Journal of Mammalogy, 101(6):1542–1547, 2021
DOI:10.1093/jmammal/gyaa154
Published online January 6, 2021

Local trends in abundance of migratory bats across 20 years

Dana M. Green,* Liam P. McGuire, Mark C. Vanderwel, Craig K. R. Willis, Matthew J. Noakes, Shelby J. Bohn, Eric N. Green, and R. Mark Brigham

Department of Biology, Laboratory Building LB109, University of Regina, 3737 Wascana Parkway, Regina, SK S4S 0A2, Canada (DMG, ENG, RMB)
Department of Biological Sciences, University of Waterloo, 200 University Avenue West, Waterloo, ON, Canada N2L 3G1 (LPM)
Department of Biology, Laboratory Building LB248, University of Regina, 3737 Wascana Parkway, Regina, SK S4S 0A2, Canada (MCV)
DST-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, Department of Zoology and Entomology, University of Pretoria, Private Bag x20, Hatfield 0028, South Africa (MJN)
Department of Integrative Biology, University of Guelph, 50 Stone Road E, Guelph, ON N1G 2W1, Canada (SJB)
Department of Biology and Centre for Forest Inter-Disciplinary Research (C-FIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada (CKRW)

*Correspondent: dana.green.eco@gmail.com

Hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) are species of conservation concern because of the documented annual mortality that occurs at wind energy facilities. Several recent studies have predicted continental-scale declines of hoary bat populations due to interactions with wind turbines. We predicted a decrease in captures at a summer site over 20 years where researchers have captured bats using generally consistent methods. We developed a hierarchical Bayesian model to estimate the relative change in the expected number of captures while controlling for time of year, temperature, and netting effort. We found no decrease in the number of captures for either species. We suggest that the lack of decrease observed at our study site may be a result of compensatory immigration, despite potential broader-scale population declines.

Key words: compensatory immigration, conservation, *Lasionycteris noctivagans*, *Lasiurus cinereus*, migration, wind energy

Wind energy is a fast-growing, renewable energy resource having indirect positive effects on the environment (Leung and Yang 2012). While the benefits of wind energy are evident, wind turbines also can negatively affect wildlife (Arnett et al. 2008; Saidur et al. 2011). Bats and other volant wildlife are being killed by wind turbines (Arnett et al. 2008; Baerwald et al. 2008; Arnett and Baerwald 2013) potentially leading to population declines. While regional differences exist, most bat fatalities at wind energy facilities in the United States and Canada are comprised of three species: hoary bats (*Lasiurus cinereus*), eastern red bats (*Lasiurus borealis*), and silver-haired bats (*Lasionycteris noctivagans*) (Arnett and Baerwald 2013; Davy et al. 2020).

The most recent continental-scale estimates of fatality rates suggested that, as of 2012, there were more than 400,000 bats killed annually at wind energy facilities in North America (Arnett and Baerwald 2013; Hayes 2013). Since then, the number of wind energy facilities continue to increase, heightening concerns about the conservation of migratory bat populations (Winhold et al. 2008; Arnett and Baerwald 2013; Frick et al. 2017b). From 2000 to 2020, wind energy production has grown substantially, increasing from a capacity of 114 MW in 2000 to 13,413 MW in 2019 (CanWEA 2019) and in the United States from 2,502 MW in 2000 to 107,443 MW in 2019 (AWEA 2019). Alberta is the third largest wind energy producer in Canada and Saskatchewan is anticipating an increase in production of 377 MW by 2021, more than doubling the current output in the province (CanWEA 2019). As wind energy facilities become more abundant in North America, populations of migratory bats, especially hoary bats, could experience declines and potentially even extinction (Frick et al. 2017b). Estimating population size is challenging, particularly for migratory species that travel long distances during their annual cycle, are found across large geographic scales (Cryan 2003), and roost solitarily or in small colonies (O'Shea 1976; Willis and Brigham 2005; Kunz et al. 2007; Bohn 2017). In addition,

population trends can vary depending on geographic scale and environmental conditions, so considering entire populations or individual abundance at local scales may yield different trends (Royle et al. 2007; Thogmartin and Knutson 2007).

