hibernation later in spring could reduce risks of unpredictable spring weather and predation (Bieber & Ruf, 2009; Stawski & Geiser, 2010). For females, although maximum spring T_a has potential to be higher in maternity roosts compared with hibernacula, minimum T_a could also be dramatically colder. Considerable energy reserves may be necessary to survive cold spring weather as torpid metabolic rate must increase when T_a falls below the minimum T_b set point (Hock, 1951). Together, these results support Michener's (1983) hypothesis that early emergence of male ground squirrels is driven by reproductive pressure and highlight the influence of reproductive timing on hibernation phenology.

We also found that energy reserves influenced emergence phenology with females in the best fall condition emerging earliest in spring. This supports the hypothesis that early emergence is a 'high risk/high reward' strategy with fat bats the best equipped to meet the high risk of cold spring weather. Pregnant bats may need to enter torpor and delay pregnancy during inclement weather and food shortage (Racey, 1973; Racey & Swift, 1981; Willis, Brigham & Geiser, 2006), but once conditions improve, normal activities and offspring growth can resume quickly (Willis *et al.*, 2006). That subadult females also emerged later than adult females could reflect their smaller pre-hibernation fat reserves (Kunz, Wrazen & Burnett, 1998) or the fact that only some subadult females mate in their first year (Schowalter *et al.*, 1979; Frick *et al.*, 2010a). Thus, most subadult females may face less pressure than adult females to emerge early after their first hibernation.

Emergence dates of adult females were substantially less variable than those of adult and subadult males. This is con-

Table 3 Pairwise comparisons for fall activity, emergence and hibernation duration by demographic

	Fall activity			Emergence			Duration		
	AM	AF	SM	AM	AF	SM	AM	AF	SM
AF	U = 271.5 P = 0.005	–	–	U = 259.0 P = 0.001	–	–	U = 279.0 P = 0.003	–	–
SM	U = 518.5 P = 0.0913	U = 117.5 P = 0.041	–	U = 0.0 P = 1.0	U = 78.0 P = 0.011	–	U = 412.5 P = 0.397	U = 106.5 P = 0.182	–
SF	U = 492 P = 0.589	U = 119.5 P = 0.029	U = 186.5 P = 0.539	U = 287.5 P = 0.328	U = 41.5 P = 0.007	U = 56.00 P = 0.292	U = 316.0 P = 0.118	U = 87.00 P = 0.447	U = 61.0 P = 0.437

a = 0.0083. *U* = Kruskal–Wallis test statistic, AF = adult female, AM = adult male, SF = subadult female, SM = subadult male. Significant results are bolded.

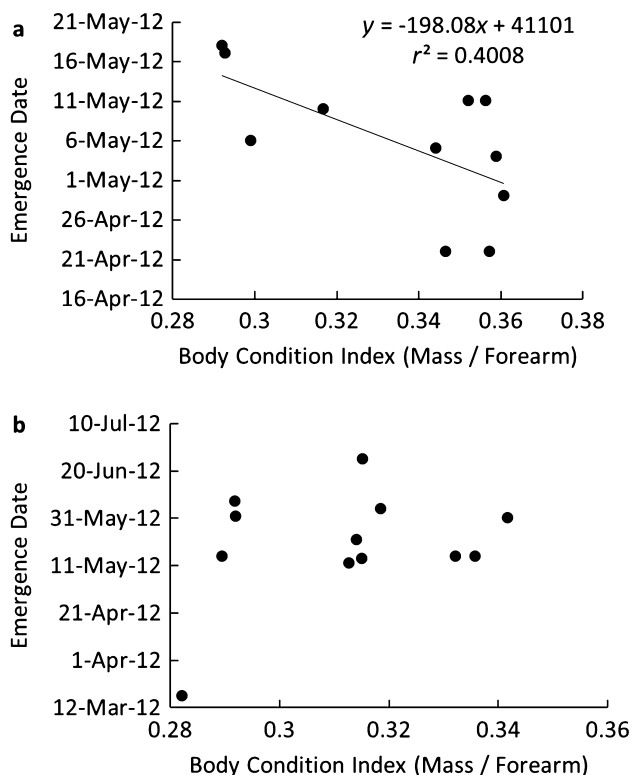


Figure 3 Relationship between emergence dates in spring 2012 for bats captured on 17 September 2011 and fall body condition indices at capture for little brown bats *Myotis lucifugus* at St. George Bat Cave. (a) Adult females; (b) adult males.

