

# Conservation implications of ameliorating survival of little brown bats with white-nose syndrome

BROOKE MASLO,<sup>1,5</sup> MICK VALENT,<sup>2</sup> JOHN F. GUMBS,<sup>3</sup> AND WINIFRED F. FRICK<sup>4</sup>

<sup>1</sup>Department of Ecology, Evolution and Natural Resources, Rutgers, The State University of New Jersey, 14 College Farm Road, New Brunswick, New Jersey 08901 USA

<sup>2</sup>Endangered and Nongame Species Program, New Jersey Division of Fish and Wildlife, 1 Van Syckels Road, Clinton, New Jersey 08809 USA

<sup>3</sup>BATS Research Center, 107 Meadow View Court, Shohola, Pennsylvania 18458 USA

<sup>4</sup>Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064 USA

**Abstract.** Management of wildlife populations impacted by novel threats is often challenged by a lack of data on temporal changes in demographic response. Populations may suffer rapid declines from the introduction of new stressors, but how demography changes over time is critical to determining long-term outcomes for populations. White-nose syndrome (WNS), an infectious disease of hibernating bats, has caused massive and rapid population declines in several hibernating species of bats in North America since the disease was first observed on the continent in 2006. Estimating annual survival rates and demographic trends among remnant colonies of hibernating bats that experienced mass mortality from WNS is needed to determine long-term population viability of species impacted by this disease. Using mark–recapture data on infected little brown bats (*Myotis lucifugus*), we estimated the first apparent annual survival rates for four years following WNS detection at a site. We found strong support for an increasing trend in annual survival, which improved from 0.68 (95% CI = 0.44–0.85) to 0.75 (95% CI = 0.51–0.89) for males and 0.65 (95% CI = 0.44–0.81) to 0.70 (95% CI = 0.50–0.84) for females. These results suggest that stabilization at remnant colonies after mass mortality from WNS may be due to improved survival and not from immigration from other areas. Despite ameliorating survival, our stochastic matrix projection model predicts continued declines for little brown bat populations ( $\lambda = 0.95$ ), raising concern for the regional persistence of this species. We conducted a vital rate sensitivity analysis and determined that adult and juvenile survival, as opposed to fecundity, are the demographic parameters most important to target to maximize recovery potential of little brown bat populations in areas impacted by WNS.

**Key words:** Barker model; *Geomyces destructans*; hibernacula; little brown bat; mark–recapture; *Myotis lucifugus*; population viability analysis; *Pseudogymnoascus destructans*; vital rate sensitivity; white-nose syndrome, WNS; wildlife disease.

## INTRODUCTION

Abrupt environmental changes caused by an introduced predator, competitor, or pathogen often result in immediate and significant declines in native or host species (Thomas et al. 2004, Rachowicz et al. 2005). Detection of novel threats typically occurs only after mass mortality within wild populations is reported (Mörner et al. 2002). Severity of population declines magnifies the urgency for timely conservation intervention; however, determination of the appropriate management strategy is hindered by the uncertainty surrounding a population's response to the threat. Novel stressors can dramatically alter the dynamics of naïve populations, typically with negative impacts (e.g., Stachowicz et al. 2002, Harvell et al. 2009, Walther

2010), but populations may also persist via a density-dependent demographic response (Lloyd-Smith et al. 2005) or rapidly developed evolutionary or ecological adaptations (e.g., Thompson 1998, Strauss et al. 2006, Hendry et al. 2008, Flajnik and Kasahara 2010). Short-term demographic analyses can assist in supporting or rejecting initial hypotheses about a population's response to a threat. Further, they may be helpful for identifying and understanding the mechanism(s) driving that response. Because populations experiencing abrupt environmental change are unstable (Fefferman and Reed 2006), sensitivity and elasticity analyses that incorporate uncertainty can be useful in identifying effective management strategies to promote short-term growth of an unstable population, which may have lasting consequences for the long-term persistence of affected populations.

White-nose syndrome (WNS), the fungal disease affecting hibernating bats, is caused by the pathogen, *Pseudogymnoascus destructans* (Gargas et al. 2009,

Manuscript received 5 January 2015; revised 4 February 2015; accepted 5 February 2015; final version received 6 March 2015. Corresponding Editor: J. R. Goheen.

