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Impact of censusing and research on wildlife populations

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Abstract

Population monitoring and research are essential for conserving wildlife, but these activities may directly impact the populations under study. These activities are often restricted to minimize disturbance, and impacts must be weighed against knowledge gained. However, few studies have quantified the effects of research or census-related visitation frequency on populations, and low visitation rates have been hypothesized to have little effect. Hibernating bats have been hypothesized to be especially sensitive to visitation because they have limited energetic stores to survive winter, and disturbance may partly deplete these stores. We examined the effect of site visitation frequency on population growth rates of three species of hibernating bats, little brown bats (*Myotis lucifugus*), Indiana bats (*Myotis sodalis*) and tri-colored bats (*Perimyotis subflavus*), both before and after detection of the disease white-nose syndrome. We found no evidence that more frequent visits decreased population growth rates for any of these species. Estimated coefficients were either the opposite sign as hypothesized (population growth rates increased with visitation frequency) or were very small (difference in population growth rates 0.067% [SE 2.5%]–1.8% [SE 9.8%]) relative to spatial and temporal variation (5.9–32%). In contrast, white-nose syndrome impacts on population growth rates were easily detected and well-characterized statistically (effect sizes 4.4–8.0; severe population declines occurred in the second and third years after pathogen detection) indicating that we had sufficient power to detect effects. These results indicate that visitation frequency (for *M. sodalis:* annual vs. semi-annual counts; for *M. lucifugus* and *P. subflavus:* 1–3 three research visits per year) had undetectable impacts on bat population growth rates both with and without the additional stress of an emerging infectious disease. Knowledge gained from censuses and research may outweigh disturbance due to human visitation if it can be used to understand and conserve the species.

KEYWORDS

census, endangered species, monitoring, multiple stressors, research impacts, wildlife management

1 | INTRODUCTION

One of the central tenets of wildlife management and conservation is monitoring populations. Populations are often counted to determine size and detect growth or decline, and finer spatial and temporal resolution censusing enables more accurate assessments (Wauchope, Amano, Sutherland, & Johnston, 2019). However, the process of censusing populations is often costly (Danielsen, Burgess, & Balmford, 2005), and in some cases, counting may negatively impact the population being studied due to disturbance (Tin et al., 2009). In addition, research aimed to understand the factors influencing populations, or management actions performed to aid species, may also have unwanted effects (Brown & Brown, 2009). As a result, populations are often monitored less than would be desirable, and research and management activities are often restricted, especially in a risk-averse system. In essence, a trade-off may exist between the benefits of monitoring, research, and management activities in terms of knowledge gained and positive impacts on species, and the costs to the species due to disturbance from these activities.

This trade-off is especially pertinent to hibernating bat populations impacted by white-nose syndrome (WNS). WNS, caused by the fungal pathogen *Pseudogymnoascus destructans* (Pd) (Warnecke et al., 2012), has caused widespread declines in populations of multiple species of bats across North America and threatens some species with extinction (Frick et al., 2015; Hoyt et al., 2020; Langwig et al., 2012; Langwig et al., 2015; Thogmartin et al., 2013). Hibernating bats are thought to be sensitive to disturbance by people visiting hibernacula for counts, research, or management because many bats arouse from hibernation during or shortly after humans pass near them (Boyles, 2017; Haarsma & de Hullu, 2012; Johnson, Brack, & Rolley, 1998; Luo, Clarin, Borissov, & Siemers, 2014; Speakman, Webb, & Racey, 1991; Thomas, 1995), and early banding activities had additional detrimental effects (Ellison, 2008). Increased arousals due to disturbance from counts, research, or other activities (e.g., recreational caving, commercial visits, etc.) is hypothesized to reduce overwinter survival because bats are energy limited during winter (Speakman et al., 1991). The potential impacts of disturbance have led to biennial counts for some species (e.g., *Myotis sodalis*; http://ecos.fws.gov/docs/recovery_plan/070416.pdf), cave closures for recreational and commercial purposes, and limitations on research activities (USFWS, 2011). However, while several studies have demonstrated that frequent visits to hibernacula (e.g., weekly) can cause bats to abandon sites (McCracken, 1989; Tuttle, 1979), no study has yet quantified the effect of hibernacula visitation frequency on bat populations. Low visitation rates (e.g., 1–3 visits per winter) have been hypothesized to have little effect (Boyles, 2017), because healthy bats often have surplus fat reserves (especially before the emergence of WNS), and have been selected to tolerate several forms of disturbance, including sound (e.g., running water in caves with streams), and predator activity (e.g., raccoons, rodents) (Luo et al., 2014).

