

ARTICLE

Rapidly declining body size in an insectivorous bat is associated with increased precipitation and decreased survival

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Abstract

Reduced food availability is implicated in declines in avian aerial insectivores, but the effect of nutritional stress on mammalian aerial insectivores is unclear. Unlike birds, insectivorous bats provision their young through lactation, which might protect nursing juveniles when prey availability is low but could increase the energetic burden on lactating females. We analyzed a 15-year capture–mark–recapture data set from 5312 individual little brown myotis (*Myotis lucifugus*) captured at 11 maternity colonies in northwestern Canada, to test the hypothesis that nutritional stress is impacting these mammalian aerial insectivores. We used long-bone (forearm [FA]) length as a proxy for relative access to nutrition during development, and body mass as a proxy for access to nutrition prior to capture. Average FA length and body mass both decreased significantly over the study period in adult females and juveniles, suggesting decreased access to nutrition. Effect sizes were very small, similar to those reported for declining body size in avian aerial insectivores. Declines in juvenile body mass were only observed in individuals captured in late summer when they were foraging independently, supporting our hypothesis that lactation provides some protection to nursing young during periods of nutritional stress. Potential drivers of the decline in bat size include one or both of (1) declining insect (prey) abundance, and (2) declining prey availability. Echolocating insectivorous bats cannot forage effectively during rainfall, which is increasing in our study area. The body mass of captured adult females and juveniles in our study was lower, on average, after periods of high rainfall, and higher after warmer-than-average periods. Finally, survival models revealed a positive association between FA length and survival, suggesting a fitness consequence to declines in body size. Our study area has not yet been impacted by bat white-nose syndrome (WNS), but research elsewhere has suggested that fatter bats are more likely to survive infection. We found evidence for WNS-independent shifts in the body size of little brown myotis, which can inform

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studies investigating population responses to WNS. More broadly, the cumulative effects of multiple stressors (e.g., disease, nutritional stress, climate change, and other pressures) on mammalian aerial insectivores require urgent attention.

KEYWORDS

aerial insectivore, body size, climate change, developmental biology, lactation, little brown bat, morphology, *Myotis lucifugus*, nutritional stress

INTRODUCTION

Globally, many aerial insectivores have declined in abundance since the mid-1980s, with steep declines documented for many insectivorous birds (Bowler et al., 2019; Nebel et al., 2011, 2020; Powell et al., 2015). Declining insect prey has been proposed as a primary driver of the concomitant decline of several avian aerial insectivores (Cox et al., 2019; Spiller & Dettmers, 2019), but the evidence is equivocal and declines are likely to be multifactorial, with the relative impact of specific factors varying among species (Michel et al., 2016). The rate of avian declines varies both geographically and taxonomically, but long-term declines have been documented for many species that are obligatory predators of aerial insects. The effect of prey declines on other taxonomic groups of aerial insectivores, such as bats, remains a key gap in our understanding of the impact of global insect declines on biological diversity.

Nutritional stress during development can affect body size at maturity in species that exhibit determinate growth (i.e., growth ceases when the individual reaches maturity). Long-bone length at maturity is determined in part by caloric intake during early development (Hermanussen et al., 1996; Romano et al., 2010), whereas body mass varies with recent caloric intake. Therefore, changes in long-bone length can act as a proxy for nutritional stress during development (Gardner et al., 2009), whereas body mass reflects recent abundance or availability of food resources (McGuire et al., 2018).

Nutritional stress can be caused by a reduction in prey abundance or quality, phenological mismatch between prey availability and foraging, or a weather-induced reduction in foraging opportunities (Cox et al., 2019; English et al., 2018). These mechanisms are not mutually exclusive and can exert cumulative effects on aerial insectivores. These effects may be exacerbated by climate change, and they each can drive decreased body size or mass under some conditions (Kelly et al., 2018; Riemer et al., 2018; Salewski et al., 2010; Teplitsky & Millien, 2014). The number of insect prey encountered by species that forage primarily using an aerial-hawking strategy, such as the little brown myotis (*Myotis lucifugus*), should be directly linked

to the abundance of aerial insects. Shifting precipitation regimes can limit foraging opportunities for aerial insectivores, even at sites where insect abundance has not declined (Cox et al., 2019; Sherwin et al., 2013). Many aerial insects suspend flight during rainfall, as do some insectivorous bats and birds that hunt them (Belwood & Fullard, 2009; Geipel et al., 2019; Voigt et al., 2011).

Effects of climate change are associated with general trends of decreasing body size in birds (Gardner et al., 2009; van Gils et al., 2016; Weeks et al., 2020), and evidence of nutritional stress in a range of avian species implicates shifting prey availability as the proximate cause of decline in some bird populations. For instance, tree swallows (*Tachycineta bicolor*) exhibited decreased body mass linked to frequency of recent rainfall and limited foraging opportunities (Cox et al., 2019).

Avian aerial insectivores provision their nestlings by capturing prey and feeding them to their young. Food availability for nestlings is therefore linked directly to availability of prey for foraging parents, whose prey consumption typically peaks during the reproductive season (e.g., Kelly et al., 2013). However, reduced availability of arthropod prey might have a less direct effect on nutritional intake by pups of insectivorous bats. Lactation is energetically costly for bats, but may provide a more stable food source for their pups when prey availability is low. Examining changes in body size of insectivorous bats would complement previous work on body size in birds, and further clarify the relative impacts of prey availability on aerial insectivores.

We used morphometric data collected from little brown myotis at a network of maternity colonies monitored over 15 years to test the hypothesis that nutritional stress is impacting mammalian aerial insectivores similarly to their avian counterparts, and to explore how increasing precipitation and temperature in our study area might affect prey availability. We were specifically interested in exploring whether maternal provisioning of pups through lactation could buffer juvenile bats against nutritional stress caused by shifts in prey availability. We considered markers of potential nutritional stress at two temporal scales. First, we used forearm length as a proxy for relative access to nutrition during development. Second, we used body mass as a proxy for access to nutrition in days prior to capture. We tested three

TABLE 1 Predictor variables included in four models of average size modeling (forearm length [mm] and mass [g]) of adult and juvenile little brown myotis (*Myotis lucifugus*; 6146 adult females; 429 juvenile females and 343 juvenile males) from Yukon, Canada, 2004–2018

Hypothesis	Predictor variables considered	Adult females		Juveniles	
		Forearm	Mass	Forearm	Mass
H ₁ . Larger bats are heavier on average	Forearm length (to account for size; Rioux Paquette et al., 2014)	...	X	...	X
	Sex (to account for sexual size dimorphism or for different energetic strategies between sexes)	X	X
Pregnant bats are heavier on average	Reproductive status: pregnant or not pregnant	...	X
H ₂ . Bats are experiencing chronic nutritional stress, either because of reduced prey availability or reduced foraging opportunities	Year	X	X	X	X
	Ordinal day (to account for changing mass over time, either due to energetic costs of pregnancy, for adult females, or to provisioning for hibernation for all individuals)	...	X ^a	...	X
	An interaction between year and ordinal day to account for seasonal variation in mass	...	X	...	X
	An interaction between year and ordinal day, to account for long-bone growth in the first year	X ^b	...
H ₃ . Weather affects foraging opportunities for insectivorous bats, with increased precipitation limiting foraging activity, and increased temperature increasing prey activity	Cumulative precipitation (CPRECIP) in the 10 days prior to capture (i.e., acute effects of reduced foraging opportunity on mass in all bats, or on long-bone growth in juveniles)	...	X	...	X
	Proportion of precipitation days (PPD) from return to maternity colonies (ordinal day 107) to date of capture (i.e., impact of seasonal precipitation on adults' foraging opportunity)	...	X	...	X
	Proportion of precipitation days (PPD) from juvenile volancy (~ ordinal day 185) to date of capture (i.e., impact of seasonal precipitation on juvenile foraging opportunities or on maternal provisioning)	X
	Mean-centered minimum temperature (a measure of how minimum temperature in the 10 days preceding capture varies from the average for that 10-day period across 15 years)	...	X	...	X
	Maternity colony ID (random effect)	X	X	X	X
H ₄ . Bigger bats experience higher survival rates	Capture–mark–recapture analysis of survival rates, including forearm length and local precipitation	X	...	X	...