<sup>5</sup> E-mail: brooke.maslo@rutgers.edu

Minnis and Lindner 2013). Following the first documentation of WNS in 2006, the disease has spread rapidly throughout eastern North America and devastated colonies of several species of hibernating bats. Colonies have declined by 99% for some species in WNS-infected hibernacula, and several previously common species are now at risk of regional or global extinction (Frick et al. 2010a, Langwig et al. 2012, Frick et al. 2015). As a psychrophilic fungus, growth of *P. destructans* is restricted to temperatures of 3–15°C and >90% relative humidity (Verant et al. 2012) and affects bats during hibernation, when individuals are torpid for extended periods (Langwig et al. 2015).

Frick et al. (2010a) conducted an early assessment of the regional population impacts of WNS mortality on little brown bats (*Myotis lucifugus*) in the northeastern USA, where WNS first emerged. Their population viability analysis (PVA) predicted regional extinction of the species within 16 years (Frick et al. 2010a). However, declines have slowed and stabilized for some species in areas where WNS has been present for a few years (Langwig et al. 2012, Reichard et al. 2014). There are several possible mechanisms for stabilization, which lead to substantially different conclusions about population persistence. One hypothesis is that documented stabilization at hibernacula in years following exposure to WNS is due to immigration of susceptible individuals from other sites. If this is true, regional populations will continue to plummet toward extinction as these infected hibernacula serve as population sinks. Alternatively, surviving bats may exhibit acquired resistance, either through effective immune response and/or by behavioral shifts (Langwig et al. 2012) that lower disease mortality. Finally, remnant colonies of bats may consist of individuals with some level of genetic resistance to the pathogen (Maslo and Fefferman 2015). Whether bats are capable of surviving within infected hibernacula or are immigrating into infected sites from elsewhere has important consequences for informing effective management intervention.

Here, we provide the first annual survival estimates for little brown bats affected by WNS after the initial mass mortality from disease. We analyze four years of mark–recapture data from a hibernaculum to determine the demographic impact of WNS. We examine sex-specific and yearly differences in survival, and we investigate whether there is a linear trend in survival over time. We then incorporate these survival rates into a stochastic population projection matrix model and conduct a vital rate sensitivity analysis to identify the most appropriate vital rate (stage specific survival and fecundity) to target for implementing effective measures to promote little brown bat recovery.

## METHODS

### *Population monitoring*

We conducted fieldwork at Hibernia Mine, a 700-m abandoned iron mine located within the Wildcat Ridge

Management Area in Rockaway, Morris County, New Jersey, USA. This mine was the roost site of the largest known hibernating colony of little brown bats in New Jersey, with pre-WNS (winter of 2008–2009) abundance estimated at ~27 000 individuals (M. Valent, unpublished data). We began the study in 2010, one year after the detection of WNS at the site. We captured little brown bats just prior to spring emergence from the mine between late March and early April 2010–2013. We banded individuals (see Plate 1) with unique 2.9-mm or 2.4-mm lipped alloy bands (Porzana, Icklesham, UK). We classified all bats as adults, as it is not possible to accurately determine age class after an individual's first summer (Brunet-Rossini and Wilkinson 2009). Because survival estimation in bats is limited by low recapture rates (e.g., O'Shea et al. 2003, 2004), we additionally resighted banded bats outside the main capture period during the late summer/early fall when bats swarm at the mine entrance. Population monitoring activities were conducted under the authority of a cooperative agreement between the New Jersey Division of Fish and Wildlife (formerly New Jersey Division of Fish, Game and Shellfisheries) and the U.S. Fish and Wildlife Service, dated 23 June 1976. National White-Nose Syndrome Decontamination Protocols were followed during all visits.

