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Cover Photograph: Juvenile Eastern Small-footed Bat parasitized by chiggers. This bat was in the crevice of a large boulder in Shenandoah National Park. Photograph © Paul Moosman.

Logo by Ashley K. Wilson.

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Patterns in Abundance of Eastern Small-footed Bats in Virginia: Long-term Trends and Responses to Disease and Climate

Paul R. Moosman, Jr.^{1,*}, David M. Marsh², Richard J. Reynolds³, and Emily K. Pody⁴

Abstract - *Myotis leibii* (Eastern Small-footed Bat) occurs in low numbers throughout its range in eastern North America. Its populations have been impacted by white-nose syndrome (WNS), but low and variable counts in hibernacula make it difficult to assess population trends. We studied numbers of bats counted in hibernacula, from 1980 to 2023, and on talus slopes in summer, from 2013 to 2025, to understand population trends in Virginia, USA. Winter bat numbers exhibited a long-term positive trend that was punctuated by low counts in the period after WNS arrived and high counts following rainy summers. Summer bat numbers showed no temporal trend, but high counts were linked with warm summers. Our results suggest that *M. leibii* populations in Virginia are stable and have survived WNS better than populations of other eastern *Myotis*. However, detecting changes in abundance of *M. leibii* with hibernacula surveys alone remains challenging; thus, biologists should include talus surveys in monitoring efforts.

Introduction

Insectivorous bats face multiple conservation threats, such as habitat loss, disease, pesticide exposure, mortality from wind-energy facilities, and climate change (Festa et al. 2023, Frick et al. 2019). Among these, white-nose syndrome (WNS), caused by the fungus *Pseudogymnoascus destructans* (Blehert and Gargas) Minnis and D. L. Lindner (Pd), has emerged as 1 of the greatest threats to North American bat populations (Blehert et al. 2009, Cheng et al. 2021). Shortly after it was discovered in 2006, WNS caused severe declines in hibernating populations of *Myotis lucifugus* (Le Conte) (Little Brown Bat), *M. septentrionalis* (Trouessart) (Northern Long-eared Bat), *Perimyotis subflavus* (Cuvier) (Tricolored Bat), and *Myotis sodalis* Miller and Allen (Indiana Bat) (Frick et al. 2017, Ingersoll et al. 2013, Johnson et al. 2021, Kurta and Smith 2020, Perea et al. 2024, Pettit and O’Keefe 2017). Hibernacula surveys, acoustic surveys, and capture efforts during summer and swarming (mating season) demonstrated clear population declines in these 4 species (Dzal et al. 2011, Ford et al. 2011, Francel et al. 2012, Hooton et al. 2023).

Quantifying the threat that WNS poses for bats that infrequently roost in caves and mines has been challenging. For example, even before the emergence of WNS, *Myotis leibii* (Audubon and Bachman) (Eastern Small-footed Bat; hereafter, Small-footed Bat) was considered rare in North America (Best and Jennings 1997), and its response to the disease has not been extensively studied. Hibernacula surveys from the first 5 years after emergence of WNS indicated that Small-footed Bats suffered reduced numbers initially but maintained positive overall population growth (Langwig et al. 2012). Summer capture rates of this species declined substantially in New Hampshire (by 68% of captures/net-night; Moosman et al. 2013) and West Virginia (by 84% of captures/net-night; Francel et al. 2012) within the same period. However, no significant changes in capture rates during summer surveys occurred in Arkansas, North Carolina, Tennessee, and West Virginia (Johnson et al. 2021, O’Keefe et al. 2019, Sasse and Perry 2023), and capture rates

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increased at swarming sites in Ontario, Canada (Hooton et al. 2023). It is unclear whether the mixed results of past studies are from differences in methods or geographic or temporal variation in the effects of WNS on Small-footed Bats.

Monitoring Small-footed Bat populations with hibernacula surveys is challenging. The number of these bats counted in winter is low and highly variable; for example, they constitute <1% of bats in hibernacula in Vermont (Trombulak et al. 2001). Small-footed Bats may be infrequently detected in hibernation because they overwinter in microsites that are under-surveyed, such as inside crevices and under rocks in caves and mines, within crevices of aboveground rock ledges (Best and Jennings 1997, Moosman et al. 2017), and possibly in deep interstitial spaces of talus slopes (Moosman et al. 2015, Saugey et al. 1993). While such roosting habits likely reduce susceptibility to WNS (Frick et al. 2017, Langwig et al. 2012), they also suggest that standard surveys of overwintering bats in caves, mines, and tunnels may not be sufficient for monitoring this species.

Climatic conditions also may add to the challenges of understanding trends in bat populations by affecting bat behavior and detectability. The number of Indiana Bats and *Pipistrellus pipistrellus* (Schreber) (Common Pipistrelles) counted in hibernation increases during severe winters (Kerbiriou et al. 2015, Thogmartin and McKann 2014), and Little Brown Bats time their arousals and emergence from hibernation with barometric changes that accompany warm-weather events in late winter (Czenze and Willis 2015, Meyer et al. 2016). Similarly, temperature influences roost selection and is suspected to affect group size during the active season (e.g., Lausen and Barclay 2002, Ruczyński 2006, Webber and Willis 2018). Such effects could bias population assessments and highlight the need for standardization, controls, and using multiple types of surveys (Ingersoll et al. 2013, Reichert et al. 2021).