^aThe adult female body mass model used a GAM with a smoothing term for ordinal day (please refer to *Methods*).

^bRemoved from the final "juvenile forearm" linear mixed model after preliminary data analyses showed no association between ordinal date and forearm length.

broad hypotheses (Table 1) including general effects of body size on mass (H₁), the hypothesis that bats in our study area experienced chronic nutritional stress due to reduced

prey availability (H₂), and the hypothesis that increased precipitation frequency reduced foraging opportunities for insectivorous bats (H₃). To assess short-term (15 years)

changes in nutritional stress experienced by developing juveniles we tested for temporal trends in long-bone length at maturity, and explored changes in average juvenile and adult body mass. To explore the potential effects of shifting climatic conditions on prey availability, we also quantified the association among body mass at time of capture, the frequency of precipitation prior to the capture event, and warming temperatures in the study area. Finally, we hypothesized that nutritional stress during early development has long-term effects on fitness (Table 1; H_4). To test the consequences of body size in our system, we modeled survival to test the prediction that survival probability was lower for smaller bats.

METHODS

Bat morphometrics

We leveraged a capture–mark–recapture (CMR) data set from 11 little brown myotis maternity colonies in Yukon, Canada, to which resident bats return before approximately 17 April each year (Slough & Jung, 2008, 2020; Appendix S1: Figure S1). The full CMR data set included 8875 captures of 5312 unique individuals over 21 years (1997–2018). Bats were captured during emergence at dusk, prior to foraging, using mist nets and harp traps at maternity colonies located in bat houses or buildings (Slough & Jung, 2008, 2020). Sex was recorded for each captured bat based on the presence or absence of a penis, and we distinguished adults (>1 year old) from juveniles (young of the year that survived to volancy) based on ossification of the phalangeal joints (Kunz & Anthony, 1982). We weighed each bat using a digital scale (± 0.1 g), and measured the forearm with digital calipers (± 0.1 mm). Pregnancy was assessed by gently palpating the abdomen of females. We applied an individually marked, 2.9 mm, lipped, aluminum band to the forearm of each bat, and then released them at the capture site. Capture and handling of bats was in compliance with guidelines from the American Society of Mammalogists (Sikes, 2016) and permitted by the Government of Yukon through regulations in the Yukon Wildlife Act.

Modeling temporal trends in bat size

We tested our hypotheses with linear mixed models using the *lme4* package to model forearm growth and the body mass of juveniles (Bates et al., 2015), and used a generalized additive model (GAM) using the *mgcv* package (Wood et al., 2016) to model body mass in adult females, which showed seasonal effects of reproduction and hibernation. All analyses were conducted in R version 4.0.0

(R Core Team, 2016). We excluded early years (pre-2004) and adult males from the data set for these analyses due to lower sample sizes, restricting our analysis to data collected at 11 colonies between ordinal day 107 and 240 (17 April and 28 August, counting from ordinal day 1 of January 1), from 2004 to 2018. We included data in the adult body mass models from all individuals for which both body mass and forearm length were measured. We excluded recaptures from the juvenile models and used only the first capture for each individual juvenile because there were insufficient within-year recaptures of juvenile bats ($n = 10$) to account for within-year, intraindividual variation in bat size.

We included forearm length as a fixed effect in models of adult and juvenile body mass, to account for effects of bat skeletal size on mass (Rioux Paquette et al., 2014; Table 1; H_1). Sex was also included as a fixed effect in models of juvenile forearm length and body mass, and reproductive status (pregnant or not pregnant) was included in models of adult female body mass to account for the effects of pregnancy. Juvenile forearms grow until individuals are 21 days old, corresponding roughly with volancy (Baptista et al., 2000; Kunz & Anthony, 1982), and may continue to increase slightly as juveniles prepare for hibernation. However, we found no effect of ordinal date on juvenile forearm length (data not shown), so capture date was removed from our forearm length models. Forearm length of mature bats should be stable over time because bats exhibit determinate growth, and ordinal date was therefore not included in models of forearm length. Juvenile bat body mass increases through late summer and fall as they prepare for hibernation, so we included capture date in the model of juvenile mass to account for body mass increase within each year. The average body mass of adult females in a maternity colony increases through pregnancy, decreases following parturition, and then increases gradually until hibernation. We used a GAM with a smoothing term for capture (ordinal) date to account for this seasonal variation in adult female body mass in response to the energetic costs of maternal investment.

Mechanisms of nutritional stress affecting bats could include a decline in aerial insect abundance over the study period, and/or reduced foraging opportunities due to increased precipitation. No trend data for aerial insect abundance were available in our study area, but we hypothesized that if bats are experiencing chronic nutritional stress (Table 1; H_2), then we would observe a negative, linear effect of “year” on mean adult forearm length over time, as juvenile bats experienced nutritional stress impacting long-bone development and resulting in smaller size at maturity (Table 1; H_2). This hypothesis also predicted that mean adult female mass would decrease over time, as females offset the effects of

nutritional stress on their young through maternal investment (pregnancy and lactation). If maternal care (lactation) buffers juvenile bats against the effects of reduced prey availability, changes in juvenile mass might be greater near the end of the summer, when the diet of weaned pups is no longer subsidized by nursing.

Bats might experience nutritional stress with shifting weather conditions even if prey abundance is stable. Increased precipitation can reduce foraging opportunities, whereas warmer nighttime temperatures may result in increased insect activity and therefore prey availability (Table 1; H_3). To incorporate the potential effects of weather on body mass in our models, we extracted data on precipitation and temperature from weather stations nearest to each monitored maternity colony. Average distance from weather stations to colonies was 44 km (range = 0.7–120 km; Appendix S1: Figure S1). Within each year, we calculated the proportion of local precipitation days (PPD) prior to each individual capture: (number of days with >1 mm precipitation between 17 April and the day preceding the capture event)/(total number of days between 17 April [approximate date of spring return to maternity colonies by adult females] or 4 July [first documented volancy for juveniles] and the day preceding the capture event). The PPD variable provided a rough proxy for aerial-hawking opportunities experienced by each individual over the active season prior to capture. Little brown myotis can also glean prey (Kaupas & Barclay, 2018; Ratcliffe & Dawson, 2003; Shively et al., 2018), but we expected that heavy rain would still interfere with navigation and foraging. We also calculated the local, cumulative precipitation volume (CPRECIP) in the 10 days preceding each capture event, as a proxy for bats' foraging opportunities prior to capture. Precipitation was recorded as a daily total by the weather stations, so these data represent rainfall over a 24-h period, as data for the evening only were not available. Low temperatures can affect insect activity, but the range of temperatures that insects can tolerate is likely to vary across species and latitudes, so identifying the correct threshold temperature to indicate reduced prey activity is challenging. Instead, we quantified mean-centered minimum temperature by averaging the minimum temperature in the 10 days prior to capture, and quantifying the deviation of that average from the average over the same sequence of ordinal days, across the study period (Bonamour et al., 2020). Therefore, mean-centered minimum temperature provides a measure of departure from "normal" minimum temperatures, for each 10-day period prior to capture.