### *Survival estimation*

We used Barker's model in Program MARK (White and Burnham 1999) to analyze encounter histories of marked, recaptured, and resighted individuals (Barker 1997). The Barker model uses a maximum-likelihood approach and allows for the simultaneous modeling of information about marked animals gathered from both within and outside the marking interval (Barker and White 2001). The model estimates the survival probability of an individual from  $i$  to  $i + 1$  (survival,  $S$ ); the probability an animal at risk of capture at  $i$  is captured at  $i$  (recapture,  $p$ ); the probability that an individual that dies between  $i$  and  $i + 1$  is found dead (recovery,  $r$ ); the probability an individual that survives from  $i$  to  $i + 1$  is resighted alive between marking occasions (resight,  $R$ ); the probability an individual that dies between marking occasions without being found dead is resighted before it died (resight,  $R'$ ); the probability that an individual at risk of capture at  $i$  is at risk of capture at  $i + 1$  ( $F$ ); and the probability an individual not at risk of capture at  $i$  is at risk of capture at  $i + 1$  ( $F'$ ) (Barker and White 2001). We simplified our analysis by reducing the parameterization of our saturated model, holding  $R$  and  $R'$  as time dependent with no differences in sex (e.g., Slattery and Alisauskas 2002, Cattet et al. 2008). Because we did not recover any dead bats between marking occasions, we set  $r = 0$ . Based on Norquay et al. (2013), we fit a model of random emigration by constraining  $F = F'$ , holding these parameters constant at 0.96 to reflect the high site fidelity of little brown bats to hibernacula.

We developed 24 a priori candidate models containing combinations of constant, yearly, time trend, and sex-specific effects on annual survival and recapture probabilities (Appendix: Table A1). Our global model included time-dependent and sex-specific survival and recapture. To test for goodness of fit, we used a parametric bootstrapping procedure with 500 simulations of our saturated model, which included all parameters. Within Program MARK, we calculated a variance inflation factor of  $\hat{c} = 1.54$  for our global model, indicating modest overdispersion in our data (Burnham and Anderson 2002). Therefore, we used small-sample-corrected quasi-Akaike's information criterion (QAIC<sub>c</sub>) adjusted by  $\hat{c} = 1.54$  (Burnham and Anderson 2002). We ranked candidate models by  $\Delta\text{QAIC}_c$  and quasi-Akaike weights ( $w$ ), which represent the relative likelihood of the model, given the data (Johnson and Omland 2004). To reduce model selection bias and uncertainty, we calculated estimates by averaging parameters within all models contributing to  $w \geq 0.95$  (Burnham and Anderson 2002, Burnham et al. 2011).

#### Population projection models

To examine the effect of survival on long-term population growth, we incorporated our estimates into four two-stage Lefkovich matrices (Caswell 2001, Morris and Doak 2002), each representing one study year from 2010–2013:

$$\begin{bmatrix} S_j \times B_j \times \text{Fe} & S_a \times B_a \times \text{Fe} \\ S_j & S_a \end{bmatrix}$$

where  $S$  represents survival of female little brown bats;  $B$  represents the probability that a female returns to a maternity colony to breed; and subscripts  $j$  and  $a$  indicate values for juveniles or adults, respectively. Little brown bats have a single pup each year and are sexually mature by the end of their first summer (Watt and Fenton 1995, Frick et al. 2010b), so we held fecundity (Fe) constant for both age classes at  $\text{Fe} = 1$ . We assigned probability of breeding for adults and juveniles to values of  $B_j = 0.38$  and  $B_a = 0.85$ , respectively, based upon published estimates generated from either 15 years of pre-WNS mark–recapture data or post-WNS adult reproductive rates (Reichard and Kunz 2009, Frick et al. 2010a, b). We fixed juvenile survival as a constant proportion of adult survival ( $S_j = 0.47S_a$ ; Frick et al. 2010a).

We chose an initial vector of  $N = 1000$  to represent an infected bat colony that has experienced some stabilization after WNS arrival (USFWS, unpublished data), and we assumed a stable age structure. We projected our population through the 2010–2013 matrices and then continued the projection an additional 96 years, allowing mean survival to continue ameliorating by 0.01 until it equaled its 10-year pre-WNS average of 0.77 (Frick et al. 2010a). We ran a 10 000-iteration Monte Carlo simulation, allowing  $S_a$  and  $B_j$  to vary stochas-

tically based on random number generation of beta distributions derived from the means and variances of each parameter, and we generated a mean stochastic yearly growth rate,  $\lambda$ .

Informed conservation strategies for WNS-infected bat populations also require an understanding of the annual population growth rates over the short term, which can be influenced dramatically by population structure (Mills 2012). We have no data on the actual population structure of the Hibernia Mine colony, but populations experiencing abrupt environmental change rarely exhibit stable age distributions (Fefferman and Reed 2006). If WNS has a greater impact on juvenile (first-year) than adult survival, the population could become skewed toward adults. To investigate differences in population trajectories between a stable and adult-skewed population structure, we artificially generated an adult-skewed initial population vector of 800 adults and 200 juveniles. We then examined differences both in annual short-term growth rates (prior to model convergence) and resulting population sizes.