During summer, Small-footed Bats are strongly associated with emergent rock formations (Kearny et al. 2023, Moosman et al. 2023), and visual searches have been found to be useful for documenting distribution, occupancy, and abundance of multiple species of rock-roosting bats (Johnson et al. 2024, Kearny et al. 2022, McEwan and Bachen 2017, Moosman et al. 2020, Whitby et al. 2013). In 2013, we initiated annual visual surveys of Small-footed Bats on talus slopes during summer (e.g., Moosman et al. 2015, 2020), to supplement hibernacula data and improve monitoring of this species in Virginia, where WNS was first documented in winter 2008–2009 (Powers et al. 2015). To improve understanding of population trends of this species in the state and to guide future monitoring programs, we estimated changes in winter bat numbers associated with the arrival of WNS and year-to-year fluctuations in both types of surveys, and tested whether bat numbers correlated with climatic conditions during the preceding or current year.

Field-site Description

We surveyed bats in 11 hibernacula in the Valley and Ridge physiographic province of western Virginia (Fig. 1). The Valley and Ridge province is a karst region of long, parallel valleys and ridges, with respective elevations in Virginia of approximately 300 and 1400 m (Fenneman 1938, Keyes et al. 1995). Its ridges are vegetated by secondary mixed-deciduous forests, but valleys have mostly been converted to pasturelands. We also surveyed Small-footed Bats at 6 talus slopes in the Blue Ridge physiographic province, which is located east of the Valley and Ridge province and forms the easternmost chain of the Appalachian Mountains (Fenneman 1938, Keyes et al. 1995). The Blue Ridge province is covered by mature secondary mixed-deciduous forest, with elevations in Virginia >1200 m. Its flanks and ridgetops have exposed greenstone and quartz-sandstone that has fragmented into talus slopes (rocks ≥ 30 -cm wide) or scree fields (rocks <30-cm wide). These aggregations of rock create canopy-free patches with abundant crevices, most commonly on southern flanks and summits (Moosman et al. 2020).

Methods

Review of historical winter surveys

We examined data from 11 caves surveyed between November and March 1980–2023. Most winter surveys were completed by biologists from Virginia Department of Wildlife Resources and Virginia Department of Conservation and Natural Resources. We excluded surveys at Hupman's Saltpeter Cave in 1994 and 1996 and a survey from Shires Saltpeter Cave in 1987 because we suspected they were incomplete (i.e., only Indiana Bats may have been recorded). Additionally, we excluded surveys at Hupman's Saltpeter Cave in 1949 and Starr Chapel Cave in 1979 because contemporaneous counts at other sites did not exist. An average of 2.6 ± 2.1 (SD) years occurred between surveys at each site, but with gaps of 12–15 years at 4 sites. Two surveys were conducted within the same year at Higgenbotham No. 1 Cave and Starr Chapel Cave; therefore, to avoid pseudoreplication we only used data from the survey at each site that was conducted closest to mid-winter.

Summer surveys

We quantified Small-footed Bat numbers during parturition and lactation by visually searching for bats roosting on talus slopes, between 24 May and 26 July 2013–2025. We searched rock crevices in circular plots of 5–10-m radius that were distributed randomly in the non-forested portion of talus slopes, with the number of plots per site varying from 3 to 8, based on area of talus (Moosman et al. 2020). Two or 3 trained observers searched plots, recording the number of bats visible and whether bats were solitary or in groups. We marked crevices with colored chalk after surveying, to prevent redundant efforts and to reduce chances of leaving crevices unsearched. Moosman et al. (2020) estimated detection in talus surveys to be ~64%, with surveyors failing to detect 18% of bats due to human error and another 18% of bats because they roosted in hidden locations. Work for this study was conducted under scientific collection permits from the Virginia Department of Wildlife Resources and with approval from the Animal Subjects Committee at the Virginia Military Institute.

Assessing trends in bat numbers

We studied trends in winter bat numbers, using each survey as the sampling unit. Surveys conducted within the same hibernation season were coded by year, corresponding to the start of

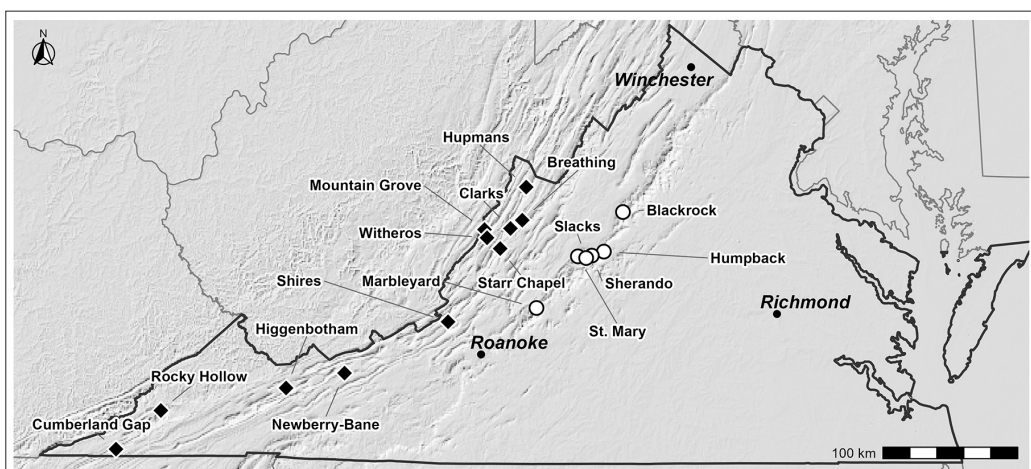


Figure 1. Approximate locations of Eastern Small-footed Bat (*Myotis leibii*) hibernacula (black diamonds) that were surveyed in winter from 1980 to 2023 and talus slopes (white circles) that were surveyed in summer from 2013 to 2025, in the Appalachian Mountains of Virginia, USA.

each winter. Because we had a single winter survey per site per year, we were unable to estimate observation error independently from abundance (Kéry et al. 2009, Udell et al. 2024). Thus, our study only addressed changes in the number of bats counted, rather than changes in abundance per se, but we considered additional lines of evidence that bear on which processes (e.g., bat movement vs. survival) had the most influence on our results. We fit bat numbers to mixed models using package glmmTMB (McGillcuddy et al. 2025) in R version 4.4 (R Core Team 2024). Our coding and data are available through Open Science Framework (<https://osf.io/f7bzv/overview>).