Effect and interaction plots were created using the *Itools* and *Interactions* packages (Long, 2019). Assumptions of model fit were checked with diagnostic plots of

residuals. Maternity colony ID was included as a random intercept effect for all models reflecting the high site fidelity of females to the study colonies (Slough & Jung, 2020).

Survivorship analysis to test correlates of bat fitness

To test whether potential shifts in body size or precipitation might also affect individual fitness (Table 1; H_4), we estimated annual survival from 1997 to 2018 at 11 colonies and a subset of these data from 2011 to 2018 using the Cormack–Jolly–Seber CMR model (Cormack, 1964; Jolly, 1965; Seber, 1965). This model estimates two fundamental parameters (1) the probability of apparent survival to the next year, (ϕ ; a product of survival and residency probability) and (2) recapture probability (p). The subset data concentrated on a period of time in which individuals' forearm lengths were measured, and when temperature and precipitation data at the colonies were available. We hypothesized that if nutritional stress during early development has carry-over effects on individual fitness, then bats with longer forearms would have a greater probability of survival, and we also hypothesized that survival might be associated with access to foraging opportunities, for which precipitation is a proxy. For the complete data set, we considered survival and recapture probability to be constant or vary in combinations (additive and interactions) of year, sex (male or female), colony, and age (juvenile or adult). For the subset data, we hypothesized p to be constant, vary by year, sex (male or female), colony, age (juvenile or adult), or an additive or interaction effect between year and sex. We hypothesized ϕ to vary by year, age, sex, colony, forearm length, total precipitation at the colony, the number of days of precipitation at each colony, or a mixed combination. Individuals determined to be juveniles were classified as juveniles for that year, and subsequently reclassified as adults. We fitted models in program MARK (White & Burnham, 1999) and compared models using Akaike's information criterion (AIC) with a correction for small sample size (AIC_c ; Burnham & Anderson, 2002). We used AIC_c weights to evaluate the probability each model is the best in terms of minimizing the Kullback–Leibler discrepancy, given the data and model set. To assess the effect size, we calculated pseudo R^2 values for each fixed effect in the top model.

RESULTS

Factors affecting bat size

The data subset used to explore temporal changes in bat size (2004–2018) included 6918 sets of measurements

from 5136 unique individuals (4371 adult females, 422 juvenile females, and 343 juvenile males). Body mass increased with forearm length (H_1). Adult female body mass increased, on average, by 0.15 g for every 1 mm of forearm length (pseudo $R^2 = 0.028$), and juvenile body mass increased by 0.30 g for every 1 mm of forearm length (pseudo $R^2 = 0.024$).

The factors we tested generally had statistically significant effects on body size, although the effect sizes were consistently very small. Forearm length of adult females declined significantly across our study period, decreasing on average by 0.02 mm/year (pseudo $R^2 = 0.004$; H_2 ; Table 2, Figure 1). Forearm length of juvenile bats decreased by 0.04 mm/year, on average (pseudo $R^2 = 0.01$), and juveniles displayed sexual size dimorphism with mean male forearms being 0.40 mm shorter than females (pseudo $R^2 = 0.028$; Figure 1). This

represents an estimated decrease in forearm length of 0.3 mm for adult females and 0.6 mm for juveniles across the 15-year study period, but with very small effect sizes.

In support of our hypothesis (H_2), average body mass decreased during our study period. Cumulative precipitation provided no predictive power and we omitted it from the final adult and juvenile models. As there was also no significant interaction between year and capture date for adult female body mass, this term was also omitted from the final model for adult female body mass (Appendix S1: Table S1). All other tested variables were significant predictors of body mass in adult females, which decreased on average by 0.026 g/year (pseudo $R^2 = 0.013$; Table 3, Figure 2). Ordinal date of capture was a significant predictor of adult female body mass (pseudo $R^2 = 0.053$), which was 1.380 g more, on

TABLE 2 Parameter estimates and SE from linear regression models exploring shifts in average forearm length (mm) of little brown myotis (*Myotis lucifugus*) in Yukon, Canada, 2004–2018.

Fixed effects	Adult females ($n = 3314$)			Juvenile ($n = 765$)		
	β	SE	p	β	SE	p
Intercept (female, year 1)	75.049	14.373	<0.001	113.805	30.794	<0.001
Year	−0.018	0.007	0.011	−0.037	0.015	0.015
Sex (male)	−0.399	0.084	<0.001

Note: Bold font indicates statistical significance at α -level 0.05.

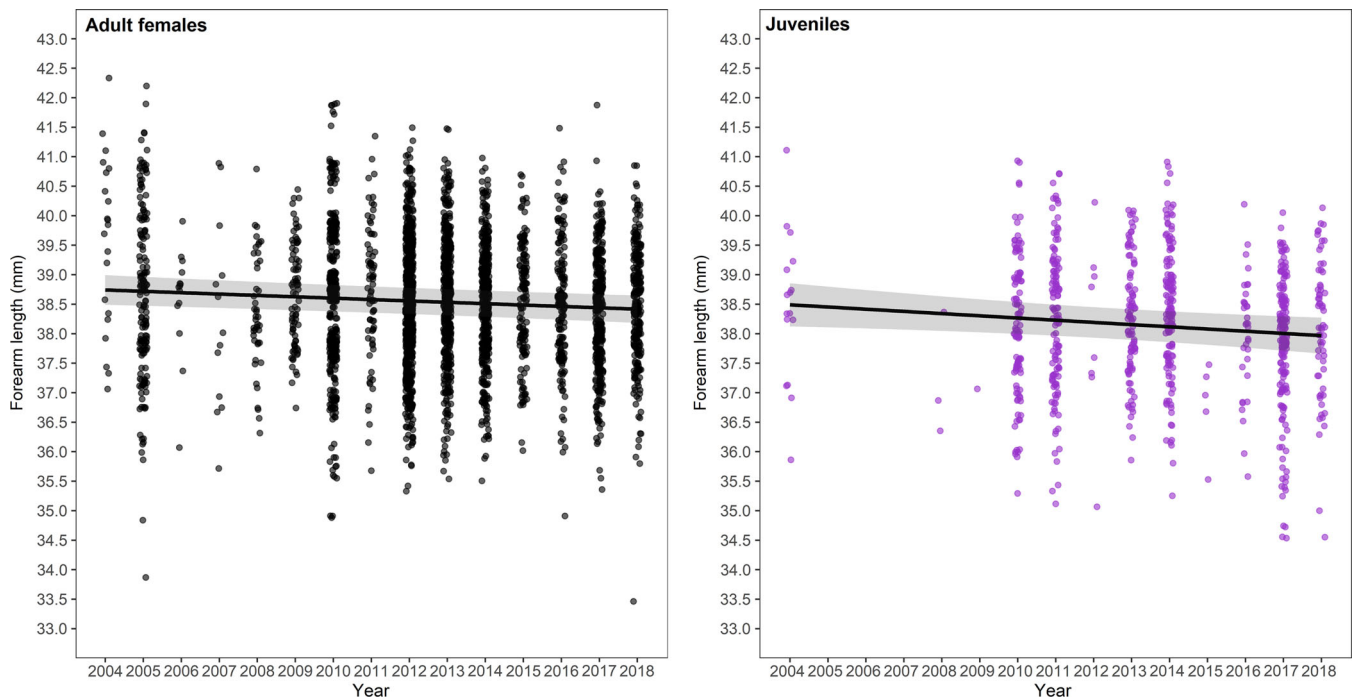


FIGURE 1 Average forearm length (mm) of adult female and juvenile little brown myotis (*Myotis lucifugus*) monitored at 11 maternity colonies in Yukon, Canada, decreased significantly over 15 years (2004–2018).