Our goal was to determine the effects of hibernacula visitation frequency on bat populations before and after the arrival of WNS. We examined population growth rates of three species, *M. sodalis*, *Myotis lucifugus*, and *Perimyotis subflavus*, at sites that had been visited at varying frequencies for counts or research (e.g., sampling for Pd; Langwig et al., 2015), including multiple visits per year or different numbers of years between counts. We accounted for some other factors that might influence populations or their sensitivity to disturbance from a visit, including number of surveyors performing a census and whether a site was gated (and thus might be less visited by the public). We hypothesized that the impact of low frequency visitation (e.g., 1–3 times per year) would be small, especially relative to natural variability and the impacts of WNS on bat population growth rates.

2 | METHODS

We examined the effect of hibernacula visitation frequency on bat populations using the yearly average population growth rate, λ, between pairs of population counts, N, separated by T years, as the response variable:

$$\lambda = (N_{t+T}/N_t)^{1/T} \quad (1)$$

Each pair of counts yields a single data-point, a value of λ, which measures the average yearly proportional change in a population over the time interval, T, and, as a result, sites of different sizes and those sampled at different intervals can be directly compared (e.g., a 50% decrease in a population over 1 year produces the same λ, regardless of whether population declines from 100 to 50 or 2000 to 1,000). Similarly, a population that declines by 50% over 1 year produces the same value of λ (0.5) as a population that declines by 75% over 2 years ($\lambda = 0.25^{1/2} = 0.5$). We $\log_{10}$-transformed λ to meet assumptions of normality. Log(λ) values of 0 indicate population stability (no change between counts), positive numbers indicate increasing populations, and negative numbers indicate declining populations. Values on a log scale are

symmetric so that a doubling of the population ($\lambda = 2$; $\log(\lambda) = 0.301$) has the same magnitude as a halving of the population ($\lambda = 0.5$; $\log(\lambda) = -0.301$). When the second of each pair of counts, N_{t+T}, was 0 (i.e., the population was extirpated; making $\lambda = 0$, and $\text{Log}(\lambda) = -\infty$) we used a value of $N_{t+T} = 0.5$ in calculating λ so that these extirpations would be included in the analysis.

We analyzed data for two species (*M. lucifugus* and *P. subflavus*) in one state (Wisconsin) and a third species, *M. sodalis*, across its distribution in the US. *M. lucifugus* and *P. subflavus* were counted by 1–7 people that searched sites visually with headlamps between November and March. *M. sodalis* were counted by $3.3 \pm SD$ 2.2 (1–18) surveyors and clusters of bats were counted manually, photographed and counted later, or cluster dimensions and bat density were separately estimated and the number of bats were estimated from their product (Meretsky et al., 2010). The presence of *P. destructans* at sites in Wisconsin was determined using swab-sampling and qPCR for the presence of *P. destructans* (Langwig, Frick, et al., 2015; Muller et al., 2013). The presence of the disease WNS at *M. sodalis* sites was determined by a combination of swab-sampling and qPCR, histology of wing punches, or visual observations (Janicki et al., 2015; Langwig, Frick, et al., 2015; Meteyer et al., 2009; Muller et al., 2013; USFWS, 2011). Where multiple methods were used, qPCR and WNS were usually detected in the same year (Frick et al., 2017; Janicki et al., 2015). *P. destructans* or WNS was detected at 86% of the 28 *M. lucifugus* sites, 79% of the 33 *P. subflavus* sites, and 80% of the 243 *M. sodalis* sites during the study period.

In Wisconsin, we examined whether visiting hibernacula once, twice, or three times per winter influenced population growth rates of colonies of bats at the 76 sites with complete counts between 2011 and 2018. Visits to sites were relatively short in duration (0.5–4 hr underground), and primarily included counting bats (most site-years with a single visit per year), and swab-sampling bats (for sites visited 2–3 times). Since sites that were visited at a higher frequency also consisted of activities that would be more likely to be disruptive to bats (i.e., tactile disturbance), the comparison provides an overestimate of the disturbance impact of counting sites two or three times per year.