We assessed whether winter bat numbers increased or decreased over time and across sites and examined whether the arrival of WNS changed temporal trends in the numbers of bats counted. We modeled bat numbers as negative binomial and used a log-link function to relate the bat numbers to predictor variables and random effects. Thus, we reported β for trend estimates but expressed annual changes in numbers as a percentage and as a model-estimated finite rate of increase ($\lambda = e^\beta$), for comparison with published population growth rates. In all models, a random intercept for site accounted for differences in the magnitude of bat numbers across sites, and a random effect for year (“YearCAT”) accounted for spatial and temporal autocorrelation in trends. Most models included a random slope for Site, to allow different trends across sites (Table 1). For Time, we used the year 1980 as the starting point (i.e., 0) and increased to 43 for the year 2023.

We considered that WNS could have 2 distinct effects on winter bat numbers. First, numbers could be reduced across sites following the arrival of WNS, and we evaluated this by adding a fixed effect for “Period”, corresponding to data before or after the disease was first detected in Virginia (winter 2008–2009). Second, we considered that WNS could change the trends in bat numbers after that winter. This was evaluated as an interaction between period and year (Table 1). We compared models using the Akaike Information Criterion corrected for small sample size (AIC_c) and used trend estimates that were model averaged across the most parsimonious models (Burnham and Anderson 2002).

We compared estimated annual trends from the summer and winter data for the same set of years. For both data sets, we used a model that included a time variable for years when data existed

Table 1. Models used to assess trends in the number of Eastern Small-footed Bats (*Myotis leibii*) counted during winter surveys in Virginia, USA, from 1980 to 2023. Terms in parentheses indicate a normally distributed random effect. “YearCAT” is a categorical variable for year that accounts for correlated fluctuations among sites, whereas “Year” is a numerical variable for year since 1980 that accounts for trends in counts over time. Bat numbers were modelled as negative binomial in all cases.

Terms in the model	Explanation
1 + (1 Site) + (1 YearCAT)	No changes over time, but bat numbers vary among sites and years
Year + (1 Site) + (1 YearCAT)	Bat numbers change over time and vary among sites and years
Year + (1 Site) + (1 YearCAT)	Only examines data before 2008; bat numbers change over time, and vary among sites and years
Year + (1+Year Site) + (1 YearCAT)	Bat numbers change over time and trends vary among sites; bat numbers vary among sites and years
Year + Period + (1 Site) + (1 YearCAT)	Bat numbers change over time and may decrease post-2008; bat numbers vary among sites and years
Year + Period + (1+Year Site) + (1 YearCAT)	Bat numbers change over time and may decrease post-2008; trends vary among sites and bat numbers vary among sites and years

for both survey types (since 2012), a random effect for site, and a random effect for survey year. Because summer data included multiple plots within sites, we accounted for this with a random intercept for plot nested within site (Moosman et al. 2020). We additionally accounted for the number of crevices searched, which was an important predictor of bat numbers in a prior study (Moosman et al. 2020). Lastly, we used a yearly random effect to compare whether winter and summer bat numbers were correlated.

Relationships between bat numbers and climatic factors

We assessed the relationship between climatic variables and bat populations (precipitation in the previous summer; temperature in the previous winter) and detectability (temperature in the winter of each hibernacula survey; temperature in the summer of each talus survey). For winter, we focused on whether warm or cold external conditions influenced hibernation site selection; for summer, we also examined whether temperature drove changes in roost selection or group size on talus slopes. For each county and year combination from 1980 to 2025, we obtained average temperature and precipitation for the 3-month period that closely coincided with the summer reproductive season (June–August) or winter hibernation season (December–February of the following year) (NOAA 2025). Climatic data were available for 7 counties (Bath, Bland, Craig, Highland, Lee, Tazewell, and Wise) with hibernacula counts and for 3 counties (Augusta, Rockbridge, and Rockingham) with talus survey sites. We regressed both winter temperature and summer precipitation with the year of study, using site as a random intercept and assuming that temperature and precipitation were normally distributed. Since bat counts exhibited high fluctuations from year to year, we assessed whether fluctuations in numbers were associated with warm versus cold winters or with wet versus dry summers.

We quantified extremes in climatic variables by regressing each variable on a fixed effect for year of study (i.e., a trend parameter) and a random effect for site that allowed overall differences in temperature or precipitation across sites. We then extracted residual values for each year and site combination to represent climate anomalies, which indicated whether a given year was unusually warm or wet after accounting for climatic trends and site differences. We incorporated these residuals, 1 at a time, into a model for bat numbers, including the terms from the most supported model from the trend analysis. This approach addressed whether warm winters (current or prior winter) or wet summers were associated with yearly changes in bat numbers on top of any overall trends in the data or effects of WNS.