TABLE 3 Parameter estimates and SE from linear and generalized additive regression models exploring shifts in average mass (g) of little brown myotis (*Myotis lucifugus*) in Yukon, Canada, 2004–2018.

Fixed effects	Adult females (n = 6123)			Juvenile (n = 765)		
	β	SE	p	β	SE	p
Intercept	56.057	9.510	<0.001	-2267.744	447.417	<0.001
Forearm	0.153	0.011	<0.001	0.304	0.020	<0.001
Year	-0.026	0.005	<0.001	1.123	0.222	0.156
Sex (male)	-0.143	0.046	0.002
Reproductive status (pregnant)	1.380	0.028	<0.001
Ordinal day	<0.001*	10.428	2.098	0.036
Year × Ordinal day
-1 SD (day 206)	0.059	0.012	<0.001
Mean (day 215)	0.013	0.009	0.156
+1 SD (day 223)	-0.032	0.014	0.023
PPD	-0.007	0.002	0.001	-0.012	0.003	<0.001
MCMTemp	0.006	0.009	0.498	0.086	0.026	0.001

Note: PPD = proportion (percentage) of precipitation days between estimated spring arrival at maternity sites (adults) or onset of volancy (juveniles), and capture date. MCMTemp = mean-centered minimum temperature (please refer to “Methods” for details). Bold font indicates statistical significance at α -level 0.05.

*Significant ($p < 0.001$), non-linear relationship modeled with GAM (Appendix S1: Figure S2).

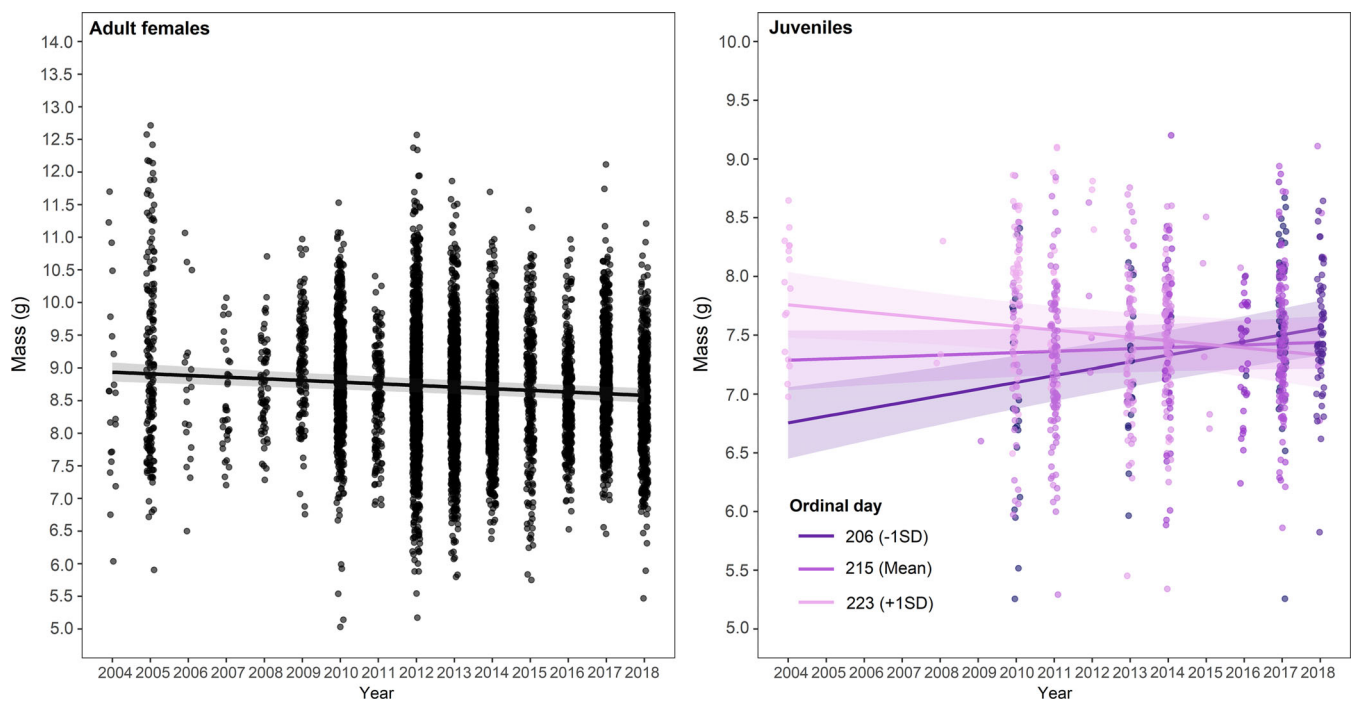


FIGURE 2 Average mass of adult female and juvenile little brown myotis (*Myotis lucifugus*) at 11 maternity colonies in Yukon, Canada, decreased significantly over 15 years (2004–2018), but with a significant interaction between ordinal day of capture and year for juvenile bats, indicating that a yearly decrease in average mass occurred at different rates depending on the time of capture. Lines indicate model-predicted averages and shaded areas indicate 95% confidence intervals. For the juvenile plot, lines show model-predicted averages for bats captured in three time periods, corresponding to the mean sampling date (day 215) and 1SD on either side. Note different range on y-axes.

average, in pregnant females (pseudo $R^2 = 0.254$). Female body mass decreased following parturition, and increased steeply after pups were weaned (Appendix S1: Figure S2). Weather conditions prior to capture partially predicted body mass of adult females (H_3), which decreased as the PPD prior to capture increased (Table 3; pseudo $R^2 = 0.011$; Figure 3) but was not affected by mean-centered minimum temperature (Appendix S1: Figure S3).

Juvenile body mass was significantly affected by the interaction between year and ordinal date (pseudo $R^2 = 0.068$; Table 3, Figure 2). Juvenile mass decreased on average by 0.032 g/year (pseudo $R^2 = 0.0006$), but only for individuals captured in the post-weaning period (near day 223; 11 August), when juveniles are foraging independently and no longer subsidized by their mothers. Juveniles captured around the time the pups became volant (day 206; 25 July 25) actually increased in mass by 0.059 g/year over the study period, whereas juveniles caught around the mean sampling date for juvenile captures (day 215; 3 August) showed no significant changes in mass over the study period (Figure 2). Weather conditions affected juvenile body mass, which declined by 0.012 g, on average, with each 1% increase in PPD (pseudo $R^2 = 0.026$; Figure 3), but was higher, on average, in bats captured after warmer-than-average periods (pseudo $R^2 = 0.019$; Appendix S1: Figure S3).