#### Vital rate sensitivity analyses

We used vital rate sensitivity analysis of our post-WNS estimates to identify which vital rates should be targeted to most rapidly increase population size over a short time frame. Vital rate sensitivity analyses are more advantageous than traditional sensitivity analyses (e.g., Morris and Doak 2002) because the stable age distribution assumption can be relaxed (Fefferman and Reed 2006), which is beneficial when populations are undergoing rapid declines (e.g., Fefferman and Reed 2006, Reed et al. 2009). Further, vital rate sensitivity analyses focus on maximizing population size over a short time frame, which can be critical for rapid conservation action (Field et al. 2007).

Based on current research projects on WNS management and published literature on potential management strategies (e.g., Boyles and Willis 2010, Willis et al. 2011, Cornelison et al. 2014), we developed three objectives for increasing short-term population growth of infected bat colonies: (1) increasing adult and juvenile annual survival by 6%; (2) increasing adult reproduction by 10%; and (3) increasing both adult and juvenile reproduction by 10%. We evaluated the effect of these objectives on the 15-year cumulative growth rate ( $\lambda^{15}$ ) and final size of our representative colony. Although it would be informative to identify the sensitivity of age-based survival, WNS infection and subsequent mortality occur most often during the winter (Langwig et al. 2015), when all age classes are hibernating together. Therefore, any management action targeting survival, such as anti-fungal treatments or provisioning of supplemental water or electrolyte sources (Cryan et al. 2013a, Cornelison et al. 2014), probably will influence all age classes.

We projected our stable and adult-skewed populations through the yearly matrices identified previously

TABLE 1. Model selection results of the top six a priori candidate models for survival ( $S$ ) and recapture ( $p$ ) probabilities for little brown bats *Myotis lucifugus* ( $N = 656$ ) at Hibernia Mine, Rockaway, New Jersey, USA.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	$w$
<b><math>S(\text{time, sex}) + p(\text{year})</math></b>	<b>1279.39</b>	<b>0.00</b>	<b>0.33</b>
<b><math>S(\text{time}) + p(\text{year, sex})</math></b>	<b>1279.57</b>	<b>0.18</b>	<b>0.30</b>
<b><math>S(\text{time, sex}) + p(\text{year, sex})</math></b>	<b>1280.23</b>	<b>0.84</b>	<b>0.22</b>
<b><math>S(\text{time}) + p(\text{year})</math></b>	<b>1281.28</b>	<b>1.89</b>	<b>0.13</b>
$S(\text{year, sex}) + p(\text{year})$	1286.56	7.17	0.01
$S(\text{constant, sex}) + p(\text{year, sex})$	1287.15	8.57	0.00

Notes: For all models, recoveries ( $r$ ) were set to 0 to indicate that no animals were recovered dead between marking occasions, and all models were set to constant resight probability and random emigration ( $F = F' = 0.96$ ). The top four models (in boldface;  $w = 0.98$ ) were used for model-averaged survival parameter estimation. QAIC<sub>c</sub> is the quasi-Akaike's information criterion corrected for small sample size; ΔQAIC<sub>c</sub> is the difference between the QAIC<sub>c</sub> value between each model and the top model;  $w$  is the quasi-Akaike weight. Time is the linear time trend and year represents yearly variation.

and began vital rate perturbations in year 5. For management objectives 1–3, we calculated the change in colony size ( $\Delta N$ ) between the first and 15th year of the simulation. The objective resulting in the largest short-term population growth of infected bat populations ( $\Delta N$ ) was considered the most effective alternative (Fefferman and Reed 2006). To account for uncertainty, we ran 10 000 iterations of the vital rate sensitivity analysis projections for each population structure in a Monte Carlo simulation. We incorporated stochasticity (as before) in adult and juvenile survival, and we assigned a certainty of management recommendations as the percentage of times a given management goal resulted in the largest positive  $\Delta N$ .

RESULTS

Population monitoring

We conducted mark–recapture operations on 12 occasions during the four-year study period, and we resighted individuals on eight occasions outside the main capture period in those years. We captured 656 little brown bats (256 females, 400 males); of these, 274 and 57 individuals were recaptured and resighted, respectively.