For each climate residual (temperature in the current survey season, prior winter temperature, prior summer precipitation), we examined whether confidence intervals for regression coefficients overlapped 0 and whether the model that included each variable had a lower AIC_c value ($\Delta\text{AIC}_c > 2$) than a model without that variable. We also explored if climate might influence long-term trends in bat numbers, rather than just year-to-year fluctuations in 2 ways—by not detrending the climate data, to check whether coefficients for climate variables remained similar to those from detrended models, and by comparing models of bat numbers with or without the yearly trend (but including climate variables) (see Supplemental File 1, available online at <https://osf.io/t7bzv/overview>).

For summer surveys, we added each climatic variable, 1 at a time, to a model for bat numbers that included year of the study, the number of crevices searched, and a random intercept for site and plot within site. Based on initial results, we conducted post-hoc analyses, to understand if summer temperature residual influenced the size or prevalence of reproductive groups on talus slopes. Similar to our approach with summer bat numbers, we modeled numbers of hibernating bats roosting in groups by using a negative binomial generalized linear mixed model, and we examined the binary presence of groups (0 = no group observed; 1 = group observed) with a logistic model.

Results

Trends in bat numbers

Winter numbers were generally low and variable between years (median = 2 bats; range = 0–64), with 6 sites having median counts of 0–2 bats and the remainder having median counts of 4–5 bats (Fig. 2). The most parsimonious model for winter numbers included a positive annual trend, a decrease in number of bats counted following arrival of WNS, and a random slope for site (i.e., trends varied across sites) (Table 2). A model that also included an interaction between period and year, to allow for changes in population trends following arrival of WNS, had less support ($\Delta\text{AIC}_c = 2.08$). Confidence intervals in this model for period (-2.19 – 1.24) and the period * year interaction (-0.068 – 0.046) were wide, indicating that the data were insufficient to distinguish these additional effects. A model that lacked a WNS period effect had an AIC_c 4.08 units higher than the best model, and all other models had negligible support ($\Delta\text{AIC}_c > 32$), with the no-trend model being the least supported.

The annual trend parameter was positive in all models that included this term. In models without a WNS period effect, the model-averaged trend estimate from 1980 to 2023 was 0.043 (95% CI: 0.003–0.078), representing a 4.4% annual increase in bat numbers. In models that included a WNS period effect, the annual trend estimate was larger ($\beta = 0.068$; 95% CI: 0.024–0.113), corresponding to a 7.6% annual increase, because the trend term compensated for lower counts after 2008. In models that contained a main effect for period, the model-averaged WNS effect was -0.785 (95% CI: -1.407 – 0.162), representing a 54.4% reduction in counts after 2008. In a model that only examined trends in numbers before arrival of WNS, with inter-annual and site-level variation, winter counts increased ($\beta = 0.061$; 95% CI: 0.006–0.116) by 6.3% (95% CI: 0.58–12.32%) per year from 1980 to 2007.

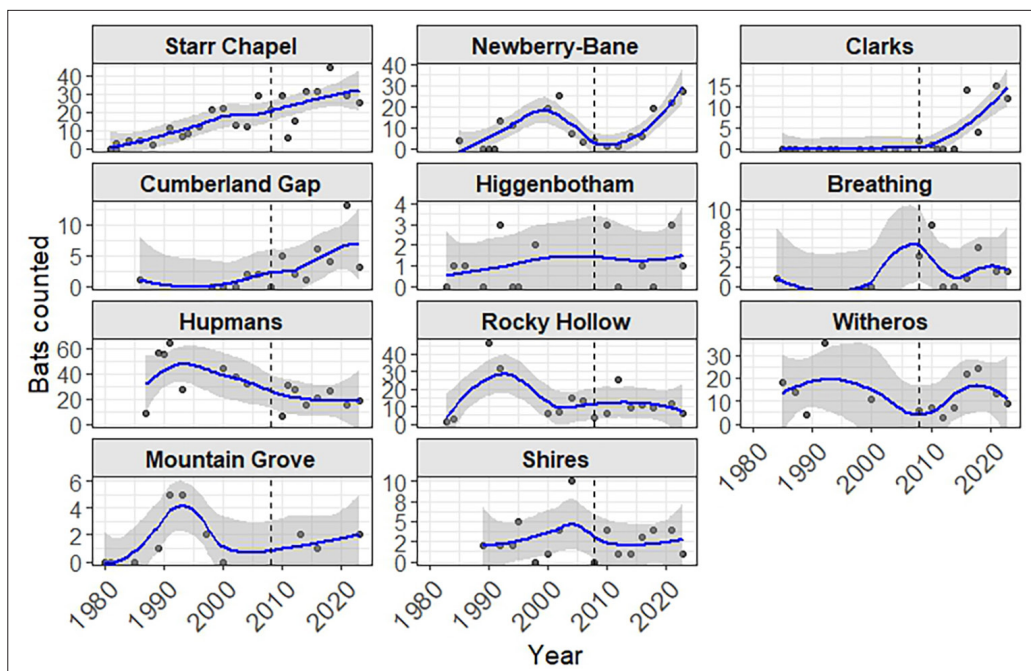


Figure 2. Numbers of hibernating Eastern Small-footed Bats (*Myotis leibii*) counted at 11 sites in Virginia, USA, from 1980 to 2023. Dashed vertical line indicates when white-nose syndrome was first documented in the state (winter of 2008–2009). Smoothed trend lines and 95% confidence ribbons are shown for individual hibernacula.