Analyzing weather trends in detail was beyond the scope of this study, but temperature and precipitation in our study area both generally increased over the study period. Linear models of weather station data estimated that yearly mean minimum temperatures during the active season for bats increased by 0.7°C (Appendix S1: Figure S4), and the number of days with >1 mm precipitation increased by 6.5 days during our 15-year study period (Appendix S1: Figure S5).

Survival analysis

The number of individuals captured and recaptured varied by year (Appendix S1: Table S2) and across colonies (Appendix S1: Table S3). We caught a total of 5158 individuals (4701 female, 457 male) at least once. Of these, we initially caught 923 individuals as juveniles and 4235 as adults. Model selection results using the complete data set identified a single model with all AIC_c weight (Appendix S1: Table S4), in which survival varied by age, sex, and colony, whereas recapture probability varied by year and sex (Appendix S1: Table S5). Recapture probability of females was much higher than males in all years, and increased over time, most likely to reflect increased sampling effort (Appendix S1: Figure S6). There was support for strong spatial variation in survival across the

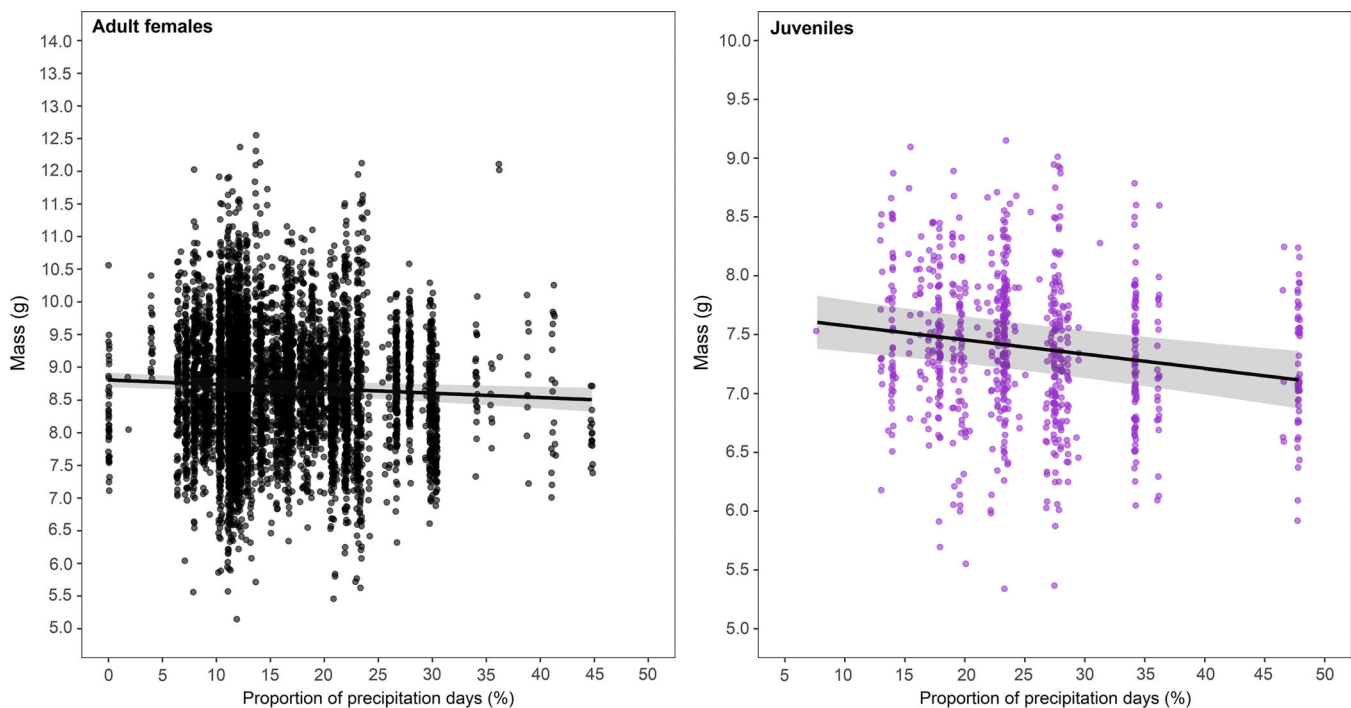


FIGURE 3 Average mass of adult female and juvenile little brown myotis (*Myotis lucifugus*) monitored at 11 maternity colonies in Yukon, Canada, was associated with the proportion of precipitation days (in the active season) experienced prior to capture; shaded areas indicate 95% confidence intervals. Note different axis ranges on the two plots.

different colonies, and for lower juvenile survival probabilities compared with adults ($\beta = -1.41, -1.76$ to -1.06 , 95% CI; Appendix S1: Figures S7, S8). There was no support for lower male survival compared with females ($\beta = 0.516, -1.279$ to 2.311 95% CI), although there was a smaller sample size for males.

The subset of data from 2011 to 2018 included 3042 individuals (2465 female, 577 male). We found support for a single model with all the AIC_c weights (Appendix S1: Table S8), in which survival varied by age, sex, colony, and forearm length, and recapture probability varied by year and sex (Appendix S1: Table S7). In support of our hypothesis (Table 1; H₄), forearm length positively influenced survival probability ($\beta = 0.167, 0.076$ – 0.257 95% CI). In other words, the log-odds of surviving increased by 0.167 for each 1 mm increase in forearm length. In considering the full range of observed forearm lengths (33.9 and 42.3), a bat at the higher length was 2.05 times more likely to survive. We found no evidence that precipitation influenced annual apparent survival.

DISCUSSION

Little brown myotis bats in the boreal forest of northwestern Canada appear to be getting smaller, which is consistent with experiencing nutritional stress, reflecting reduced prey abundance, reduced foraging opportunities, or a combination thereof. Declining bat body size in our data set is associated with increased precipitation and reduced survival probability, and parallels trends detected in insectivorous birds that may be linked to climate change (Gardner et al., 2009; Weeks et al., 2020). We consider two likely mechanisms to explain our results, which could operate independently or cumulatively (1) declining prey (arthropod) abundance) and (2) limited foraging opportunities due to increasing frequency and amount of precipitation. We could not test the first mechanism directly as there are no robust data on insect abundance in our study area. Abundance of flying insects has declined precipitously in some places (Conrad et al., 2006; Hallmann et al., 2017; Lister & Garcia, 2018; Shortall et al., 2009), but evidence for global declines in insect abundance remains equivocal and trends in abundance vary widely among regions and taxa (Didham et al., 2020; Wagner et al., 2021). We were able to test the effects of changing weather, and we observed effects of precipitation and temperature on bat body mass. Declining prey abundance and altered foraging opportunities with shifting weather regimes and global climate change are not mutually exclusive mechanisms, and could interact cumulatively to aggravate nutritional stress.

Little brown myotis are long lived relative to their body size (>20 years; Davis & Hitchcock, 1995; Florko et al., 2017). Therefore, we had expected that even if forearm length of juveniles decreased over time, high survival of older adults from one year to the next might mask any signal of reduced forearm length in smaller individuals recruited to the breeding population each year. Despite their longevity, average forearm length at maturity of little brown myotis females in our data set decreased significantly over 15 years, and we observed a steeper decrease in juvenile forearm length.