sistent with stabilizing selection on female emergence timing due to the trade-off between benefits of early emergence and costs of encountering inclement spring weather. Interestingly, although delayed by 1–2 weeks, emergence dates of juvenile females were distributed similarly to adult females, even though most subadult females do not reproduce. This could reflect sex-specific, and potentially heritable, sex difference in emergence date, given that emergence timing is heritable in at least one other hibernator (Lane *et al.*, 2011). Male *M. lucifugus* appears to have more flexibility in emergence

timing than females but factors driving their decisions to emerge remain unclear. Some males emerged as early as 19 March 2012 during a brief period of unseasonably warm weather when daily maxima reached 25°C (Fig. 1), dramatically exceeding previous *T_a* records for the area by 9°C. Interestingly, however, despite what is presumably strong pressure on females for early emergence, no females responded to these unusually warm conditions. The cave entrance is typically still snow covered in March with the closest weather station in Hodgson, Manitoba (<50 km) reporting only 3 of the last 20 years as snow free on 17 March (Environment Canada 2012). As snow melts earlier with climate change, bats may adjust emergence timing, but as for Columbian ground squirrels, this could lead to reduced survival if spring weather remains unpredictable (Lane *et al.*, 2012). Earlier springs also have the potential to shift the timing of parturition. Timing of the formation of maternity colonies of the Ozark big-eared bat *Corynorhinus townsendii ingens* varies from year to year, presumably with spring weather (Clark, Clark & Leslie, 2002).

There are a number of possible explanations for the longer period of activity by male bats in the fall. First, males that are active late in the fall could maximize reproductive interactions by mating with the few females that are still active or by entering multiple hibernacula to mate with torpid females. Second, since males undergo expensive spermatogenesis and mate in late summer/fall, they may need to compensate for this energetic cost of reproduction by remaining active to forage (Gustafson, 1979; Hosken *et al.*, 1998). Females in fall may prioritize energy accumulation in order to enter hibernation with enough fat to support pregnancy after spring emergence (Jonasson & Willis, 2011) and, without the cost of spermatogenesis, females may also be able to obtain adequate mass for hibernation sooner than males.

Patterns of phenology we observed suggest that females and males may experience differential mortality and reproductive consequences from WNS (Jonasson & Willis, 2011). The low variability of female emergence dates we observed supports the hypothesis that emergence timing reflects a trade-off between reproduction and survival. Emerging early is likely beneficial for reproduction but emerging too early will be detrimental. Given that WNS advances emergence timing, even if bats survive and have sufficient fat to initiate pregnancy in spring, a higher likelihood of encountering

unpredictable spring weather may limit female reproductive success and spring survival. Hibernation duration for bats in our study (230–240 days) is a month longer than the <200 days reported for any other bat population (e.g. Fenton, 1970). It has been suggested that bats in northern climates will experience high mortality from WNS compared with southern populations because early-emerging bats must survive longer with no access to food (Flory *et al.*, 2012). Although this is a reasonable prediction, northern populations have likely evolved characteristics (e.g. ability to carry more fat) to help them hibernate through longer winters. Therefore, although northern populations are clearly suffering tremendous mortality from WNS (Frick *et al.*, 2010b; Langwig *et al.*, 2012), they may fare better than some predictions suggest, especially in years with early springs.

We found that, as in better studied rodent and marsupial hibernators, demographic variation in hibernation phenology corresponded with the mismatched reproductive timing of male and female bats. Decoupling of mating with fertilization appears to have reversed phenological patterns compared with other species and led to the evolution of differences in emergence behaviour of males and females. Individual females apparently balance advantages of early parturition and possible access to passively and socially heated maternity roosts against risks of predation and unpredictable spring weather and food availability. Males appear to delay emergence until weather conditions are highly favourable. Future research is needed to understand cues employed by bats to make decisions about emergence. Climate change may benefit females by allowing earlier emergence and, consequently, earlier parturition dates. This could allow northward range expansion for little brown bats that may currently be limited by winter duration and hibernaculum temperature (Humphries *et al.*, 2002). However, if climate change reduces predictability of spring weather, bats that respond to warmer T_a by emerging could face reduced chance of survival and reproductive success.

Acknowledgements

We thank the University of Winnipeg Bat Lab and volunteers for help with fieldwork, and W. Frick, S. Lingle, M.B. Fenton and an anonymous reviewer for excellent comments on earlier drafts. Funding was provided by a Natural Sciences and Engineering Research Council (NSERC) Canada Graduate Scholarship, and a Manitoba Graduate Scholarship to K.J.O.N., and by grants to C.K.R.W. from NSERC, the Canada Foundation for Innovation, Manitoba Hydro, and the University of Winnipeg Chancellor's Research Chair in Wildlife Health.

