Survey Methods for Monitoring Bat Populations
2024 *Journal of North American Bat Research* Special Issue 1:1–10

Fluctuations in Bat-house Colony Size May Hamper Estimation of Population Changes

Robert M. R. Barclay[1,*], Thiago A. Monteiro[1], Erin N. Miller[1], and Lara E. Hiles[1]

Abstract - One method of assessing changes in bat population sizes is to count individuals emerging from roosts. Government agencies and conservation organizations use such counts. We conducted almost nightly counts at a *Myotis lucifugus* (Little Brown Bat) maternity colony in Calgary, Alberta, as well as 2–3 counts per week at another Little Brown Bat maternity colony in the Rocky Mountains west of Calgary. In both cases, the number of bats fluctuated widely from night to night, especially before parturition had occurred (Calgary colony, 8–154 bats; Rocky Mountains colony, 161–681 bats). After the start of parturitions, fluctuations were smaller, but still considerable (Calgary, 59–152 bats; Rocky Mountains, 197–464). This suggests that single, or even several, emergence counts conducted annually, as is often recommended, may not accurately document changes in colony size from year to year.

Introduction

Monitoring how population sizes of organisms respond to short- and long-term changes to their environment from such things as natural disasters (e.g., fires, floods), habitat loss, and climate change, is important for management and conservation. Populations of bat species that form maternity colonies or hibernate in permanent structures, such as caves, may be relatively easy to monitor repeatedly (e.g., Frick et al. 2010, Hooton et al. 2023). Other species are more difficult to monitor accurately because they form colonies in less permanent structures, such as trees, or display fission-fusion colony behaviors in which individuals move asynchronously among several roosts (e.g., Garroway and Broders 2007, Olson and Barclay 2013, Willis and Brigham 2004). Some species can be monitored by measuring echolocation activity (e.g., North American Bat Monitoring Program 2024). However, not all species of bats are unambiguously identifiable via their echolocation calls (Barclay 1999, Russo et al. 2018).

Some synanthropic species of bats regularly form maternity colonies in buildings and/or bat houses (Lausen et al. 2023, Lewis 1995, Rueegger 2016). Various government agencies and non-governmental organizations have established monitoring protocols to track population changes of colonies in these structures. These protocols frequently involve public participation and are thus useful in engaging citizen scientists and increasing public awareness of bats and the environmental challenges they face, such as white-nose syndrome. It is often recommended that several counts of bats emerging from a maternity-colony roost take place per year to increase the accuracy of population estimates (Alberta Community Bat Program 2023, Canada Bat Box Project 2024, Community Bat Programs of BC 2023, Conserve Wildlife Foundation of New Jersey 2024, Maine Department of Inland Fisheries and Wildlife 2024, New Hampshire Fish and Game Department 2024, Vermont Fish and Wildlife Department 2024, Wisconsin Department of Natural Resources 2024). Multiple counts are appropriate because the number of emerging bats changes, for example, as the colony builds up in the spring and once the juveniles start to fledge later in the summer.

[1]Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1B4, Canada.
*Corresponding author - barclay@ucalgary.ca.

Associate Editor: Aaron Corcoran, University of Colorado

Over 4 years, we counted *Myotis lucifugus* (Le Conte) (Little Brown Bat) emerging from a maternity colony occupying a bat house in a city park in Calgary, Alberta, Canada. Multiple counts were conducted per year, and we noted that the number of bats emerging varied greatly, even among counts conducted within a few days of each other. We thus conducted more frequent emergence counts at this bat house, as well as at a larger colony in the Rocky Mountains west of Calgary. Our goals were to determine how accurate individual emergence counts might be in assessing changes in population size over several years, and what factors influenced changes in colony sizes over the summer. We hypothesized that numbers fluctuate in response to ambient temperature extremes. In hot conditions, bats may disperse among multiple roosts to prevent over-heating. In cold conditions, they may disperse to allow individuals to go into torpor as a way to conserve energy (Bergeson et al. 2021, Patriquin et al. 2016). We also hypothesized that human disturbance might cause bats to vacate the bat house in the city park. For this urban colony, we therefore predicted that numbers would decline on weekends due to increased human activity.