Survival estimation

Model selection results show strong support for a linear increase in survival over time (Table 1). Of the 24 candidate models proposed, 98% of the QAIC<sub>c</sub> weights were captured in the top four models, which all provided strong support for a linear trend in survival (Table 1). Model-averaged survival increased from 0.68 (95% CI = 0.44–0.85) to 0.75 (95% CI = 0.51–0.89) for males and 0.65 (95% CI = 0.44–0.81) to 0.70 (95% CI = 0.50–0.84) for females across the study period (Fig. 1). Recapture rates ranged from 0.30 (95% CI = 0.18–0.44) to 0.67 (95% CI = 0.52–0.80) for males and 0.27 (95% CI =

0.15–0.44) to 0.57 (95% CI = 0.37–0.76) for females between 2011 and 2013.

Population projections

The long-term population projection converged on a mean yearly stochastic growth rate of 0.95, predicting persistent annual declines of 5% in colonies of little brown bats infected with WNS. However, short-term annual growth rates varied between the two population structures. The stable and adult-skewed populations demonstrated opposite patterns, exhibiting a marked decline and growth, respectively, before stabilizing within five years of WNS emergence (Fig. 2).

Vital rate sensitivity analyses

For both population structures, increasing survival of both age classes (objective 1) had the largest positive effect on short-term population growth and was reported as the best management recommendation with 100% certainty (Table 2). Although this management action returns both colonies to positive growth after five years (Fig. 3), the adult-skewed colony results in the greatest  $\Delta N$ , increasing by 395 individuals over the 15-year period.

DISCUSSION

Implications of survival rates on long-term population dynamics

Our work provides the first annual survival estimates for little brown bats affected by WNS based on mark–recapture data. Increasing annual survival after initial mortality from WNS suggests an adaptive response of little brown bats to this novel pathogen (Fig. 1). Massive mortality was first observed at Hibernia Mine during the

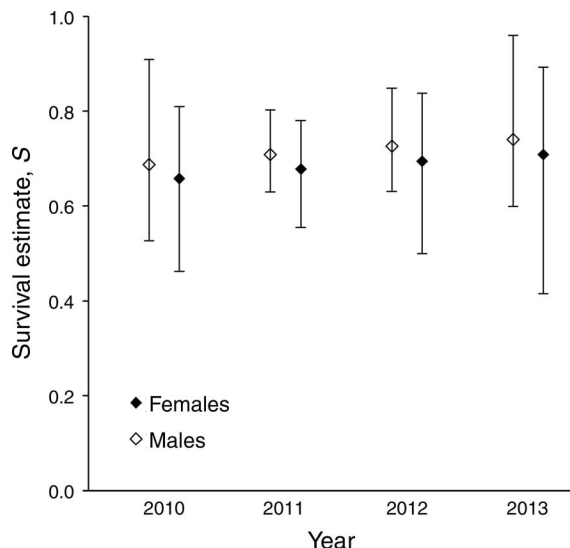


FIG. 1. Model-averaged survival estimates and 95% confidence intervals for female and male little brown bats (*Myotis lucifugus*) infected with white-nose syndrome (WNS) in Hibernia Mine, Rockaway, New Jersey, USA, 2010–2013.

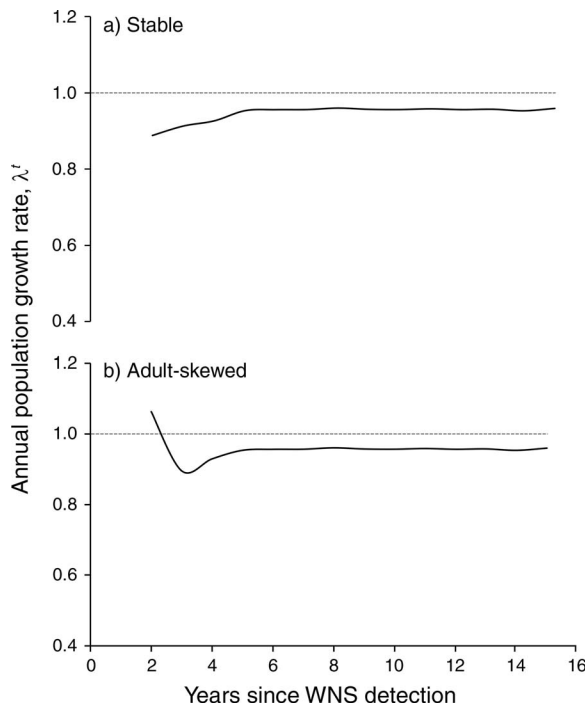


FIG. 2. Short-term annual population growth rates for (a) stable and (b) adult-skewed populations of little brown bats (*Myotis lucifugus*) infected with white-nose syndrome, modeled by number of years since WNS detection. For both population structures, annual growth stabilizes at annual growth rates of 0.95 within five years of disease emergence.