For the past 20 years, research on multiple bat species has occurred in Cypress Hills Interprovincial Park (hereafter Cypress Hills) in Canada, including work on two migratory species: hoary bats (e.g., Willis and Brigham 2005; Willis et al. 2006; McGuire et al. 2013) and silver-haired bats (e.g., Fraser 2011; Bohn 2017). Straddling the provincial border in southwestern Saskatchewan and southeastern Alberta, Cypress Hills rises 430 m above the surrounding prairie landscape (Kulig 1996). Beginning in the spring, hoary and silver-haired bats migrate to Cypress Hills and arrive in mid-June to give birth and raise their young (Willis and Brigham 2005; Willis et al. 2006; Fraser 2011; Bohn 2017). In addition, large numbers of hoary and silver-haired bats migrate through the prairie provinces each year (Baerwald et al. 2014) and therefore many migratory bats likely pass through Cypress Hills *en route* to other breeding grounds further north. Given recent analyses predicting continental-scale and regional declines of hoary bats (Frick et al. 2017b; Rodhouse et al. 2019; Davy et al. 2020), we aimed to use long-term data from the Cypress Hills to determine if patterns of abundance for migratory bats at this localized study site mirror the predictions for larger spatial scales. Patterns of abundance at Cypress Hills could reflect the general, continental- and regional-scale declines that have been reported (Frick et al. 2017b; Rodhouse et al. 2019) or, alternatively, could reflect smaller regional-scale processes affecting local abundance.

We collated capture data from various studies across 20 years (2000–2019) on migratory bats in Cypress Hills to assess temporal trends in abundance. We tested the hypothesis that long-term, local-scale abundance data collected from Cypress Hills would reflect the continental-scale population declines that have been suggested for migratory bats and predicted a decrease in migratory bat captures over the study period.

Materials and Methods

We compiled available summer capture data on silver-haired and hoary bats from Cypress Hills (Fig. 1). Our final data set included captures from June to August of 2000 – 2002; July to August in 2008; July 2009; and June to August in 2015, 2016, 2018, and 2019. All data were based on mist-net captures along a 10- to 15-km segment of Battle Creek in the West Block of Cypress Hills in southwestern Saskatchewan (49°34′N, 109°53′W). Battle Creek is the main water body bisecting the park and acts as a flyway and water resource for these bats. The Cypress Hills is unique in the prairie ecosystem of Saskatchewan because of historical geological processes that left the area as an uplifted glacial refugium. We collected weather data recorded by the nearest Environment Canada weather station in Cypress Hills (49°38′N, 109°30′W; climate.weather.gc.ca), approximately 17 km from our capture area along the Battle Creek. The vegetation of the park is 50% grassland, 45% woodland, and 5% wetland (Sauchyn 1993). The wooded areas are a mix of coniferous and deciduous trees; predominantly lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*—Widenmaier and Strong 2010).

The number of hoary and silver-haired bats captured each night (n = 171 nights) were recorded during the years when netting was undertaken (9 of the 20 years). Precision in the estimates of netting effort, defined as the number of net-hours per night (i.e., number of nets multiplied by the number of hours) varied by year, with known values in some years and relatively coarse estimates in other years. For example, in 2000 – 2002, before wind energy effects and possible decreases of migratory bats were widely appreciated, bats were captured for radiotelemetry studies of habitat selection and torpor expression (*L. cinereus*; e.g., Willis and Brigham 2005, 2006) rather than for estimates of abundance trends. Similarly, in 2018 the documentation of the numbers of nets and hours netted was not relevant to the study and therefore, these data were not precisely recorded. Thus, for 2000 – 2002 and 2018, overall net-hours were estimated based on a range of values. The researchers for those years estimated the minimum and maximum number of nets and number of hours nets were open per night, from which we derived a distribution of estimates for capture effort. Our netting effort variable was calculated as the log-product of the hours and number of nets. In the majority of years there were no records of the type of net (i.e., monofilament or 2-ply), the length of nets, or net height. Therefore, these were not considered in our calculation of netting effort.

We developed a hierarchical Bayesian model to estimate the relative change in the expected number of captures for each bat species between 2000 and 2019 while controlling for time of year, temperature, and our estimate of netting effort. The number of captures on a given night was modeled by a negative binomial distribution whose expected value was related to a linear combination of predictor variables through a log-link function. Our predictor variables included Julian date, year, minimum temperature, and log-effort. The effect of year included both a linear trend and a random intercept that accounted for year-to-year differences in captures around the linear trend. Log-effort was modeled as a latent variable whose true value was uncertain in years when nightly effort was not recorded. For those years, log-effort was modeled as a normal random variable whose distribution approximated the estimated range of net-hours on a natural log scale (3.11 ± 0.26 for 2000–2002; 1.39 ± 0.36 for 2018).