The random slope for site was variable ($SD = 0.057$), demonstrating heterogeneity in annual trends among sites. Estimated site-specific trends ranged from 0.015 at Hupman’s Saltpeter Cave, Highland County, to 0.121 at Clark’s Cave, Bath County, corresponding to between a 1.5% and 12.9% annual increase in winter bat numbers, respectively. The model set suggests an increase in bat numbers over time, with moderate variation among sites, and some evidence of declines corresponding with WNS period. Adding a period effect did not substantially alter the estimated inter-annual fluctuations in winter numbers. Models with and without the period term were highly correlated ($r = 0.86$), indicating years with high or low numbers of bats remained so regardless of whether the period variable was included.

Summer counts on talus slopes exhibited no significant change in bat numbers from 2013 to 2025 (Fig. 3). The model that included the number of crevices searched and random intercepts for plot and site showed a non-significant trend in bat numbers of -0.02 (95% CI: -0.075–0.033), corresponding to an annual change of about -2.0% with 95% CI of -7.2–3.4%. Change in winter bat numbers within the same period (2013–2023) was not statistically distinguishable from zero ($\beta = 0.05$; 95% CI: -0.023–0.116), with an estimated annual change of 4.8% (95% CI: -2.3–12.3%). When we directly compared summer and winter bat numbers, the correlation between the random effects for the different survey types was positive ($r = 0.38$), but the confidence intervals were large due to the small number of years (95% CI: -0.63–0.90).

Table 2. The most parsimonious models of winter numbers of Eastern Small-footed Bats (*Myotis leibii*) in hibernacula in Virginia, USA, from 1980 to 2023. The number of parameters (K), Akaike Information Criterion corrected for small sample size (AIC_c), support compared to the top model (ΔAIC_c), AIC weight (AIC_c Wt), and log-likelihood value (LL) are shown for each model.

Terms in the model	K	AIC_c	ΔAIC_c	AIC_c Wt	LL
Period + Trend, random slope	8	985.84	0.00	0.67	-484.48
Period * Trend, random slope	9	987.92	2.08	0.24	-484.41
Trend, random slope	7	989.92	4.08	0.09	-487.62
Period + Trend	6	1018.37	32.53	0.00	-502.93
Trend	5	1020.37	34.53	0.00	-505.01
Intercept only	4	1030.62	44.78	0.00	-511.19

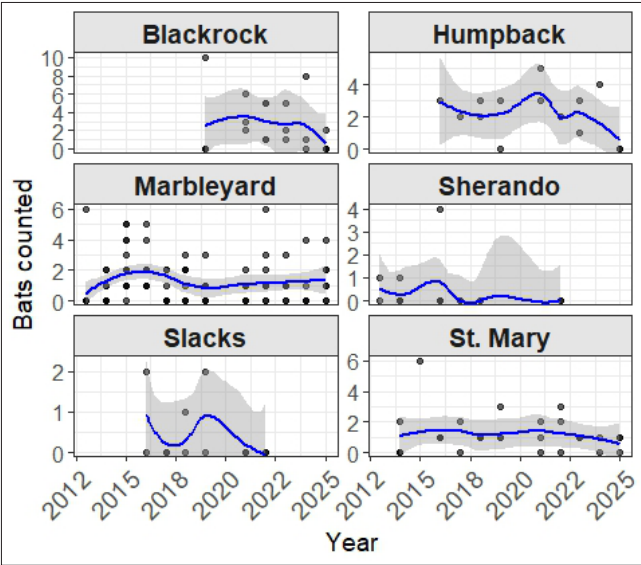


Figure 3. Numbers of Eastern Small-footed Bats (*Myotis leibii*) counted per randomized plot on 6 talus slopes during summer, in Virginia, USA, from 2013 to 2025. The number of bats in each plot, smoothed trend lines, and 95% confidence ribbons are shown for individual sites.

Relationship between bat numbers and climatic factors

From 1980 to 2025, average temperature and precipitation for counties in the Valley and Ridge province with hibernacula was $1.3 \pm 1.7\text{ }^{\circ}\text{C}$ and $27.1 \pm 8.2\text{ cm}$ in winter (December–February) and $20.9 \pm 1.2\text{ }^{\circ}\text{C}$ and $32.0 \pm 7.2\text{ cm}$ of precipitation in summer (June–August) (NOAA 2025). At talus study sites in the Blue Ridge province, winters were similar ($1.6 \pm 1.5\text{ }^{\circ}\text{C}$) and had less precipitation ($22.0 \pm 7.5\text{ cm}$), and summers were warmer ($21.9 \pm 0.8\text{ }^{\circ}\text{C}$) and drier ($30.8 \pm 8.2\text{ cm}$), compared with counties in the Valley and Ridge province. Climatic conditions at hibernacula shifted substantially from 1980 to 2025. Winters grew warmer ($0.045\text{ }^{\circ}\text{C}/\text{year}$; 95% CI: $0.029\text{--}0.061$) and wetter ($0.130\text{ cm}/\text{year}$; 95% CI: $0.059\text{--}0.201$). Summers also warmed ($0.010\text{ }^{\circ}\text{C}/\text{year}$; 95% CI: $0.001\text{--}0.019$) but had inconsistent changes in rainfall ($0.031\text{ cm}/\text{year}$; 95% CI: $-0.046\text{--}0.107$).

Bat numbers in winter showed a modest positive association with precipitation in the prior summer ($\beta = 0.022$; 95% CI: $<0.001\text{--}0.043$). This corresponds to an estimated 11.4% increase in winter bat numbers for every 5 cm above normal summer precipitation, although the 95% CI for this effect was wide ($0.0\text{--}24.1\%$), and the relationship appeared site specific (Fig. 4). Fluctuations in winter bat numbers were not significantly related to temperature residuals in the previous winter ($\beta = 0.029$; 95% CI: $-0.071\text{--}0.128$) or to temperature residuals within the same winter of each survey ($\beta = 0.070$; 95% CI: $-0.032\text{--}0.172$), although graphical trends in the latter were apparent at some sites (see Supplemental File 2, available online at <https://osf.io/f7bzx/overview>).