Evidence for increasing nutritional stress in some avian aerial insectivores is growing (Cox et al., 2019; Rioux Paquette et al., 2014; Spiller & Dettmers, 2019), but most birds' ability to provision their young relies heavily on prey availability. Our data allowed us to test whether lactation in mammalian aerial insectivores provides a mechanism to mitigate the immediate effects of reduced prey availability (reduced prey abundance and/or limited foraging opportunities) on their offspring. The mean mass of recently volant juveniles in our data set increased slightly over the study period, indicating that lactating little brown myotis were apparently able to better protect juveniles from the nutritional stress they were experiencing relative to birds. Reproductive females may be allocating additional resources to lactation to protect nursing pups during periods of reduced prey availability, but this hypothesis was not supported by the decreasing trend in juvenile forearm length. Alternately, parturition dates may be slightly earlier each year as temperatures in the study area increase. This shift would result in slightly older (i.e., heavier) pups being measured in similarly timed surveys each year, but we cannot directly test this with the available data. Regardless, the protective effect of lactation did not carry over after weaning, as juvenile mass decreased on average over the study period for juveniles that were weaned and foraging independently.

The observed magnitude of declines in long-bone length in our study is small, as are the estimated effects of the variables we considered, but forearm length in little brown myotis is not highly variable and is likely to have limited plasticity. There are undoubtedly constraints on how much nutritional stress a developing pup can survive (i.e., how much of an effect nutritional stress could have on long-bone length before survival is affected). Our data set represents only the forearm length and mass of juveniles that had survived to volancy, and the magnitude of the observed effects on this population may be greater than our data indicate. The observed decline in body mass may also appear small. However, the magnitude of decline in fully weaned juveniles is non-trivial: the estimated, cumulative decline of 0.48 g over the 15-year study period represented 5%–6% of the body mass of even the heaviest

juveniles in the data set (e.g., individuals >8 g). The association between bat size and survival probability also suggests that decreasing body size has fitness implications.

We detected opposite effects of more frequent precipitation and increased mean-centered minimum temperature on bat mass. The negative effect of precipitation on bat mass is consistent with our hypothesis of reduced foraging opportunities. Decreased body mass was also reported in little brown myotis during a particularly rainy year on Haida Gwaii (Burles et al., 2009), and poor body condition in the congeneric greater mouse-eared bat (*M. myotis*) was associated with particularly wet conditions in Germany and Poland (Zahn et al., 2007). Little brown myotis are aerial-hawking predators, but can also target non-aerial arthropods (Shively et al., 2018), providing some flexibility during periods of increased precipitation. Nevertheless, the foraging success of little brown myotis is more strongly affected by heavy rain than that of conspecifics such as long-eared bats (*M. evotis*) that are specialized gleaners (Burles et al., 2009). Annual precipitation in Yukon has increased by 6% over a 50-year period (1948–2015) and is projected to increase by 10%–20% over the next 50 years (Streicker, 2016). Therefore, whereas increased drought frequency may pose a threat to little brown myotis elsewhere in their range (Frick et al., 2009), increased precipitation may be a greater concern in northwestern Canada and Alaska. Temperatures in the region are also increasing, which might have a positive effect on abundance or activity of some insect prey. Bats that had recently experienced particularly warm periods were heavier on average than bats captured after cooler than average periods. However, the general decrease in body size across the study period as temperature increased does not imply a long-term benefit from warmer conditions.

We recognize that yearly declines in average mass of adult females could reflect a reduced frequency of reproduction over the study period. We are unable to directly test this hypothesis with the available data, but increased precipitation was associated with delayed parturition and a reduced proportion of reproductive females in colonies of little brown myotis and Yuma bats (*M. yumanensis*) in British Columbia (Grindal et al., 1992). Delayed parturition in particularly wet or dry conditions is likely to be a response to reduced prey availability (Sherwin et al., 2013), and later parturition dates are typically associated with reduced pup survival (Barclay, 2012; Frick et al., 2009; Sherwin et al., 2013). If lower reproductive rates are partly responsible for the yearly reduction in mean mass, this would represent a potential impact of ongoing climate change on the fitness of high-latitude populations of little brown myotis. The unexplained variance in our data set may also reflect other environmental factors that we could not quantify. For example, in the boreal forest, fires have become more

frequent and severe (de Groot et al., 2013; Stephens et al., 2014), and the consequences to bats are largely unknown (Jung, 2020). However, both the fires themselves and smoke arriving from nearby or distant fires could impact insect availability and foraging conditions for aerial-hawking bats.

Measuring long-bone length of small, live animals in the field is subject to several sources of measurement error. These include small movements by the animal, variation among observers (i.e., calipers may be held slightly differently by different observers despite training to standardize methods), and variation in measurements by the same observer (i.e., slightly different caliper placement among measurements; e.g., Peers et al., 2021). However, these types of measurement error are typically distributed evenly throughout large data sets and are more likely to obscure patterns than create them (Lank et al., 2017). It is unlikely that measurement error could cause the observed trends in our large data set.

The trends we observed are comparable with body size declines reported previously for a range of avian aerial insectivores that were associated with climate change (Weeks et al., 2020), as are the magnitudes of the effects. Body mass in a population of mountain wagtail (*Motacilla clara*) decreased by 0.035 g/year on average over 23 years (~4% decline in body mass over the study period; Prokosch et al., 2019). Similar reductions in body mass and wing length were observed in a group of British passerines (Yom-Tov et al., 2006), and body mass and wing chord decreased significantly in a group of spring migrants over 46 years (van Buskirk et al., 2010). Average wing length in a yellowhammer (*Emberiza citrinella*) population declined by ~2.12% over 21 years, with a steeper decline in body size of juveniles than in the adult population (Dunn et al., 2017) that mirrored the steeper decline in forearm length and body mass we observed for post-weaning juvenile bats. Notably, these studies reported very small statistical effect sizes similar to those reported here, which may also reflect constraints on plasticity in body size of small vertebrates.

The bat colonies we studied have not yet been impacted by bat white-nose syndrome (WNS), but the fungus that causes WNS is getting closer (<https://www.whitenosesyndrome.org/spreadmap>). In impacted populations of little brown myotis, individuals that have survived hibernation in some WNS-affected caves and mines have a higher percent body fat and higher body mass, on average, than bats sampled before the first mass mortalities (Cheng et al., 2018), suggesting selection by WNS for higher body condition. Bats that may already be struggling to find sufficient nutrition may be less likely to survive the arrival of WNS, although this requires

investigation. Applying our analyses to a larger range of locations (where time series data are available) will allow us to explore geographic variation in the observed trends, and consider other factors such as latitude, length of the active season, and the potential interactive effects of WNS on body size.

Ongoing nutritional stress on bats and a concomitant decrease in body size and mass has conservation implications for endangered little brown myotis. Declining populations of bats and other aerial insectivores could have substantial effects on trophic webs. Aerial insectivores are top predators in the aerosphere. Decline or extirpation of these species could trigger trophic cascades in the aerial trophic web (Kelly et al., 2013), given that aerial insectivores consume millions of tons of insects per year (Boyles et al., 2011; Nyffeler et al., 2018). Although the exact ecological effects of aerial insectivore declines are difficult to predict, they are just as important to understand as the declines in aerial insects themselves. More broadly, the cumulative effects of multiple stressors (e.g., disease, nutritional stress, climate change, and other pressures) on bats suggest that each require urgent research attention.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Von Zuben, 2022) are available in the Open Science Framework repository at <https://osf.io/3q9cm/>.