Methods

We visually counted Little Brown Bats emerging from the roosts used by 2 maternity colonies. In 2021, we counted bats emerging from 3 wooden, multi-chamber bat houses attached to the wall of the Discovery and Information Centre in Peter Lougheed Provincial Park, Alberta (PLDC; 50º40’48”N, 115º6’36”W). The bat houses were 2–3 m apart, and we considered the bats to be a single maternity colony because radio-tagged reproductive females moved among the 3 boxes (Monteiro 2023). The bat houses were in a restricted area behind the park visitors’ center, and thus had limited disturbance from the public. The surrounding area was mature coniferous forest.

From 2019 to 2023, we counted bats emerging from a wooden, single-chamber bat house in Bowness Park in Calgary (51º6’0”N, 114º12’0”W). The bat house was 5 m above the ground, attached to a tree immediately beside a walking trail along the Bow River. The park is popular with the public and attracts large gatherings during the summer, especially from Friday through Sunday and on holidays.

At both sites, trained observers with several years experience, counted the number of bats emerging from mid-May to the end of August. Emergence occurred under relatively bright ambient conditions. Counts rarely differed between observers, and if they did, a mean number was recorded. At PLDC, 2–3 observers counted emerging bats every 1–5 days (excluding rainy evenings). Exit counts at the Bowness bat house from 2019 to 2022 involved 1–2 observers and occurred every 5–7 days. In 2023, observers counted emergence at the Bowness bat house every 1–2 days, again excluding rainy evenings. At both colonies, observers arrived at least 10 min prior to the anticipated start of emergence and stood silently, no closer than 10 m from the bat houses. Counting continued until no further bats emerged for a minimum of 10 min. We then visually checked the bat houses from the ground with a flashlight to ensure that all bats had emerged, and to look for non-volant juveniles.

We created scatter plots for visual inspection of the relationships between the Bowness bat house colony size in 2023 and each predictor variable—days since the colony became established (28 May) and daily maximum and minimum ambient temperatures (Government of Canada 2024). Polynomial regression was employed to model potential nonlinear trends and a multiple linear regression model was constructed using the lm() function and visualized using the package ggplot2 (version 3.3.5) in the program R (version 3.6.2). The model’s residuals were checked for normality and homoscedasticity through a histogram

and fitted versus residual plot. Autocorrelation in model residuals was examined using the acf() function, and additional coefficient testing was performed using the coeftest() and vcovHC() functions. A lagged variable was also introduced (the number of bats from the following day) to investigate the effect of correlation between subsequent observations. Alpha was set at 0.05, and all means are stated as ± *SD*.

Results

Our emergence counts at the Bowness bat house fluctuated considerably within each year from 2019 through 2022 (Table 1). This occurred during both the pre-parturition period in May and June and after the first juveniles (pups) were observed in the box. The maximum number of volant bats occupying the box consistently occurred during the pre-parturition period each year. In each of the 4 years, emergence counts during the pre-parturition period varied from as low as 0–25 bats, to as high as 100–132. During the post-parturition period, the minimum number of bats emerging was larger (25–56), while the maximum was generally smaller (60–112) (Table 1).

The more frequent emergence counts in 2023 also revealed large fluctuations in the colony size (Fig. 1). The colony was well established by 17 May (77 bats). Numbers then varied between 8 and 154 bats during the pre-parturition period (17 May–23 June). For example, counts occurred every night between 2 and 8 June, with numbers initially increasing from 8 to 122 bats, then declining to 88 and increasing again to 154.

Table 1. Number of adult Little Brown Bats counted emerging from the bat house in Bowness Park, Calgary, Alberta on different dates in 2019–2022. "No pups" indicates that no juveniles were observed in the bat house after emergence had finished (i.e., pre-parturition). "Pups" indicates that non-volant juveniles were observed in the bat house after emergence had finished. For 2023, the means and maxima for the 2 periods of the season are presented. See Figure 1 for the complete 2023 data.

Year	Date	#adults	Notes	Mean	SD	Maximum
2019	8 June	25	no pups			
	16 June	102	no pups	62.7	38.5	102
	23 June	61	no pups			
2020	18 May	10	no pups			
	20 May	55	no pups			
	24 May	0	no pups			
	25 May	11	no pups	36.3	34.1	100
	28 May	12	no pups			
	3 June	46	no pups			
	11 June	100	no pups			
	25 June	56	no pups			
	2 July	60	pups			
	8 July	59	pups	58.5	1.73	60
	15 July	59	pups			
	21 July	56	pups			

From the first evidence of pups in the bat house (24 June 2023) to the start of colony dispersal (approximately 1 August), the colony size was initially relatively stable with between 122–152 bats emerging. It then dropped from 126 to 67 and remained between 59 and 102 bats from 29 June to 5 July. It was again stable (51–65 bats) from 9 to 26 July, which included the time when the first juveniles likely started to fly (approximately 3 weeks after birth; Fenton and Barclay 1980, Lausen et al. 2023).