In additional models for which winter numbers were not de-trended, allowing climatic variables to capture both long-term trends and interannual variation, only summer precipitation residuals

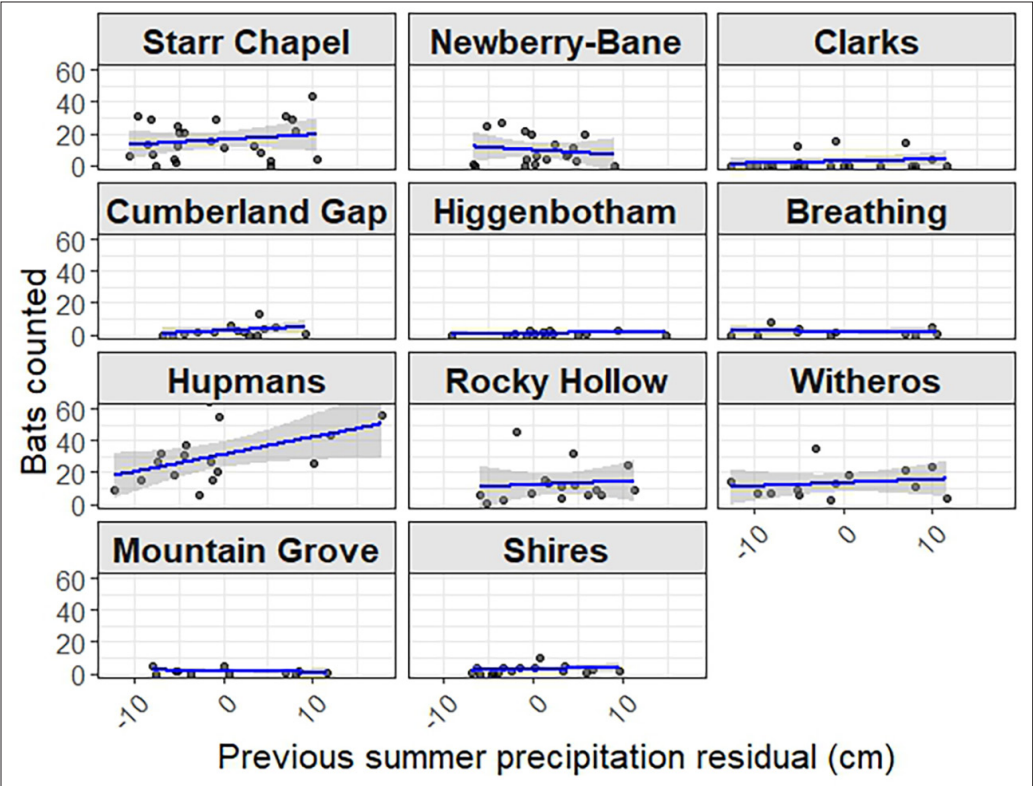


Figure 4. Relationship between the number of Eastern Small-footed Bats (*Myotis leibii*) counted in hibernation and the departure from normal rainfall in the summer preceding each survey, at 11 sites in Virginia, USA, from 1980 to 2023. Plots include trend lines and 95% confidence ribbons.

were supported as a driver of variation in bats counted (Supplemental File 1). The estimated effect of summer precipitation in this model was virtually unchanged from the detrended model ($\beta = 0.022$; 95% CI: 0.001–0.044). Similarly, when we compared models that included a long-term annual trend in winter bat numbers, summer precipitation residuals, or both, the model with both predictors had the strongest support. This indicates that summer precipitation residual and the long-term trend explained distinct components of variation in winter counts.

In contrast to winter bat count data, summer bat numbers were not closely related to either temperature residuals in the prior winter ($\beta = -0.006$; 95% CI: -0.161–0.150) or rainfall residuals in the prior summer ($\beta = -0.008$; 95% CI: -0.031–0.015), but the number of bats counted was positively correlated to temperature residual within the summer of the survey ($\beta = 0.37$; 95% CI: 0.034–0.709). This effect represents a 44.7% increase in expected summer bat numbers with each 1 °C increase above normal mean summer temperature (Fig. 5). Post-hoc models examining whether summer temperature residual influenced size of groups or their prevalence within plots suggested there was no significant relationship for either variable. For both group size ($\beta = 0.892$; 95% CI: -0.544–2.328) and the presence or absence of groups ($\beta = 0.717$; 95% CI: -0.357–1.791), the estimated effect for summer temperature residual was positive but with wide confidence intervals that overlapped zero.