hibernation period of 2008–2009, when the colony declined from an estimated ~27 000 to 1756 individuals during that first year, suggesting a first-year post-WNS survival rate of <10%. Since that time, annual survival appears to have rebounded considerably, and although annual survival rates remain lower than typical pre-WNS levels (Frick et al. 2010b), our results show a trend of increasing survival rates over time.

Although the mechanisms of increasing survival are not known, overwinter survival could improve from several causes, including an acquired immune response to infection (Richmond et al. 2009), changes in

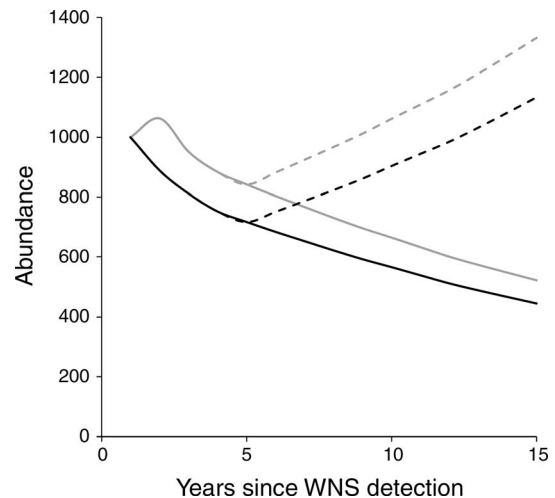


FIG. 3. Predicted trajectories for stable and adult-skewed populations of little brown bats (*Myotis lucifugus*) with and without management targeting increasing survival after emergence of white-nose syndrome. Black lines represent stable populations; gray lines represent adult-skewed populations. Solid lines indicate no management action and dashed lines indicate management intervention to increase survival.

hibernating behavior (Langwig et al. 2012), and evolutionary selection for genetically resistant individuals (Loehle 1995, Harvell et al. 2009, Matthews et al. 2013, Maslo and Fefferman 2015). Langwig et al. (2012) suggested that little brown bats alter their social behavior after the arrival of WNS by roosting solitarily rather than in dense clusters, which could limit exposure and transmission of *P. destructans* and reduce mortality. *Pseudogymnoascus destructans* may also be undergoing epidemic fade-out if transmission is density dependent and host populations have dropped below the threshold for invasion (Lloyd-Smith et al. 2005). Our analysis here is based on a relatively short time period immediately following the emergence of WNS. Long-term mark-recapture studies could help to determine whether survival rates of bats at sites with WNS continue to increase toward pre-WNS levels (Frick et al. 2010b), or if WNS will regulate host populations and colony sizes

TABLE 2. Vital rate sensitivity analysis results for each simulated age distribution of little brown bats, based upon the three management scenarios.

Age structure	Management scenario					
	Increase adult and juvenile survival by 0.06		Increase adult reproduction by 0.1		Increase adult and juvenile reproduction by 0.1	
	$\Delta N$	$\lambda'$	$\Delta N$	$\lambda'$	$\Delta N$	$\lambda'$
Stable	187	1.01	-448	0.96	-426	0.96
Adult-skewed	395	1.02	-326	0.97	-326	0.97

Notes: We ran vital rate sensitivity analyses on two artificially generated age distributions: stable (40% juveniles) and adult-skewed (20% juveniles). In both cases, certainty of management recommendation was 100% based upon 10 000 iterations of Monte Carlo simulation.  $\Delta N$  values represent the change in population size from 2010 (year 0) to 2025 (year 15) of the vital rate sensitivity analysis, and  $\lambda'$  represents the cumulative annual population growth rate derived from the vital rate sensitivity analysis.



PLATE 1. Little brown bat (*Myotis lucifugus*) banded at Hibernia Mine, Rockaway, New Jersey, USA in 2012. Photo credit: Eden Buenaventura.

will remain small and similar to those in Europe, where the disease is endemic (Frick et al. 2015).