For *M. sodalis*, we used the distribution-wide historic count database maintained by the US Fish and Wildlife Service for this federally endangered species (243 total sites in 15 states across the eastern USA, 1931–2017, with 93.4% of the population growth rates from >1980, and 95% from nine states: Kentucky [30.6% of population growth rates], Missouri [15.7%], Indiana [11.6%], West Virginia [8.1%], Arkansas [8.0%], New York [6.7%], Tennessee [6.6%], Virginia [4.8%], and Illinois [3.2%]). These sites were counted at different intervals, with substantial variation among states in counting frequencies. There was also variation in counting frequency within several states, allowing for comparisons of population growth rates at sites with different counting intervals within these states. It is worth noting that the counting frequency for a given site was not randomly determined by the surveyors. It was often based on a combination of factors, including the difficulty in coordinating access and cost of surveying the site, and state and federal policies on counting frequencies. However, we have no reason to suspect that the counting frequency at a site was selected based on the population trend at that site in a way that would bias the results towards finding or not finding an effect of count frequency on population growth rates.

For all three species, we only included estimates of population growth rates in the analyses if the earlier colony count (N_t in Equation (1)) was >10 bats, because immigration and other variation in colony counts has disproportionately large effects when initial colony sizes are small. A cutoff of 10 bats was a natural separation in the data, and the results were qualitatively robust to other cutoffs between 8 and 15 bats. For *M. sodalis*, this cutoff excluded only 19% of population growth rate estimates (from 3,366 to 2,737 population growth rates) because colony sizes of this species are generally large (mean maximum colony size: 9,918 bats; range 11-123,800).

We used linear models and linear mixed effects models (the latter using the *lmer* function in *lme4* package in R v3.6.1) to examine relationships between the $\log_{10}$ average yearly population growth rate from year t to year t + T and visit frequency in year t, both before and after WNS was detected at each site. Analyses with all pre- and post-WNS detection data combined (w/ an interaction between visits and WNS status) gave qualitatively identical results. We used Akaike's Information Criterian (AIC) to compare models using categorical, presence-absence, or continuous values of years since WNS detected and to compare models with and without an interaction term between visit frequency and WNS year because WNS impacts varied strongly among years for some species and sensitivity to disturbance could vary similarly. We included random effects for Year (as a categorical variable) and Hibernacula (site) to account for repeated measures and within-site or within-year correlations; in some models variances for these effects were estimated to be zero and had to be dropped to avoid singularities. We ran additional analyses that included the number of surveyors performing a census and whether a site was gated. For *M. sodalis* analyses we also examined survey duration (in hours; mean 2.4, *SD* 1.9, range

0.5–16), number of surveyor-hours (survey duration multiplied by number of surveyors), and interactions with average roost height or a subjective categorical variable describing whether surveys disturb the bats at the site. These auxiliary data were only available for a subset of sites and years, so we report both sets of analyses. In analyses of *M. sodalis* we also included a random effect for State because there were differences among states in count frequencies and we did not want to confound regional differences in population growth rates with effects of counting frequencies. Including State as a random effect accounts for unmeasured variability among states (leading to correlations in the response variable within a state) and thus focuses the analyses on differences in population growth rates within each state associated with counting frequencies. More biologically relevant spatial units would be better, but counting frequencies were usually determined at the state level. Finally, as noted above, *M. sodalis* colony sizes varied over five orders of magnitude (11-123,800), so we also performed analyses that weighted population growth rates from different colonies with weights = $2^{(4\text{-priority number})}$. Priority numbers are designations of *M. sodalis* hibernacula associated with colony size (Priority number 1: >10,000; 2:1,000-9,999; 3:50-999; 4: <50; [Pruitt & TeWinkel, 2007]), resulting in weights of 8, 4, 2, and 1 for priority 1, 2, 3, and 4 colonies, respectively. For all analyses, to calculate *p*-values from t-values (estimated for each fixed effect coefficient by the lmer function), we conservatively assumed that random effects required 1 df per level for each site, year, and state.