As part of another study (R.M.R. Barclay, University of Calgary, Calgary, Alberta, Canada, unpubl. data), 13 adult female Little Brown Bats from the Bowness bat house were fitted with radio-transmitters. When not roosting in the bat house, these tagged bats roosted in 7 different buildings, 1 other bat house, and 1 tree, all within 3 km of the maternity colony bat house.

Table 1, continued. Number of adult Little Brown Bats counted emerging from the bat house in Bowness Park, Calgary, Alberta on different dates in 2019–2022. "No pups" indicates that no juveniles were observed in the bat house after emergence had finished (i.e., pre-parturition). "Pups" indicates that non-volant juveniles were observed in the bat house after emergence had finished. For 2023, the means and maxima for the 2 periods of the season are presented. See Figure 1 for the complete 2023 data.

Year	Date	#adults	Notes	Mean	SD	Maximum
2021	31 May	63	no pups			
	3 Jun	108	no pups			
	9 June	6	no pups			
	14 June	132	no pups	78.7	47.9	132
	18 June	81	no pups			
	22 June	128	no pups			
	28 June	33	no pups			
	5 July	112	pups			
	11 July	36	pups			
	15 July	48	pups	65.8	29.8	112
	22 July	56	pups			
	27 July	77	pups			
2022	29 May	44	no pups			
	1 June	46	no pups			
	8 June	15	no pups	68.3	38.6	112
	18 June	112	no pups			
	23 June	95	no pups			
	28 June	98	no pups			
	5 July	25	pups			
	10 July	100	pups	72.3	41.2	100
	16 July	92	pups			
2023			no pups	88.7	42.4	154
			pups	101.9	29.2	152

There was no evidence that human activity on weekends caused bats to leave the bat house. Indeed, the opposite was apparent. Over 8 weekends involving emergence counts on Friday and Sunday, numbers increased from Friday to Sunday by 1.7–850% (mean 193 ± 325%) on 6 occasions and declined twice by 1.7 and 5.1%.

During the pre-parturition period, the number of bats emerging from the bat box varied significantly (multiple regression with date and daily minimum and maximum temperature: $R^2 = 0.79$, $F_{3, 16} = 19.87$, $P < 0.001$). We observed significant correlation between subsequent observations of nightly emergence counts within the original model, possibly due to previous day and temperature variables. However, introducing a lagged variable into the model, whereby the emergence count of the previous night was used with the following day's independent variables, confirmed that the significance of the model persisted ($R^2 = 0.82$, $F_{4, 14} = 16.45$, $P < 0.001$). Additionally, the updated model confirmed that the day a count was conducted still significantly influenced the colony size estimate ($t_{14} = 3.38$, $P < 0.001$). Numbers initially increased and then decreased with date ($t_{16} = 4.87$, $P < 0.001$), and were higher with higher minimum ambient temperature ($t_{16} = 3.24$, $P = 0.005$). There was no significant effect of maximum temperature ($t_{16} = 1.92$, $P = 0.07$). After the first pups were born, the numbers emerging from the roost also varied significantly ($R^2 = 0.55$, $F_{3, 30} = 12.3$, $P < 0.001$) but only with date, with numbers declining over time ($t_{30} = 5.36$, $P < 0.001$). Neither maximum nor minimum daily temperature had a significant effect ($P > 0.05$).

It was not possible to determine when the first juveniles started to fly, but all were volant by 31 July 2023, as evidenced by the fact that no bats were left in the Bowness bat box after emergence. This was consistent with previous years (2020–2022) when the first observation of all bats emerging occurred between 2 and 5 August.