References

Bieber, C. & Ruf, T. (2009). Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* **96**, 165–171.

Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T.H.,

Darling, S.R., Gargas, A., Niver, R., Okoniewski, J.C., Rudd, R.J. & Stone, W.B. (2009). Bat white-nose syndrome: an emerging fungal pathogen? *Science* **323**, 323–323.

Blumstein, D.T. (2009). Social effects on emergence from hibernation in yellow-bellied marmots. *J. Mammal.* **90**, 1184–1187.

Brittingham, M.C. & Williams, L.M. (2000). Bat boxes as alternative roosts for displaced bat maternity colonies. *Wildl. Soc. B.* **28**, 197–207.

Buchanan, G.D. (1987). Timing of ovulation and early embryonic development in *Myotis lucifugus* (Chiroptera: Vespertilionidae) from northern central Ontario. *Am. J. Anat.* **178**, 335–340.

Charmantier, A. & Gienapp, P. (2013). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evol. Appl.* **7**, 15–28.

Clark, B.S., Clark, B.K. & Leslie, D.M.J. (2002). Seasonal variation in activity patterns of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*). *J. Mammal.* **83**, 590–598.

Davis, W.H. & Hitchcock, H.B. (1965). Biology and migration of the bat, *Myotis lucifugus*, in New England. *J. Mammal.* **46**, 296–313.

Environment Canada (2012). Monthly data report 1982 - 2012, Hodgson2. Retrieved from http://climate.weather.gc.ca/climateData/monthlydata_e.html?timeframe=3&Prov=&StationID=3745&mlyRange=1966-01-01%7C2007-11-01&Year=1982&cmdB1=Go#.

Fenton, M.B. (1970). Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. *Life Sci. Contrib. R. Ont. Mus.* **77**, 1–34.

Flory, A.R., Kumar, S., Stohlgren, T.J. & Cryan, P.M. (2012). Environmental conditions associated with bat white-nose syndrome mortality in the north-eastern United States. *J. Appl. Ecol.* **49**, 680–689.

Frick, W.F., Reynolds, D.S. & Kunz, T.H. (2010a). Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *J. Anim. Ecol.* **79**, 128–136.

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M. & Kunz, T.H. (2010b). An emerging disease causes regional population collapse of a common North American bat species. *Science* **329**, 679–682.

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239–274.

Geiser, F. (2013). Hibernation. *Curr. Biol.* **23**, R188–R193.

Geiser, F. & Drury, R.L. (2003). Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *J. Comp. Physiol. [B.]* **173**, 55–60.

Gustafson, A.W. (1979). Male reproductive patterns in hibernating bats. *J. Reprod. Fertil.* **56**, 317–331.

Hock, R.J. (1951). Metabolic rates and body temperatures of bats. *Biol. Bull.* **101**, 289–299.