We fit our statistical model using the "brms" (version 2.12.0) library for the R programming language (version 3.6.2). The posterior distribution of model parameters was estimated using Markov chain Monte Carlo (MCMC) sampling with four chains of 8,000 iterations, the first 4,000 of which were discarded during a warm-up period. All parameters were checked for convergence and suitable effective sample size. To investigate the potential of subadult captures inflating capture rates, we ran an additional model excluding data from captures after 22nd July

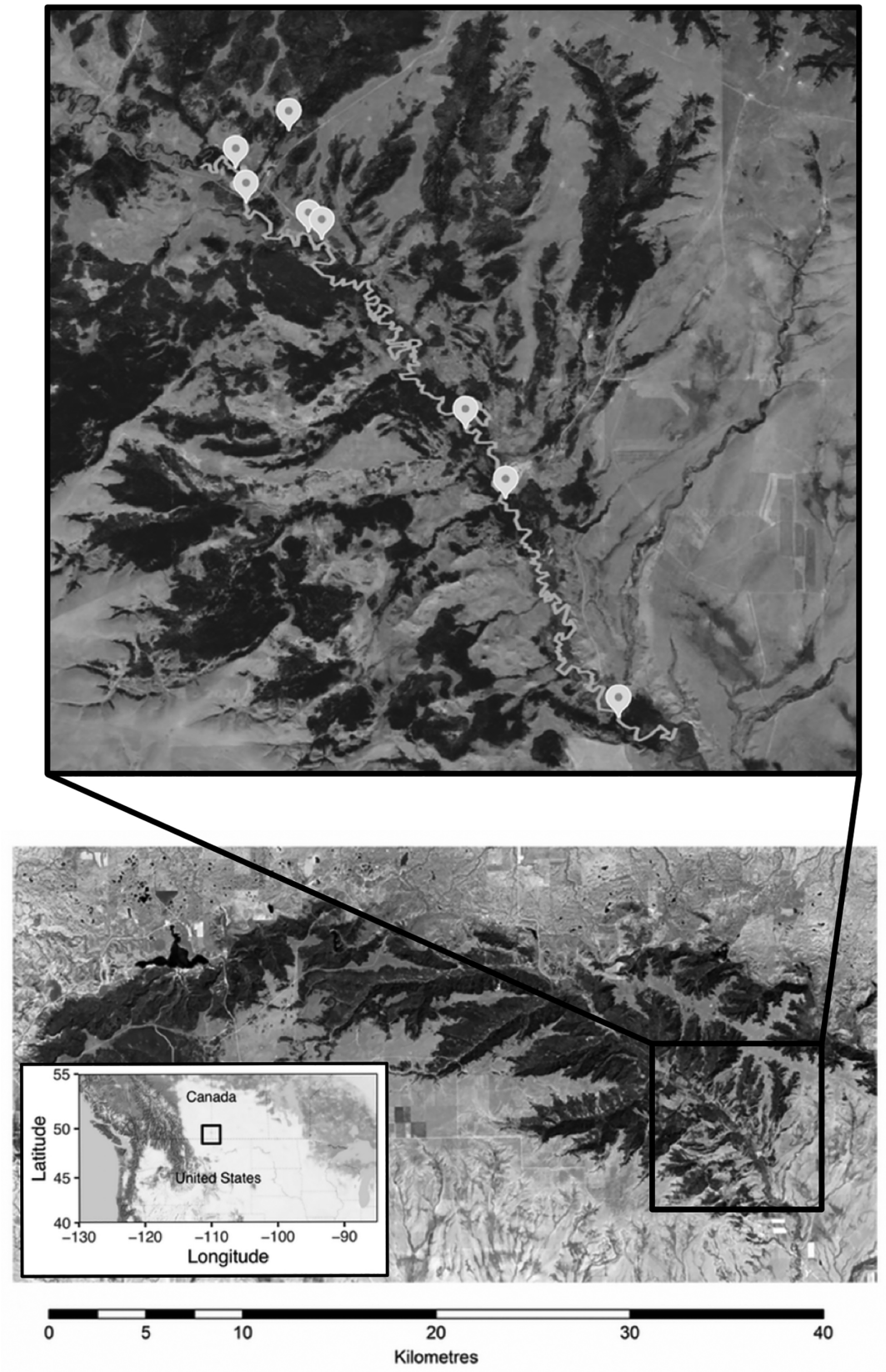

Fig. 1.—Bottom map depicts the geographic location of Cypress Hills, highlighting the isolation of this forested area in the prairies of North America and the dramatic difference of vegetative cover of Cypress Hills compared to the surrounding prairie landscape. Cypress Hills supports a comparatively small breeding population, and likely serves as a stopover site for bats migrating to breeding areas in the boreal forest. Larger, top inset map represents an approximately 10 km^2 section of Cypress Hills where research has occurred since 2000 (Inset map of points; earth.google.com/web/). The white line follows the section of Battle Creek where mist netting has occurred from 2000 – 2019 and the points represent netting locations from 2018 and 2019.

(approximately when subadults become volant—Kunz 1982; Shump and Shump 1982).

Results

Overall, 289 migratory bats were captured during 171 nights with netting effort that ranged from 1 to 8 nets deployed for 1.0–7.5 h per night. Based on our models, there was no clear evidence of a positive or negative change in capture rate over time for hoary bats (year effect = 0.01 ± 0.03; 95% confidence interval [*CI*] = −0.05 – 0.07). Captures of silver-haired bats, however, appeared to increase over time (year effect = 0.09 ± 0.04; 95% *CI* = 0.00 – 0.17). Nightly minimum temperature had a net positive effect on captures of both species (hoary: 0.09 ± 0.04; 95% *CI* = 0.01 – 0.16; and silver-haired: 0.09 ± 0.04; 95% *CI* = 0.01 – 0.17), as did day of year (hoary: 0.02 ± 0.01; 95% *CI* = 0.01 – 0.04; and silver-haired: 0.03 ± 0.01; 95% *CI* = 0.02 – 0.05).

Based on our results, there is a low probability that local numbers of hoary bats have declined meaningfully. We estimate there is an 18% probability that numbers have declined by more than 30% over a 20-year period and a 7% probability they have declined by more than 50%. Our results are more suggestive of either a small change in local numbers (40% probability they have changed by <30%) or an increase of at least 30% (41% probability). Our results are even more striking for silver-haired bats, for which we estimate there is a 1% probability that local numbers have declined by at least 30% and a 96% probability that they have increased by at least 30% over a 20-year period. Excluding the potential for subadults in the analysis increased the uncertainty in model estimates but did not fundamentally change the patterns we observed.