3 | RESULTS

There was no evidence that *M. lucifugus* or *P. subflavus* had lower population growth rates at sites that were visited 2 or 3 times than at sites visited a single time either before WNS was detected or when WNS was present (Figure 1; Tables S1-S4). In contrast, the effects of WNS on both species were clearly evident, with stable populations before and in the first year of *P. destructans* detection, and sharply declining populations afterward (Figure 2; Table S2, S4). The coefficient for visit frequency was either positive (i.e., for *P. subflavus* both before and after WNS detection, and for *M. lucifugus* before WNS detection) or negative but extremely small and non-significant (Table S2: for *M. lucifugus* in the first year after WNS detection; the visits coefficient of −0.0025 in Table S2 translates into a 0.6% [SE 17%], 1.1% [SE 34%], and 1.7% [SE 51%] decrease in λ with 1, 2, or 3 visits) relative to year-to-year variation (yearly *SD* in λ based on random effect = 32%), indicating that poor power was not the reason we did not detect a significant negative effect. The number of surveyors (which ranged between 1 and 6) and whether a site was gated or not had no significant effect on population growth rates (*M. lucifugus*: # surveyors coef. −0.022, SE 0.039, t = −0.56; p = .58, gate coef. 0.093, SE 0.077, t = 1.21; p = .23; *P. subflavus* # surveyors coef. −0.023, SE 0.032; t = −0.73; p = .47; gate coef. 0.011, SE 0.052, t = 0.22; p = .82), and including these predictors had no qualitative effect on the effects of visit frequency before or after WNS detection at a site.

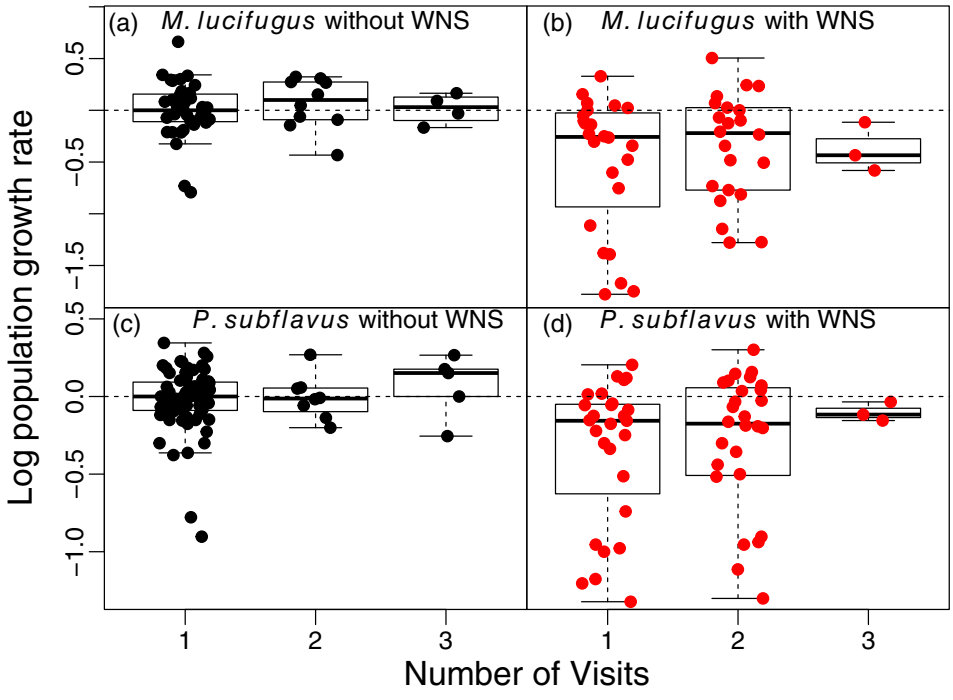

FIGURE 1 Box-plot of $\log_{10}$ population growth rates ($\log_{10}[N_{t+1}/N_t]$) for *Myotis lucifugus* (a, b) at 28 sites and *Perimyotis subflavus* (c, d) at 33 sites in Wisconsin with 1, 2, or 3 visits during the same winter, before (a, c) or after (b, d) the detection of WNS at that site (years 1–4 in Figure 2). Values below 0 indicate colonies that declined between years (e.g., a value of −0.5 indicates a population that was only $10^{-0.5} = 0.32$ times as large in the second of the 2 years, representing a 68% decline), whereas values above zero indicate populations that grew. A small amount of jitter has been added along the x-axis to facilitate presentation