Although emergence counts at the PLDC bat boxes were conducted less often than at the Bowness bat box, a similar pattern was evident, with significant fluctuations in number of

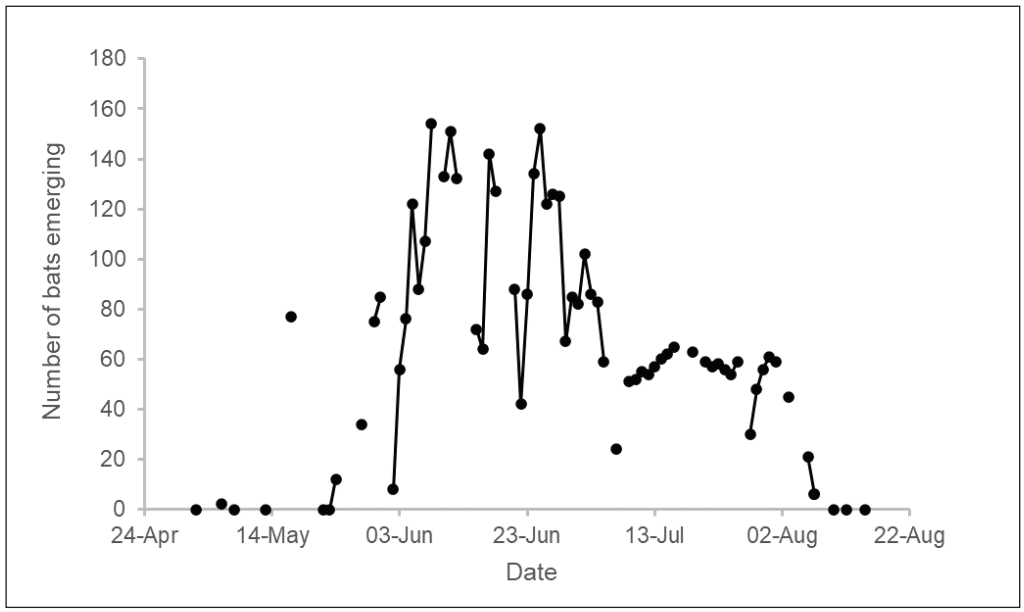

Fig. 1. Number of Little Brown Bats counted emerging from the Bowness Park bat house in 2023. Gaps in the line indicate days when counts were not made. The first juveniles were seen in the bat box on 24 June.

bats (Fig. 2). Once the colony was established, exit counts ranged from 161 to 681 during the pre-parturition period (421.2 ± 166.5, n = 13), and from 197 to 464 after the first pups were born (285.0 ± 123.7, n = 4). As part of another project (Monteiro 2023), 29 adult females from the PLDC colony were radio-tagged. Sixteen of these, including both reproductive and non-reproductive females, switched back and forth between roosting in the PLDC bat boxes and in several cabins almost 4 km away.

To assess changes in colony sizes from year to year (e.g., in response to white-nose syndrome), various agencies recommend making several emergence counts each year to increase the reliability of the population estimates. Using the time frames for counts recommended by the Alberta Community Bat Program (2023) and the Canadian Bat Box project (2024), emergence counts at both colonies varied greatly each year (Table 2). The most relevant protocol for the Bowness colony is the one developed by the Alberta Community Bat Program (2023), which suggests 2 counts during the pre-fledging period (specifically 1 June–7 July) and 2 more after fledging of pups has started (15 July–7 August). Using these time frames and a random number generator to select specific emergence-count dates from the 2023 data, we developed 25 pairs of counts during each phase to assess how variable the average emergence counts would have been for the Bowness maternity colony, depending on the dates chosen for counts. For the pre-fledging period, the average of 2 randomly selected counts ranged from 65.5 to 134 individuals (94.4 ± 19.8). The mean was close to the overall mean for our nightly counts (96.5 ± 38.2), but with a smaller range compared to that of the nightly counts (8–154). For the fledging period, the averages of randomly selected pairs of counts ranged from 13.5 to 63 (50.8 ± 12.4). Again, the mean was close to the overall mean (50.5 ± 16.4), but the range was similar to that of the nightly counts (6–65).