Discussion

Our prediction that we would detect a decrease in migratory bat abundance in Cypress Hills was not supported. In contrast, we found no evidence of a decrease in captures of hoary or silver-haired bats across the 20-year range of our data set. Rather, we report a high probability that there was no change in local abundance of hoary bats in the Cypress Hills across our study period, and that silver-haired bat captures appear to have increased at this site. However, a range of studies on North American migratory bats suggest that overall population sizes have significantly decreased over the past several decades, especially for hoary bats (Winhold et al. 2008; Frick et al. 2017b; Rodhouse et al. 2019; Davy et al. 2020). The summer resident bats in Cypress Hills represent a tiny subset of the continental population and our data represent a small geographic scale relative to other studies (Frick et al. 2017a; Rodhouse et al. 2019; Davy et al. 2020). Moreover, determining overall population size and abundances for migratory bats is difficult, and even rough estimates do not exist (Lentini et al. 2015). We therefore suggest alternative explanations that may explain our results. Potential explanations include changes in climate, the quality of forest habitat for migratory bats throughout the study period at Cypress Hills, and compensatory immigration.

Changing climate has influenced populations and local abundance of many wildlife species and the habitats they occupy. A variety of taxa, including fishes (Perry et al. 2005), birds (Gillings et al. 2015), and mammals (MacLeod et al. 2005; MacLeod 2009), are experiencing range shifts suspected to have been induced by changes to climate. Often, the shifts in range and abundance are latitudinal (Chen et al. 2011). While it has been established that hoary and silver-haired bats give birth and rear their young in northern latitudes (Kunz 1982; Shump and Shump 1982), their seasonal movements are not well understood and it is possible that more individuals that normally would have roosted further south are now migrating further north. In addition, climate change can influence forest communities (Vose et al. 2012; Grimm et al. 2013), thereby changing available habitat to bats. Cypress Hills has experienced an increase in forest cover over the last 50 years (Widenmaier and Strong 2010), potentially increasing the roosting habitat available for migratory bats. Both climate change and changes in habitat therefore could have favored compensatory immigration to the Cypress Hills and masked the signal of large-scale population declines in our local-scale capture data.