There was also no evidence that populations of *M. sodalis* that were counted more frequently had a lower population growth rate than populations counted less frequently either before or after the arrival of WNS. This was true whether the analysis was a comparison between colonies counted every year or every other year (Figure 3; pre-WNS: Table S5; post-WNS: Table S6; Figure S1 for individual state comparisons) or count frequencies of every year to every 4 years (Figure S2; pre-WNS: Table S7; post-WNS: Table S8), and the results were very similar if we used a weighted regression with site-weights that scale with colony size (see Methods; counting frequency coefficients for all models were negative or *p*-values were all >.6). Specifically, pre-WNS detection, population growth rates between counts done every year (log λ = −0.078, SE 0.032) were the same to the fourth decimal place as counts separated by 2 years (difference in log λ = 0.00029); the difference in non-logged population growth rates was 0.067% ± 2.5% which is not significantly different from zero (p = .99) and much smaller than year-to-year variation (SD = 0.03 or 5.9% for non-logged population growth rates) or variation among sites (0.073 or 18% for non-logged population growth rates) based on random-effect coefficients (Table S5). Post-WNS detection, population growth rates were much lower than pre-WNS detection (WNS coeff. For counts separated by 1–2 years: −0.13, SE 0.025, t = −5.30, $p = 1.3 \times 10^{-7}$; WNS coeff. for counts separated by 1–4 years: −0.14, SE 0.023, t = −6.06, $p = 1.6 \times 10^{-9}$), but again, population growth rates were essentially identical between counts separated by 1 year (log λ = −0.41, SE 0.23; λ = 0.39, 0.14–1.09) and counts separated by 2 years (log λ = −0.41 SE −0.0077 = −0.42); the difference in non-logged population growth rates is 1.8% (SE 9.8%) which is much smaller than year to year variation (SD = 0.03 or 5.9% for non-logged population growth rates) or variation among sites (SD 0.073 or 18% for non-logged population growth

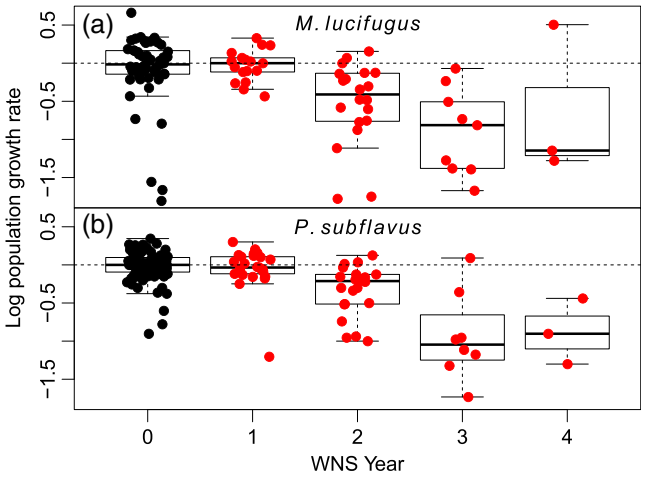

FIGURE 2 Box-plot of $\log_{10}$ population growth rates ($\log_{10}[N_{t+1}/N_t]$) in Wisconsin for *Myotis lucifugus* (a) at 28 sites and *Perimyotis subflavus* (b) at 33 sites before (black circles) and in the first to fourth year after WNS arrival (red circles). Values below 0 indicate colonies that declined between years (e.g., a value of −0.5 indicates a population that was only $10^{-0.5} = 0.32$ times as large in the second of the 2 years, representing a 68% decline), whereas values above zero indicate populations that grew. A small amount of jitter has been added along the x-axis to facilitate presentation