- Hosken, D.J., Blackberry, M.A., Stewart, T.B. & Stucki, A.F. (1998). The male reproductive cycle of three species of Australian vespertilionid bat. *J. Zool. (Lond.)* **245**, 261–270.
- Humphrey, S.R. & Cope, J.B. (1976). Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. *Am. Soc. Mammal.* **4**, 1–79.
- Humphries, M.M., Thomas, D.W., Hall, C.L., Speakman, J.R. & Kramer, D.L. (2002). The energetics of autumn mast hoarding in eastern chipmunks. *Oecologia* **133**, 30–37.
- Humphries, M.M., Thomas, D.W. & Kramer, D.L. (2003). The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiol. Biochem. Zool.* **76**, 165–179.
- Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D. (2000). Climate change is affecting altitudinal migrant and hibernating species. *PNAS* **97**, 1630–1633.
- Jonasson, K.A. & Willis, C.K.R. (2011). Changes in body condition of hibernating bats support the thrifty female hypothesis and predict consequences for populations with white-nose syndrome. *PLoS ONE* **6**, e21061.
- Jonasson, K.A. & Willis, C.K.R. (2012). Hibernation energetics of free-ranging little brown bats. *J. Exp. Biol.* **215**, 2141–2149.
- Körtner, G. & Geiser, F. (1998). Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* **113**, 170–178.
- Kunz, T.H., Wrazen, J.A. & Burnett, C.D. (1998). Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). *Ecoscience* **5**, 8–17.
- Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O., Coltman, D.W., Buoro, M., Raveh, S. & Dobson, F.S. (2011). A quantitative genetic analysis of hibernation emergence date in a wild population of Columbian ground squirrels. *J. Evol. Biol.* **24**, 1949–1959.
- Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O. & Dobson, F.S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**, 554–558.
- Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H. & Kilpatrick, A.M. (2012). Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecol. Lett.* **15**, 1050–1057.
- Lausen, C.L. & Barclay, R.M.R. (2006). Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *J. Mammal.* **87**, 362–370.
- Lorch, J.M., Meteyer, C.U., Behr, M.J., Boyles, J.G., Cryan, P.M., Hicks, A.C., Ballman, A.E., Coleman, J.T.H., Redell, D.N., Reeder, D.M. & Blehert, D.S. (2011). Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* **480**, 376–378.
- Lyman, C.P., Willis, J.S., Malan, A. & Wang, L.C.H. (1982). *Hibernation and Torpor in mammals and birds*. New York: Academic Press.
- McRitchie, W.D. & Monson, K.M. (2000). *Caves and Karst in Manitoba's Interlake Region from Surveys Conducted by the Speleological Society of Manitoba*. Winnipeg: Speleological Society of Manitoba.
- Michener, G.R. (1978). Effect of age and parity on weight gain and entry into hibernation in Richardson's ground squirrels. *Can. J. Zool.* **56**, 2573–2577.
- Michener, G.R. (1979). The circannual cycle of Richardson's ground squirrels in Southern Alberta. *J. Mammal.* **60**, 760–768.
- Michener, G.R. (1983). Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? *Behav. Ecol. Sociobiol.* **14**, 29–38.
- Michener, G.R. (1998). Sexual differences in reproductive effort of Richardson's ground squirrels. *J. Mammal.* **79**, 1–19.
- Murie, J.O. & Boag, D.A. (1984). The relationship of body weight to overwinter survival in Columbian ground squirrels. *J. Mammal.* **65**, 688–690.
- Pearce, R.D., O'Shea, T.J. & Wunder, B.A. (2008). Evaluation of morphological indices and total body electrical conductivity to assess body composition in big brown bats. *Acta Chiropt.* **10**, 153–159.
- Pfeiffer, B. & Mayer, F. (2012). Spermatogenesis, sperm storage and reproductive timing in bats. *J. Zool.* **289**, 77–85.
- Racey, P.A. (1973). Environmental factors affecting the length of gestation in heterothermic bats. *J. Reprod. Fertil. Suppl.* **19**, 175–189.
- Racey, P.A. (1974). Ageing and assessment of reproductive status of Pipistrelle bats, *Pipistrellus pipistrellus*. *J. Zool.* **173**, 264–271.
- Racey, P.A. & Entwistle, A.C. (2000). Life-history and reproductive strategies of bats. In *Reproductive biology of bats: 363–414*. Crichton, E.G. & Krutzsch, P.H. (Eds). San Diego: Academic Press.
- Racey, P.A. & Swift, S.M. (1981). Variations in gestation length on a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *J. Reprod. Fertil.* **61**, 123–129.
- Reynolds, D.S., Sullivan, J.C. & Kunz, T.H. (2009). Evaluation of total body electrical conductivity to estimate body composition of a small mammal. *J. Wildl. Mgmt.* **73**, 1197–1206.
- Schowalter, D.B., Gunson, J.R. & Harder, L.D. (1979). Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. *Can. Field Nat.* **93**, 243–251.
- Stawski, C. & Geiser, F. (2010). Fat and fed: frequent use of summer torpor in a subtropical bat. *Naturwissenschaften* **97**, 29–35.
- Thomas, D.W., Fenton, M.B. & Barclay, R.M.R. (1979). Social behaviour of the little brown bat, *Myotis lucifugus*. *Behav. Ecol. Sociobiol.* **6**, 129–136.
- United States Fish and Wildlife Service (USFWS). (2011). National White-nose Syndrome Decontamination Protocol. Retrieved from <https://www.whitenosesyndrome.org/resource/revised-decontamination-protocol-june-25-2012>

- Visser, M.E. & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proc. Roy. Soc. B.* **272**, 2561–2569.
- Warnecke, L. & Geiser, F. (2010). The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions. *J. Comp. Physiol. [B.]* **180**, 437–445.
- Warnecke, L., Turner, J.M., Bollinger, T.K., Lorch, J.M., Misra, V., Cryan, P.M., Wibbelt, G., Blehert, D.S. & Willis, C.K.R. (2012). Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *PNAS.* **109**, 6999–7003.
- Willis, C.K.R. & Brigham, R.M. (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behav Ecol Sociobiol.* **62**, 97–108.
- Willis, C.K.R., Brigham, R.M. & Geiser, F. (2006). Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* **93**, 80–83.
- Wimsatt, W.A. & Kallen, F.C. (1957). The unique maturation response of the Graafian follicles of hibernating vespertilionid bats and the question of its significance. *Anat. Rec.* **129**, 115–131.