Along with changes to range and habitat, climate change also may influence local abundances, similar to fishes (Last et al. 2011) and birds (Maclean et al. 2008). For example, as high-quality habitat becomes available for some migratory and nonmigratory birds (through death or emigration of territorial individuals), new individuals fill the vacancy (Krebs 1971; Betts et al. 2008), complicating extrapolation of local abundance trends to changes in the whole population. This phenomenon is known as compensatory immigration (Pulliam 1988; Turgeon and Kramer 2012). Studies of local abundance can provide indices of overall population trends, although such inferences may be complicated because local studies only capture variation for a small subset of the overall population (Thogmartin and Knutson 2007; Rushing et al. 2016). Local population (i.e., small spatial scale) dynamics often are the result of movement decisions by individuals within that smaller population. In Cypress Hills, if historically "resident" migratory bats experience mortality (e.g., at wind turbines) before returning the following summer, the newly vacant habitat could be occupied by new individuals. In subsequent seasons, individuals that might otherwise have continued migrating to more northern breeding areas remain and occupy the newly vacant habitat. Occupation by new individuals would give the impression of a locally stable population.

Given that reproductive female hoary and silver-haired bats use Cypress Hills, it is possible that overall population decreases due to wind turbines lead to higher turnover and thus more available maternity roosting habitat in high-quality sites. By remaining in Cypress Hills, transient bats could reduce energy expenditure by minimizing migration distance while taking advantage of newly available foraging and roosting areas, as well as reducing risks associated with prolonged migration (Alerstam and Lindström 1990; Hedenström 2009).

Considering there is mounting evidence that migratory bat populations are decreasing (Rodhouse et al. 2019; Davy et al. 2020), it is important to protect locations such as the Cypress Hills to help conserve migratory bat species where local abundance appears to be stable.

Although our data have limitations (e.g., netting effort, age, and sex of individuals missing from data sets), they provide an opportunity to assess the long-term trend for a local subset of two migratory bat populations (O'Shea et al. 2003; Ingersoll et al. 2013). However, our results must be interpreted cautiously and likely do not reflect population trends for hoary bats and silver-haired bats across North America. Long-term, range-wide data are critical for revealing trends and predicting potential decreases. Hoary bats are predicted to decrease further as new wind energy facilities are constructed (Frick et al. 2017b) and silver-haired bats are experiencing local abundance declines (Davy et al. 2020). Similar effects also seem likely for other migratory bats including eastern red bats, due to similar ecology and life history (Arnett et al. 2008; Arnett and Baerwald 2013; Davy et al. 2020). Online resources can allow access to data that include aggregated content for large-scale analyses (Costello et al. 2013; Hardisty and Roberts 2013), rather than at the small scale we considered. If bat populations continue to decrease due to wind energy (Frick et al. 2017b; Rodhouse et al. 2019), white-nose syndrome (Frick et al. 2017a), and other potential causes, online databases (i.e., Bat Acoustic Monitoring Project, North American Bat Monitoring Program) should be considered as a resource to collate large data sets that cover large geographic areas. As online databases become more comprehensive, long-term and large-scale data analyses will be more robust and can aid in detecting trends across many contexts.

Acknowledgments

The work accomplished herein was all conducted on Treaty 4 lands with a presence in Treaty 6. These are the territories of the Nêhiyawak, Anihšināpēk, Dakota, Lakota, and Nakoda, and the homeland of the Métis/Michif Nation. We thank Jody Wynen, Carter Casmaer, and Lynn Wynen-Chamberlain, for their continuous support during the production of this paper. We also thank Adam Sprott for assistance in providing mapping information for Cypress Hills. There was no outside funding directly for this study but we thank NSERC (Natural Sciences and Engineering Research Council (Canada)) and the Canadian Queen Elizabeth II Diamond Jubilee Scholarship program for support of the studies that ultimately contributed to this work. The authors declare that they have no conflicts of interest.

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Submitted 3 June 2019. Accepted 9 November 2020.

Associate Editor was Roger Powell.