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REFERENCES

- Baptista, T. L., C. S. Richardson, and T. H. Kunz. 2000. "Postnatal Growth and Age Estimation in Free-Ranging Bats: A Comparison of Longitudinal and Cross-Sectional Sampling Methods." *Journal of Mammalogy* 81: 709–18.
- Barclay, R. M. R. 2012. "Variable Variation: Annual and Seasonal Changes in Offspring Sex Ratio in a Bat." *PLoS One* 7: 1–7.
- Bates, D. M., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Belwood, J. J., and J. H. Fullard. 2009. "Echolocation and Foraging Behaviour in the Hawaiian Hoary Bat, *Lasiurus cinereus cermotus*." *Canadian Journal of Zoology* 62: 2113–20.
- Bonamour, S., L. M. Chevin, D. Réale, C. Teplitsky, and A. Charmanier. 2020. "Age-Dependent Phenological Plasticity in a Wild Bird." *Journal of Animal Ecology* 89: 2733–41.
- Bowler, D. E., H. Heldbjerg, A. D. Fox, M. de Jong, and K. Böhning-Gaese. 2019. "Long-Term Declines of European Insectivorous Bird Populations and Potential Causes." *Conservation Biology* 33: 1120–30.
- Boyles, J. G., P. M. Cryan, G. F. McCracken, and T. H. Kunz. 2011. "Economic Importance of Bats in Agriculture." *Science* 332: 41–2.
- 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: 132–8.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.
- Cheng, T. L., A. Gerson, M. S. Moore, J. D. Reichard, J. DeSimone, C. K. R. Willis, W. F. Frick, and A. M. Kilpatrick. 2018. "Higher Fat Stores Contribute to Persistence of Little Brown Bat Populations with White-Nose Syndrome." *Journal of Animal Ecology* 88: 591–600.
- Conrad, K. F., M. S. Warren, R. Fox, M. S. Parsons, and I. P. Woiwod. 2006. "Rapid Declines of Common, Widespread British Moths Provide Evidence of an Insect Biodiversity Crisis." *Biological Conservation* 132: 279–91.
- R Core Team. 2016. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing.
- Cormack, R. M. 1964. "Estimates of Survival from the Sighting of Marked Animals." *Biometrika* 51: 429–38.
- Cox, A. R., R. J. Robertson, Z. Lendvai, K. Everitt, and F. Bonier. 2019. "Rainy Springs Linked to Poor Nestling Growth in a Declining Avian Aerial Insectivore (*Tachycineta bicolor*)." *Proceedings of the Royal Society B: Biological Sciences* 286: 20190018.
- Davis, W. H., and H. B. Hitchcock. 1995. "A New Longevity Record for the Bat *Myotis lucifugus*." *Bat Research News* 36: 6.
- de Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. "Climate Change Impacts on Future Boreal Fire Regimes." *Forest Ecology and Management* 294: 35–44.
- Didham, R. K., Y. Basset, C. M. Collins, S. R. Leather, N. A. Littlewood, M. H. M. Menz, J. Müller, et al. 2020. "Interpreting Insect Declines: Seven Challenges and a Way Forward." *Insect Conservation and Diversity* 13: 103–14.

- Dunn, J. C., K. C. Hamer, and T. G. Benton. 2017. "Dynamics of Phenotypic Change: Wing Length Declines in a Resident Farmland Passerine despite Survival Advantage of Longer Wings." *Ibis* 159: 152–7.
- English, P. A., J. J. Nocera, and D. Green. 2018. "Nightjars May Adjust Breeding Phenology to Compensate for Mismatches between Moths and Moonlight." *Ecology and Evolution* 8: 5515–29.
- Florko, K. R., S. J. Bohn, M. C. Kalcounis-Rueppell, and R. M. Brigham. 2017. "A 23-Year-Old Little Brown Bat (*Myotis lucifugus*) Record from Southwest Saskatchewan, Canada." *Northwestern Naturalist* 98: 57–9.
- Frick, W. F., D. S. Reynolds, and T. H. Kunz. 2009. "Influence of Climate and Reproductive Timing on Demography of Little Brown Myotis *Myotis lucifugus*." *Journal of Animal Ecology* 79: 128–36.
- Gardner, J. L., R. Heinsohn, and L. Joseph. 2009. "Shifting Latitudinal Clines in Avian Body Size Correlate with Global Warming in Australian Passerines." *Proceedings of the Royal Society B: Biological Sciences* 276: 3845–52.
- Geipel, I., M. J. Smeeke, W. Halfwerk, and R. A. Page. 2019. "Noise as an Informational Cue for Decision-Making: The Sound of Rain Delays Bat Emergence." *Journal of Experimental Biology* 222: jeb192005.
- Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. "The Influence of Precipitation on Reproduction by *Myotis* Bats in British Columbia." *American Midland Naturalist* 128: 339–4.
- Hallmann, C. A., M. Sorg, E. Jongejans, H. Siepel, N. Hofland, H. Schwan, W. Stenmans, et al. 2017. "More than 75 Percent Decline over 27 Years in Total Flying Insect Biomass in Protected Areas." *PLoS One* 12: e0185809.
- Hermanussen, M., M. de Los Angeles, A. P. Roi de Lama, C. A. Romero, J. B. Ruiz, and J. A. F. Tresguerres. 1996. "Differential Catch-Up in Body Weight and Bone Growth after Short-Term Starvation in Rats." *Growth Regulation* 6: 230–7.
- Jolly, G. M. 1965. "Explicit Estimates from Capture-Recapture Data with both Death and Immigration-Stochastic Model." *Biometrika* 52: 225–47.
- Jung, T. S. 2020. "Bats in the Changing Boreal Forest: Response to a Megafire by Endangered Little Brown Bats (*Myotis lucifugus*)." *Écoscience* 27: 59–70.
- Kaupas, L., and R. M. R. Barclay. 2018. "Temperature-Dependent Consumption of Spiders by Little Brown Bats (*Myotis lucifugus*), but Not Northern Long-Eared Bats (*M. septentrionalis*), in Northern Canada." *Canadian Journal of Zoology* 96: 261–8.
- Kelly, J., E. S. Bridge, W. F. Frick, and P. B. Chilson. 2013. "Ecological Energetics of an Abundant Aerial Insectivore, the Purple Martin." *PLoS One* 8: 1–8.
- Kelly, R., R. Friedman, and S. E. Santana. 2018. "Primary Productivity Explains Size Variation across the Pallid bat's Western Geographic Range." *Functional Ecology* 32: 1520–30.
- Kunz, T. H., and E. L. P. Anthony. 1982. "Age Estimation and Post-Natal Growth in the Bat *Myotis lucifugus*." *Journal of Mammalogy* 63: 23–32.
- Lank, D. B., C. Xu, B. A. Harrington, R. I. G. Morrison, C. L. Gratto-Trevor, P. W. Hicklin, B. K. Sandercock, et al. 2017. "Long-Term Continental Changes in Wing Length, but Not Bill Length, of a Long-Distance Migratory Shorebird." *Ecology and Evolution* 7: 3243–56.
- Lister, B. C., and A. Garcia. 2018. "Climate-Driven Declines in Arthropod Abundance Restructure a Rainforest Food Web." *Proceedings of the National Academy of Sciences* 115: E10397–406.
- Long, J. 2019. "jtools: Analysis and Presentation of Social Scientific Data." R Package Version 2.0.1.
- McGuire, L. P., L. A. Kelly, D. E. Baloun, W. A. Boyle, T. L. Cheng, J. Clerc, N. W. Fuller, et al. 2018. "Common Condition Indices Are no more Effective than Body Mass for Estimating Fat Stores in Insectivorous Bats." *Journal of Mammalogy* 99: 1065–71.
- Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson. 2016. "Differences in Spatial Synchrony and Interspecific Concordance Inform Guild-Level Population Trends for Aerial Insectivorous Birds." *Ecography* 39: 774–86.
- Nebel, S., J. Casey, M. A. Cyr, K. J. Kardynal, E. A. Krebs, E. F. Purves, M. Bélisle, et al. 2020. "Falling through the Policy Cracks: Implementing a Roadmap to Conserve Aerial Insectivores in North America." *Avian Conservation and Ecology* 15: 1–8.
- Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2011. "Declines of Aerial Insectivores in North America Follow a Geographic Gradient." *Avian Conservation and Ecology* 5: 1.
- Nyffeler, M., Ç. H. Şekercioglu, and C. J. Whelan. 2018. "Insectivorous Birds Consume an Estimated 400–500 Million Tons of Prey Annually." *Science of Nature* 105: 47.
- Powell, L. L., N. J. Cordeiro, and J. A. Stratford. 2015. "Ecology and Conservation of Avian Insectivores of the Rainforest Understory: A Pantropical Perspective." *Biological Conservation* 188: 1–10.
- Peers, M. J. L., Y. N. Majchrzak, E. K. Studd, A. K. Menzies, P. M. Kukka, S. M. Konkolic, R. Boonstra, S. Boutin, and T. S. Jung. 2021. "Evaluation of Gum-Line Recession for Aging Lynx (*Lynx canadensis*)." *Wildlife Society Bulletin* 45: 706–10.
- Prokosch, J., Z. Bernitz, H. Bernitz, B. Erni, and R. Altwegg. 2019. "Are Animals Shrinking Due to Climate Change? Temperature-Mediated Selection on Body Mass in Mountain Wagtails." *Oecologia* 189: 841–9.
- Ratcliffe, J. M., and J. W. Dawson. 2003. "Behavioural Flexibility: The Little Brown Bat, *Myotis lucifugus*, and the Northern Long-Eared Bat, *M. septentrionalis*, both Glean and Hawk Prey." *Animal Behaviour* 66: 847–56.
- Riemer, K., R. P. Guralnick, and E. P. White. 2018. "No General Relationship between Mass and Temperature in Endothermic Species." *eLife* 7: 1–16.
- Rioux Paquette, S., F. Pelletier, D. Garant, and M. Bélisle. 2014. "Severe Recent Decrease of Adult Body Mass in a Declining Insectivorous Bird Population." *Proceedings of the Royal Society B: Biological Sciences* 281: 20140649.
- Romano, T., J. D. Wark, and M. E. Woldek. 2010. "Calcium Supplementation Does Not Rescue the Programmed Adult Bone Deficits Associated with Perinatal Growth Restriction." *Bone* 47: 1054–64.
- Salewski, V., W. M. Hochachka, and W. Fiedler. 2010. "Global Warming and Bergmann's Rule: Do Central European Passerines Adjust their Body Size to Rising Temperatures?" *Oecologia* 162: 247–60.
- Seber, G. A. F. 1965. "A Note on the Multiple-Recapture Census." *Biometrika* 52: 249–59.