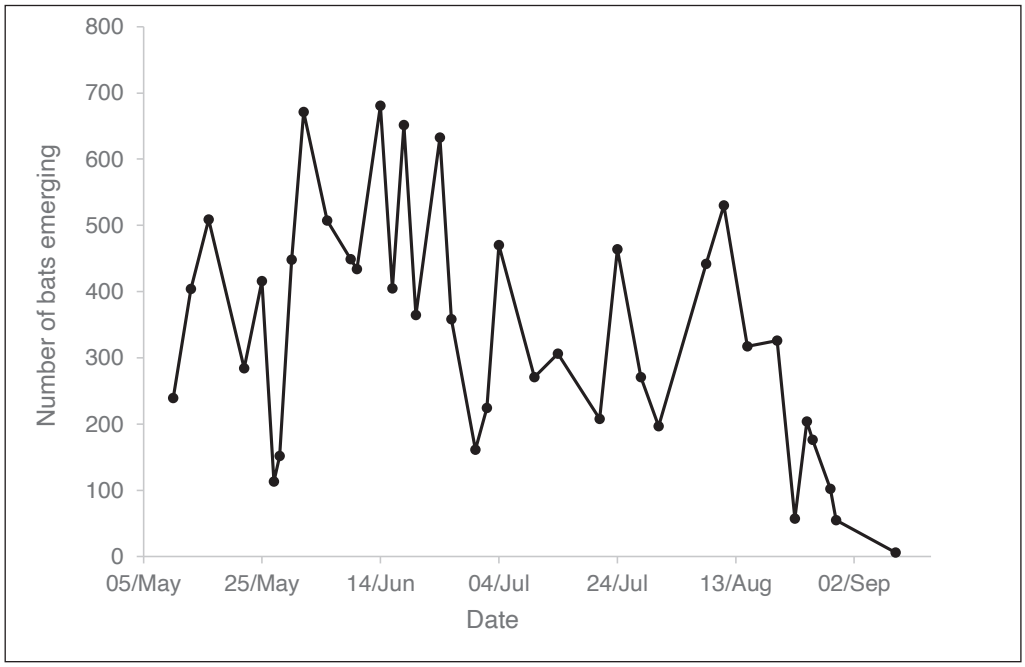

Fig. 2. Total number of Little Brown Bats counted emerging from the 3 bat houses on the Peter Lougheed Discovery Centre, Alberta, in 2021. The first juveniles were estimated to have been born on 6 July.

Discussion

In both maternity colonies of Little Brown Bats that we studied, the number of bats occupying each roost fluctuated greatly, even from one day to the next, during both the pregnancy and lactation stages. Although our data came from only 2 maternity colonies, colony size fluctuations also occur in Little Brown Bat maternity colonies occupying natural roosts, such as trees (Olson and Barclay 2013). These fluctuations also occur in other bat species and are related to a fission-fusion process whereby individuals move among

Table 2. Minimum and maximum emergence counts at the Bowness Park and Peter Lougheed Discovery Center (PLDC) bat houses, based on recommended dates for counts by the Alberta Community Bat Program (ACBP) and the Canadian Bat Box project; *n* is the number of emergence counts made during each time frame.

	Date range	Year	Min–Max	*n*
ACBP				
Bowness	1 June–7 July	2019	25–102	3
		2020	46–100	4
		2021	6–132	7
		2022	15–112	6
		2023	8–154	29
	15 July–7 August	2020	56–71	3
		2021	23–77	4
		2022	42–92	4
		2023	6–65	17
PLDC	1 June–7 July	2021	161–681	13
	15 July–7 August	2021	197–464	4
Canadian Bat Box Project				
Bowness	1–21 June	2019	25–102	2
		2020	46–100	3
		2021	6–132	4
		2022	15–112	3
		2023	8–154	15
	5 July–1 August	2020	56–59	3
		2021	36–112	5
		2022	25–100	5
		2023	24–65	22
PDLC	1–21 June	2021	365–681	8
	5 July–1 August	2021	197–464	6

roosts within their home range (e.g., Barclay and Kurta 2007, Lewis 1995, Patriquin and Ratcliffe 2016, Willis and Brigham 2004). Essentially, the colony of bats occupies multiple roosts rather than just 1. The reasons for roost switching vary and, as we found, include variation in ambient temperature that makes social thermoregulation more or less beneficial (Patriquin et al. 2016, Sunga et al. 2022). Although we found no evidence that human disturbance caused numbers in the Bowness Park bat house to fluctuate, human disturbance might influence numbers in other situations. Other factors, such as disturbance by predators, can also cause bats to move roosts (e.g., Barclay et al. 1982).

We expected that the number of bats emerging from the Bowness bat house would increase once juveniles started to fly, but this did not happen. This suggests that juveniles, and perhaps their mothers, moved from the box to other roosts in the area, although we have no data to support this. Exit counts at the PLDC were more variable during the post-parturition period, making it difficult to determine whether there was an increase once fledging started.