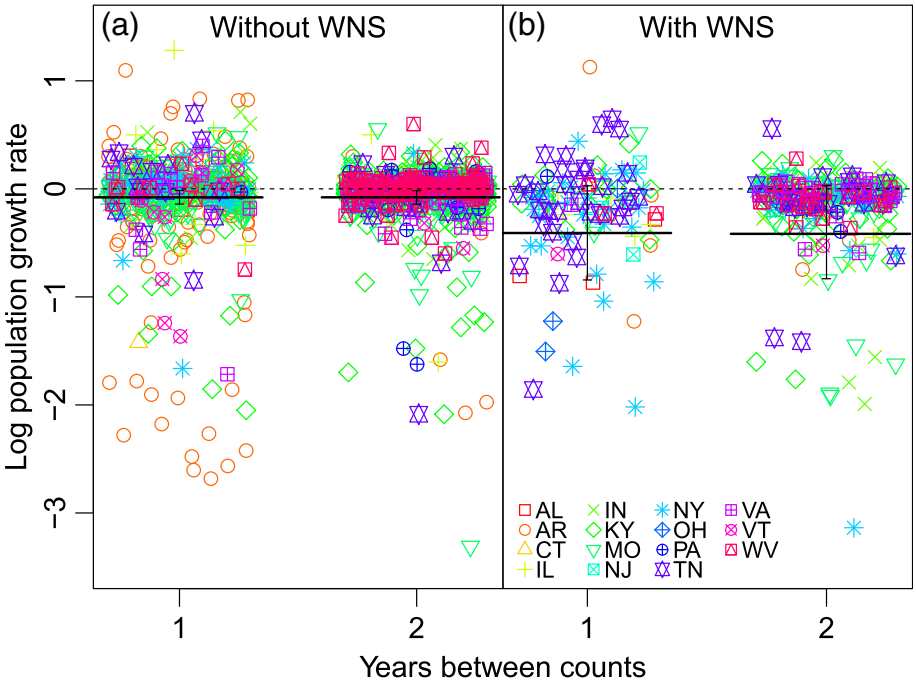

FIGURE 3 *Myotis sodalis* $\log_{10}$ population growth rate ($\log_{10}[N_{t+1}/N_t]$) plotted against the number of years between counts (yearly (1) or every other year (2)) at 220 sites before (a) or after (b) the detection of WNS at that site. Black horizontal segments and error bars show the estimated means and 95% CIs based on the fitted model. Colors show data from different states. A small amount of jitter has been added to points along the x-axis to facilitate presentation

rates) based on random effect coefficients (Table S5). There was no evidence that additional site variables explained variation in population growth rates (whether it was gated: pre-WNS: gate coef. 0.0059, SE 0.025, $p = .81$; post-WNS: gate coef. −0.013, SE 0.054, $p = .82$). Similarly, there was no evidence that longer censuses, more surveyors, more surveyor-hours, lower roosting bats, or more easily disturbed sites had low population growth rates and including these variables did not influence the effects of counting frequency (all surveying coefficients were either positive, or p-values were $> .18$).

4 | DISCUSSION

Although frequent visits to hibernacula during winter are known to disturb bats and have been shown to cause site abandonment (McCracken, 1989; Tuttle, 1979), we found no statistical evidence to suggest that small numbers (1–3) of short (95% were 0.5–4 hr) visits to bat hibernacula for research or counting during winter had negative impacts on bat population growth rates. For *M. lucifugus* and *P. subflavus* in Wisconsin there was no evidence that visit frequency (one to three visits per winter) altered population growth rates, despite higher frequency visits often being longer in duration and, for a subset of bats, including a tactile disturbance (swabbing). For *M. sodalis*, across its range, we found that population growth rates were statistically indistinguishable for populations counted at intervals of every year to every 4 years and there was no evidence of differences in population growth rates between sites counted every year or every other year. We also found no evidence that the effect of visit frequency on bat population growth rates was more negative after the arrival of WNS to each site, suggesting that bats were not significantly more sensitive to 1–3 research or counting visits in the presence of this disease. In contrast, WNS impacts were clearly evident for all three species, indicating that population variability and uncertainty in counts (e.g., counting only parts of hibernacula, bats switching between sites) did not affect our ability to detect trends in populations for any of these species. These results suggest that, for *M. lucifugus* and *P. subflavus*, visiting sites two or three times to count and swab bats had no more detectable impact on bat populations than a single counting visit, and counting populations of *M. sodalis* every year had no more effect than counting bats every other year or less frequently. As a result, annual censuses, which allow for more rigorous monitoring and assessment of population trends (Wauchope et al., 2019), and detection of disturbance to or die-offs at sites, and research that provides useful information may outweigh disturbance caused during these visits. It is worth noting that counting frequency is often constrained by financial and logistical considerations, which may still limit censuses to every other year or less frequent intervals. The main conclusion based on the analyses presented here is that disturbance associated with 1 (*M. sodalis*) or 2–3 (*M lucifugus*, *P. subflavus*) census or research visits per year did not reduce population growth rates compared with less frequent visits.