Discussion

As elsewhere, counts of the Small-footed Bat in Virginia's hibernacula were quite low and variable and composed a fraction of the counts of other species reported from the same sites (Powers et al. 2015). It is these low counts coupled with high variability that likely have excluded Small-footed Bats from some population assessments. Despite these challenges, we found strong evidence that the number of Small-footed Bats counted during winter surveys increased over the 43-year period of our study. If the increased bat numbers are true reflections of population growth, as opposed to improved detection, the model estimated annual rate of Small-footed Bat population growth (λ) prior to WNS would have been 1.06 (95% CI: 1.00–1.12). This value approaches the maximum expected population

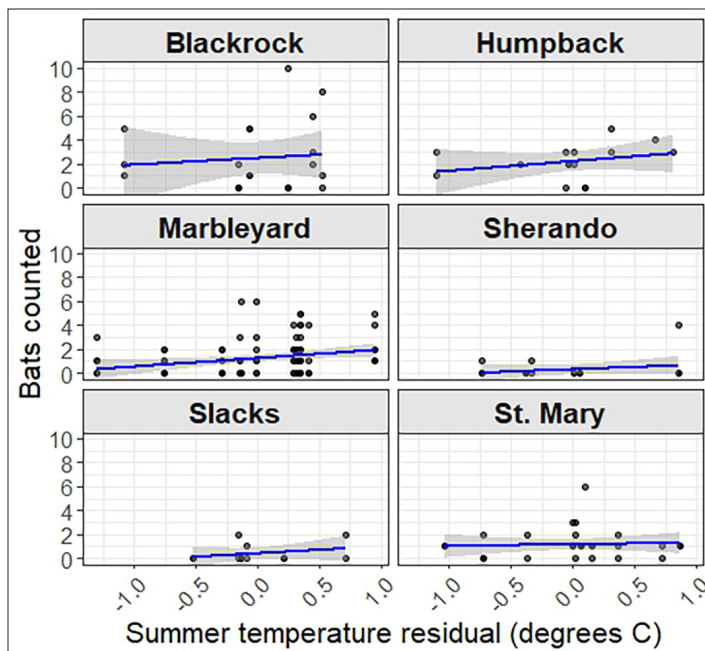


Figure 5. Relationship between the number of Eastern Small-footed Bats (*Myotis leibii*) counted per randomized plot and the departure from normal temperatures during the same summer of each survey, at 6 talus slopes in Virginia, USA, from 2013 to 2025. Graphs show abundance in each plot, with a linear trend and 95% confidence ribbon.

growth rates for Common Pipistrelles (Kerbirou et al. 2015) and approximates the realized rates for Little Brown Bats during periods of strong population growth (Frick et al. 2010b).

Johnson et al. (2021) first observed increasing summer captures of Small-footed Bats in the Central Appalachians of West Virginia beginning in 2003. What factors led to population growth for Small-footed Bats in our study region were unclear. Other North American species, including Little Brown Bats, Tricolored Bats, and *Myotis velifer* (J.A. Allen) (Cave Bats), also increased, likely because of pesticide bans, landscape changes, creation of artificial roosts, and gating of hibernacula entrances (Frick et al. 2010b, Prendergast et al. 2010). The increase in number of Small-footed Bats in Virginia's hibernacula could have been driven by similar factors. Although this species is not known to occupy bat boxes, Small-footed Bats might benefit from the construction of riprap-covered dams or embankments, rocky road cuts, and bridges (Moosman et al. 2023, Sasse and Perry 2023, Thompson 2013).

Lowered winter numbers after the hibernacula surveys of 2008–2009 suggest that WNS impacted populations of Small-footed Bats in Virginia. Our model-estimated declines associated with a 2008–2009 arrival of WNS in Virginia are consistent with those observed in the Northeast and Central Appalachian Mountains (Francel et al. 2012, Hoyt et al. 2021, Langwig et al. 2012, Moosman et al. 2013). Hoyt et al. (2021) reported declines (10–30%) in winter populations of Small-footed Bats in New York, followed by population growth after the initial impacts from WNS. Our data suggest some populations of Small-footed Bats in Virginia responded similarly, with rapid recovery at some sites (e.g., Clark's Cave) and weak or neutral trends at other locations. Such heterogeneity is typical of WNS-impacted bat populations (Frick et al. 2010a). However, some of the declines we observed happened before the first detection of WNS in North America. Causes for these early declines are uncertain, but they coincide with an earlier arrival of WNS that is suggested from molecular evidence (Thapa et al. 2021).

Small-footed Bat numbers appeared stable in summer surveys that we conducted several years after WNS was first detected in Virginia, similar to patterns seen in Arkansas (Sasse and Perry 2023). The non-significant trend in bat numbers we observed in summer is not surprising, given the high interannual variation and the limited sample size of survey years. We anticipate that trends in summer bat numbers will become clearer with continued data collection, unless Small-footed Bat densities are already near their maximums. Population growth might not translate into higher summer counts at our study sites if suitable crevices are near capacity and Small-footed Bats exclude conspecifics from occupied roosting areas. Notwithstanding the still incomplete knowledge of this species' ecology, summer surveys at least confirm that Virginia's populations have persisted and continue to form maternity colonies. This has not been the case for more WNS-susceptible species, such as Northern Long-eared Bats, which have become rare in the state and may be failing to reproduce (Kalen et al. 2022).

When examining fluctuations in winter bat numbers, we found a weak site-specific relationship with precipitation during the preceding summer. High summer precipitation is generally expected to increase insect abundance and biomass (Müller et al. 2024), which can improve bat survival and reproductive success by providing food resources for early parturition and lactation (Frick et al. 2010b, Kurta et al. 1989). Earlier parturition and abundant prey presumably give young bats time to complete development and allow adult females to recover from reproduction and build winter fat reserves (Arlettaz et al. 2001, Frick et al. 2010b). Yet, these benefits are not universal—precipitation extremes can reduce bat survival when annual rainfall is already high (Grindal et al. 1992), and insect abundance has declined globally from factors such as climate change, intensive land use, pesticides, and introduced species (Gebremariam 2024). The heterogeneous patterns we observed across sites could reflect this context dependence, with the direction and magnitude of rainfall effects varying with local conditions.