Assessing the number of bats in a maternity colony is challenging given the movement among roosts by individuals within a single colony. As we found, counting 1 roost multiple times results in fluctuating numbers of individuals. This complicates efforts to assess changes in population size over longer periods of time (i.e., years). Government agencies and other groups recommend performing 2–4 exit counts, split between the pre-fledging and post-fledging periods, to census the bats in a maternity roost of Little Brown Bats in a bat house or building (e.g., Alberta Community Bat Program 2023, Community Bat Programs of BC 2023, Conserve Wildlife Foundation of New Jersey 2024, Maine Department of Inland Fisheries and Wildlife 2024, New Hampshire Fish and Game Department 2024, Vermont Fish and Wildlife Department 2024, Wisconsin Department of Natural Resources 2024). The North American Bat Monitoring Program recommends a similar approach (Loeb et al. 2015). Given the fluctuations in bat numbers we found, 1 or 2 counts per period during a summer may lead to dramatically different estimates of colony size and thus over- or underestimate actual changes in size over the longer term.

Given our findings, if the goals of exit counts at bat maternity roosts include assessing population changes from year to year, we recommend that more counts need to be made than are currently recommended. While our study focused on Little Brown Bats, we suggest that multiple counts should also be conducted for other species that have a fission-fusion social system.

Acknowledgments

Our research in Calgary was conducted on the traditional territories of the peoples of Treaty 7, which include the Blackfoot Confederacy (comprised of the Siksika, the Piikani, and the Kainai First Nations), the Tsuut'ina First Nation, and the Stoney Nakoda (including Chiniki, Bearspaw, and Goodstoney First Nations). The City of Calgary is also home to the Métis Nation of Alberta (Districts 5 and 6). We also acknowledge that our work in Peter Lougheed Provincial Park was in the traditional territory of the Treaty 7 Nations of The Tsuut'ina Nation, the Stoney Nakoda Nation, comprised of the Chiniki, Bearspaw, Goodstoney and Wesley First Nations, and the Blackfoot Confederacy, including the Kainai-Blood Tribe, Siksika, Peigan-Piikani and Aamskapi Pikun. We recognize the Treaty 3 region of the Mètis Nation of Alberta. We thank S. Holroyd, T. Thompson, D. Maucieri and B. Steed for assistance counting bats emerging from the bat boxes. Funding was provided by the Natural Sciences and Engineering Research Council of Canada. We thank 2 anonymous reviewers for their careful review of the manuscript and helpful suggestions.

Literature Cited

Alberta Community Bat Program. 2023. Alberta bat roost reporting and monitoring instructions. Available online at www.albertabats.ca/wp-content/uploads/ACBP-Bat-Watch-Protocols-and-Forms-2023.pdf. Accessed 12 January 2024.

Barclay, R.M.R. 1999. Bats are not birds: A cautionary note regarding the use of echolocation for field identification of bats. Journal of Mammalogy 80:290–296.

Barclay, R.M.R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59, *In* M.J. Lacki, J.P. Hayes, and A. Kurta (Eds.). Bats in Forests: Conservation and Management. Johns Hopkins Press, Baltimore, MD. 329 pp.

Barclay, R.M.R., C.E. Thomson, and F.J.S. Phelan. 1982. Screech Owl, *Otus asio*, attempting to capture Little Brown Bats, *Myotis lucifugus*, at a colony. Canadian Field-Naturalist 96:205–206.

Bergeson, S.M., R.M. Brigham, and J.M. O'Keefe. 2021. Free-ranging bats alter thermoregulatory behavior in response to reproductive stage, roost type, and weather. Journal of Mammalogy 102:705–717.

Canada Bat Box Project. 2024. Canada Bat Box Project emergence count protocol. Available online at wcsbats.ca/Portals/211/OpenContent/Files/Emergence%20counts%20protocol.pdf?ver=2020-09-14-220707-797&timestamp=1600121240623. Accessed 11 January 2024.

Community Bat Programs of BC. 2023. Counting bats. Available online at https://bcbats.ca/get-involved/counting-bats/. Accessed 12 January 2024.

Conserve Wildlife Foundation of New Jersey. 2024. Summer bat count. Available online at www.conservewildlifenj.org/protecting/projects/bat/bat-count/. Accessed 12 January 2024.