- Sherwin, H. A., W. I. Montgomery, and M. G. Lundy. 2013. "The Impact and Implications of Climate Change for Bats." *Mammal Review* 43: 171–82.
- 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 Multi-Method Approach." *Canadian Journal of Zoology* 96: 31–8.
- Shortall, C. R., A. Moore, E. Smith, M. J. Hall, I. P. Woiwod, and R. Harrington. 2009. "Long-Term Changes in the Abundance of Flying Insects." *Insect Conservation and Diversity* 2: 251–60.
- Sikes, R. S. 2016. "2016 Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research and Education." *Journal of Mammalogy* 97: 663–88.
- 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: 311–20.
- Slough, B. G., and T. S. Jung. 2008. "Observations on the Natural History of Bats in the Yukon." *The Northern Review* 29: 127–50.
- Spiller, K. J., and R. Dettmers. 2019. "Evidence for Multiple Drivers of Aerial Insectivore Declines in North America." *Condor* 121: 1–13.
- Streicker, J. 2016. "Yukon Climate Change Indicators and Key Findings 2015." Northern Climate ExChange, Yukon Research Centre, Yukon College, 84 p.
- Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, et al. 2014. "Temperate and Boreal Forest Mega-Fires: Characteristics and Challenges." *Frontiers in Ecology and Environment* 12: 115–22.
- Teplitsky, C., and V. Millien. 2014. "Climate Warming and Bergmann's Rule through Time: Is there any Evidence?" *Evolutionary Applications* 7: 156–68.
- van Buskirk, J., R. S. Mulvihill, and R. C. Leberman. 2010. "Declining Body Sizes in North American Birds Associated with Climate Change." *Oikos* 119: 1047–55.
- van Gils, J. A., S. Lisovski, T. Lok, W. Meissner, A. Ożarowska, J. De Fouw, E. Rakhimberdiev, M. Y. Soloviev, T. Piersma, and M. Klaassen. 2016. "Body Shrinkage Due to Arctic Warming Reduces Red Knot Fitness in Tropical Wintering Range." *Science* 352: 819–21.
- Voigt, C. C., K. Schneeberger, S. L. Voigt-heucke, and D. Lewanzik. 2011. "Rain Increases the Energy Cost of Bat Flight." *Biology Letters* 7: 793–5.
- Von Zuben, V. 2022. "Yukon Bat Size." OSF. <https://osf.io/3q9cm/>.
- Wagner, D. L., R. Fox, D. M. Salcido, and L. A. Dyer. 2021. "A Window to the World of Global Insect Declines: Moth Biodiversity Trends Are Complex and Heterogeneous." *Proceedings of the National Academy of Sciences of the United States of America* 118: 1–8.
- Weeks, B. C., D. E. Willard, M. Zimova, A. A. Ellis, M. L. Witynski, M. Hennen, and B. M. Winger. 2020. "Shared Morphological Consequences of Global Warming in North American Migratory Birds." *Ecology Letters* 23: 316–25.
- White, G. C., and K. P. Burnham. 1999. "Program MARK: Survival Estimation from Populations of Marked Animals." *Bird Study* 46: S120–39.
- Wood, S. N., N. Pya, and B. Säfken. 2016. "Smoothing Parameter and Model Selection for General Smooth Models." *Journal of the American Statistical Association* 111: 1548–63.
- Yom-Tov, Y., S. Yom-Tov, J. Wright, C. J. R. Thorne, and R. Du Feu. 2006. "Recent Changes in Body Weight and Wing Length among some British Passerine Birds." *Oikos* 112: 91–101.
- Zahn, A., L. Rodrigues, A. Rainho, and J. M. Palmeirim. 2007. "Critical Times of the Year for *Myotis myotis*, a Temperate Zone Bat: Roles of Climate and Food Resources." *Acta Chiropterologica* 9: 115–25.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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