Although the relationship between summer precipitation residual and fluctuations in winter bat numbers was weak and site-specific, it still raises the question of whether climatic change plays a role in population growth of Small-footed Bats in Virginia. Climate change may impact bat populations by influencing geographic distribution or affecting population size (Festa et al. 2023). Our study sites grew warmer without a significant increase in summer rainfall from 1980 to 2025, and the summer precipitation residual explained annual fluctuations in winter counts rather than influencing the long-term trend in bat numbers. This suggests any population increases after summers with favorable precipitation levels were temporary, implying that other factors have constrained the long-term increase in the number of Small-footed Bats in Virginia's hibernacula.

Variables such as availability of prey (Anthony and Kunz 1977, Kurta et al. 1989), suitable roosts (Kerth et al. 2001), predation (Speakman 1991), and anthropogenic influences (Ethier and Fahrig 2011, O'Shea et al. 2016) are potential constraints in other bat species. Although we can only speculate about which of these factors limits Small-footed Bat populations in Virginia, roost availability is a plausible candidate. Rock outcrops with high solar exposure are an insular habitat in the dense closed-canopy forests of the Appalachian Mountains, and lack of suitable roost sites could hinder population growth when conditions are otherwise favorable. The availability of rock outcrops may be further constrained by fire suppression and forest mesophication, which have contributed to canopy encroachment on rock outcrops in the Appalachian Mountains (Landsman and Thiel 2021, Nowacki and Abrams 2008). Studying how Small-footed Bats respond to canopy reductions or fire could provide valuable conservation insights.

In contrast to the relationship with summer rainfall, we found no evidence that conditions during winter affected bat numbers in hibernacula the following year, matching findings for European bats examined by Culina et al. (2017). Several factors could account for independence between fluctuations in Small-footed Bat winter numbers and prior winter temperature residuals. Notably, winters in Virginia are mild, and Small-footed Bats appear more resilient to cold and dry microclimates than most other cave-hibernating species in eastern North America (Best and Jennings 1997).

Interpreting fluctuations in winter counts was complicated by the inability to estimate observation error independently from winter abundance (Kéry et al. 2009, Udellet al. 2024). However, winter bat numbers often surged annually at rates that would have exceeded reproductive potentials, suggesting that Small-footed Bats either immigrated or changed their behavior in a way that influenced detection. Our analysis did not identify a significant relationship between fluctuations in winter numbers and temperature residuals within the same survey season, suggesting movements by Small-footed Bats during hibernation are not strongly tied to the climatic conditions we examined. However, patterns at the high-abundance hibernacula (e.g., Hupman's Saltpeter, Newberry-Bane, and Rocky Hollow caves) indicated winter temperatures may have influenced distribution or detectability for some sites (Supplemental File 2).

Like winter counts, summer numbers were variable within and between years; however, unlike winter counts, summer fluctuations covaried with temperature residuals within the same season, supporting the idea that behavioral changes influenced detection in talus surveys. Small-footed Bats may preferentially select talus sites during hot summers for thermoregulatory reasons. The thermal profiles of such roosts vary with size and shape, solar exposure, and type of rock (Chruszcz and Barclay 2002, Ferreira et al. 2026, Lausen and Barclay 2002, Moosman et al. 2023). It may be that Small-footed Bats moved to the talus sites we studied from nearby rock formations because of the thermal conditions available during hot summers.

An alternative explanation for the variable number of bats observed in summer is that group size, rather than habitat selection, shifted in response to thermal conditions. In most insectivorous bats, roosting in social groups is a behavior of reproductive females and their offspring that

increases thermal stability and aids development of young (Webber and Willis 2018). We counted reproductive groups that ranged in size from mother-juvenile pairs to aggregations of ~10 bats, although outside our plots we encountered groups of up to ~60 individuals. If reproductive groups were to break into smaller units during particularly hot summers, their less clumped distribution could increase probability of encountering bats in survey plots (Moosman et al. 2020). However, neither group size nor the probability of encountering groups of bats was significantly associated with temperature residuals; thus, we believe shifts in roost selection are the likely explanation for variability.

Our results add to mounting evidence that Small-footed Bats were less impacted by WNS than their congeners (Hooton et al. 2023, Johnson et al. 2021, O’Keefe et al. 2019). Several aspects of the winter biology of Small-footed Bats may promote reduced susceptibility to WNS and persistence of populations after the initial disease impacts (Frick et al. 2017, Hoyt et al. 2021, Langwig et al. 2012). These include a high tolerance to dry and cold hibernation sites, overwintering alone or in small groups, and spending less time in hibernation than other eastern cave-hibernating bats (Godin 1977, Gunier and Elder 1973, Mohr 1936). Furthermore, hibernating in aboveground rock outcrops, which are infrequently visited by other eastern species, likely reduces exposure to *Pd* (Moosman et al. 2017).

Management implications

Virginia’s Small-footed Bat populations may have weathered the arrival and spread of WNS, but the variability in winter counts is a reminder that the ecology of this species is incompletely understood, despite decades of study. Their numbers in hibernacula surveys are so low and variable that, had mortality been higher, population declines would have outpaced efforts to assess status. For this reason, summer talus surveys are a worthwhile addition for monitoring populations. Moreover, as we show in this study, talus surveys yield counts comparable to hibernacula counts, and they expand the pool of Virginia’s monitoring sites. Our data suggest trends in summer bat numbers should be assessed with models that account for potential confounding effects of summer temperature and other relevant variables described in Moosman et al. (2020). This combined summer-winter approach provides insights that hibernacula surveys alone do not (e.g., reproductive information), and it has shown promise for other species of rock-roosting *Myotis* that have limited options for population monitoring (McEwan and Bachen 2017, Zanarini 2019).

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