The contrast between the lack of negative effects observed here and the demonstrated effects of high frequency disturbance (e.g., weekly visits) on bat populations (McCracken, 1989; Tuttle, 1979) merits discussion. The key difference is likely the frequency and duration of disturbance and the resultant impact on bats' fat stores. Healthy bats normally arouse from torpor every 2–3 weeks for a few hours over the 3–6 month winter period for a total of 8–15 arousals (Reeder et al., 2012; Thomas, Dorais, & Bergeron, 1990; Warnecke et al., 2012). Disturbance during a census may result in an additional arousal from torpor, but only for bats that had aroused in the previous few days and subsequently returned to torpor (Turner et al., 2015). In contrast, bats that have not aroused recently may alter the timing of their next arousal, resulting in relatively little loss in stored fat (Turner et al., 2015). If bats have fat stored for surplus arousals during winter hibernation, then there is likely to be little mortality from 1 to 2 additional arousals (Boyles, 2017; Thomas et al., 1990). In contrast, bats suffering from WNS have disrupted physiology and hibernation patterns (Warnecke et al., 2013), and in late hibernation arouse 2–3 times as frequently as healthy bats (Cheng et al., 2017; Reeder et al., 2012; Warnecke et al., 2012). In this case, the addition of one or two additional arousals may be of little consequence because the incremental impact of 1–3 visits is much smaller than differences either in initial mass or fat stores (Cheng et al., 2019; Hoyt et al., 2019), the timing of infection (Hoyt et al., 2018), or a bat's response to Pd infection (Cheng et al., 2017, Reeder et al., 2012, Warnecke et al., 2012). In summary, the impact of 1–3 counts or research-related visits to hibernacula on bat population growth rates was undetectable, likely because the cost to most bats from 1 to 3 short visits is relatively small, especially compared with the total number of winter arousals for both healthy and WNS-affected bats. Nonetheless, continued efforts to minimize impacts of counting and research visits (i.e., by keeping them short and efficient and minimizing sound and light) will maximize the chance for bat populations to recover from WNS and other threats. Similarly, restricting access to hibernacula during winter for recreational activities, as is done to protect other sensitive and threatened species (e.g., closing parts of beaches for nesting piping and snowy plovers (https://www.fws.gov/northeast/pipingplover/pdf/recguide.pdf), or closing rock climbing areas for nesting raptors

(https://www.fws.gov/Endangered/esa-library/pdf/f990825.pdf)), will also minimize disturbance to hibernating bats.

Effective wildlife management and conservation requires monitoring populations and performing research, and these activities may affect the populations that are being conserved. Here we examined the effect of counting frequency and research visits on population growth rates of a group of animals that are known to be highly sensitive to disturbance: hibernating bats. We found no evidence that population growth rates of three species of hibernating bats were negatively affected by the frequency of visitation when the number of annual visits was low (1–3 per winter). These data suggest that, at least for these species, the potential knowledge gained from population censuses and research may outweigh the disturbance, especially if the knowledge gained is used to understand and conserve the species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

A. Marm Kilpatrick, Joseph R. Hoyt, Kate E. Langwig, R. Andrew King, J. Paul White conceived the study. Heather M. Kaarakka, Jennifer A. Redell, J. Paul White, Joseph R. Hoyt, A. Marm Kilpatrick, Kate E. Langwig performed surveys in Wisconsin. R. Andrew King managed and organized the *M. sodalis* dataset. A. Marm Kilpatrick performed analyses with input from Joseph R. Hoyt, Kate E. Langwig, and R. Andrew King, A. Marm Kilpatrick wrote the first draft and all authors provided comments and contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

Data requests should be made to A. M. K.

ETHICS STATEMENT

All research was performed under animal use and care protocols Kilpm1705, Kilpm1509, and Frickw1106.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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