Fenton, M.B., and R.M.R. Barclay. 1980. *Myotis lucifugus*. Mammalian Species 142:1–8.

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.

Garroway, C.J., and H.G. Broders. 2007. Nonrandom association patterns at Northern Long-eared Bat maternity roosts. Canadian Journal of Zoology 85:956–964.

Government of Canada, Environment and Natural Resources. 2024. Available online at climate.weather.gc.ca/climate_data/daily_data_e.html?StationID=50430. Accessed 29 July 2024.

Hooton, L.A., A.A. Adams, A. Cameron, E.E. Fraser, L. Hale, S. Kingston, M.B. Fenton, L.P. McGuire, E.F. Stukenholtz, and C.M. Davy. 2023. Effects of bat white-nose syndrome on hibernation and swarming aggregations of bats in Ontario. Canadian Journal of Zoology 101:886–895.

Lausen, C.L., D.W. Nagorsen, R.M. Brigham, and J. Hobbs. 2023. Bats of British Columbia. 2nd ed. Royal BC Museum, Victoria, BC, Canada. 375 pp.

Lewis, S.E. 1995. Roost fidelity of bats: A review. Journal of Mammalogy 76:481–496.

Loeb, S.C., T.J. Rodhouse, L.E. Ellison, C.L. Lausen, J.D. Reichard, K.M. Irvine, T.E. Ingersoll, J.T.H. Coleman, W.E. Thogmartin, J.R. Sauer, C.M. Francis, M.L. Bayless, T.R. Stanley, and D.H. Johnson. 2015. A plan for the North American Bat Monitoring Program (NABat). United States Department of Agriculture, Forest Service Research and Development, Southern Research Station, General Technical Report SRS-208:1–100.

Maine Department of Inland Fisheries and Wildlife. 2024. Bats. Available online at www.maine.gov/ifw/fish-wildlife/wildlife/species-information/mammals/bats.html. Accessed 12 January 2024.

Monteiro, T.A. 2023. The behaviour of reproductive female Little Brown Bats (*Myotis lucifugus*) in the Albertan Rocky Mountains. M.Sc. Thesis. University of Calgary, Calgary, AB, Canada. 135 pp.

New Hampshire Fish and Game Department. 2024. NH bat counts. Available online at www.wildlife.nh.gov/wildlife-and-habitat/nongame-and-endangered-species/bats-new-hampshire/nh-bat-survey. Accessed 12 January 2024.

North American Bat Monitoring Program. 2024. NABat North American Bat Monitoring Program. Available online at www.nabatmonitoring.org/. Accessed 24 January 2024.

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.

Patriquin, K.J., and J.M. Ratcliffe. 2016. Should I stay or should I go? Fission–fusion dynamics in bats. Pp. 65–103, *In* J. Ortega (Ed.). Sociality in Bats. Springer International Publishing, Cham, Switzerland. 301 pp.

Patriquin, K.J., M.L. Leonard, H.G. Broders, W.M. Ford, E.R. Britzke, and A. Silvis. 2016. Weather as a proximate explanation for fission-fusion dynamics in female Northern Long-eared Bats. Animal Behaviour 122:47–57.

Rueegger, N. 2016. Bat boxes – A review of their use and application, past, present and future. Acta Chiropterologica 18:276–299.

Russo, D., L. Ancillotto, and G. Jones. 2018. Bats are still not birds in the digital era: Echolocation call variation and why it matters for bat species identification. Canadian Journal of Zoology 96:63–78.

Sunga, J., Q.M.R. Webber, J. Humber, B. Rodrigues, and H.G. Broders. 2022. Roost fidelity partially explains maternity roosting association patterns in *Myotis lucifugus*. Animal Behaviour 194:67–78.

Vermont Fish and Wildlife Department. 2024. Summer maternity roost monitoring instructions. Available online at https://vtfishandwildlife.com/get-involved/volunteer/monitoring-bat-colonies. Accessed 12 January 2024.

Willis, C.K.R., and R.M. Brigham. 2004. Roost switching, roost sharing and social cohesion: Forest-dwelling Big Brown Bats, *Eptesicus fuscus*, conform to the fission-fusion model. Animal Behaviour 68:495–505.

Wisconsin Department of Natural Resources. 2024. Bat roost monitoring. Available online at wiatri.net/inventory/bats/volunteer/roosts/. Accessed 12 January 2024.