Our results from Hibernia Mine do not support the hypothesis that the observed stabilization of some little brown bat colonies is primarily the result of immigration of new individuals from other sites. If bats were immigrating to new sites and dying at the same rates observed during the mass mortality phase of WNS, annual survival estimates would be significantly lower than reported. Overall, little is known about site fidelity to hibernacula for little brown bats, except for a recent study by Norquay et al. (2013), which showed that site fidelity is high, at least in the northern extent of the species' range.

Our matrix projection models predict a mean stochastic yearly growth rate of  $\lambda = 0.95$  despite ameliorating survival during the four year study period, suggesting that if survival does not continue to improve,

the long-term impacts of WNS are severe. Although these results suggest that little brown bats will persist longer than previously expected based on the first three years of mortality rates (Frick et al. 2010a), a 5% annual rate of decline still results in almost certain regional extinction (or quasi-extinction) within 100 years. Our analysis is based on a single hibernating colony of little brown bats located within a geographic region considered highly suitable for *P. destructans* (Flory et al. 2012). Population trajectories of little brown bats could vary across the WNS-infected region based upon latitudinal differences in environmental conditions and hibernacula microclimates (Flory et al. 2012, Langwig et al. 2012, Verant et al. 2012), but currently little is known about geographic variation in mortality from WNS. If the demographic patterns observed in this study are representative of the response of little brown bat

colonies to WNS, our results raise serious concerns about this species' long-term regional persistence.

#### *Short-term conservation strategies*

Given the severity of initial mortality from WNS of North American bat populations and the bleak prognosis reported here and elsewhere (Frick et al. 2010a), developing an effective strategy for mitigating WNS impacts and conserving affected species is of critical importance. Our results strongly suggest that active management is required to increase little brown bat recovery potential. Despite several advances in understanding the ecology of *P. destructans* and its effects on bats (e.g., Warnecke et al. 2012, Langwig et al. 2015), a clear path toward effective management of this pathogen is not yet apparent. Our vital rate sensitivity analysis determined that increasing survival across both age classes (as opposed to strategies focused on increasing fecundity) would be the most effective strategy for increasing little brown bat abundance over a 15-year period. Unfortunately, there are currently no established methods for improving survival of infected bats. Several methods for reducing infection intensity have been unsuccessful or are in early stages of development. For example, decontamination of the environmental reservoir in infected hibernacula could reduce exposure and transmission of *P. destructans*. Early trials are underway, but concerns about treating natural environments with anti-fungals have been raised (Foley et al. 2011). Maintenance of localized thermal refugia may lessen the energetic costs of frequent arousals of torpid bats (Boyles and Willis 2010), and provisioning of sodium and chloride may replenish depleted electrolyte levels in infected hibernating bats (Cryan et al. 2013b). However, even if either or both of these approaches prove effective for ameliorating rates of mortality, there is no current mechanism to entice bats to use thermal refugia or to deliver electrolyte supplements. Chemical and biocontrol of *P. destructans* through bacterially produced volatile organic compounds or other anti-fungal treatments is also being investigated (Cryan et al. 2013b, Cornelison et al. 2014). Although feasibility of implementing these strategies over the long term is challenged by the difficulties of disturbing bats during hibernation with single or repeated treatments, using these methods to maintain populations above a critical size threshold may prove to be the key to improving survival of infected bats.

Our vital rate sensitivity analysis indicated that targeting management to improve reproductive rates would not have a significant effect on colony size. Average pre-WNS reproductive rates for little brown bats are estimated at  $>0.93$  (Humphrey 1971, Reynolds 1999, Frick et al. 2010b). Preliminary post-WNS reproductive rates have been reported as  $\sim 0.85$  (Reichard and Kunz 2009, Frick et al. 2010a, b), generated from physical examination of female bats at maternity colonies in midsummer, when nonreproductive females

may have already vacated the roost (J. Reichard, *personal communication*). If true, these estimates probably overestimate reproductive rates. Indeed, WNS may have several negative impacts on female reproduction. Bats recovering from severe WNS infection may forego reproduction in any given year as a facultative response to physiological stress, allowing them to allocate nutritional reserves toward healing. WNS infection may also cause a delay in reproduction until the recovery process is complete and the individual has sufficient energy reserves to support reproduction. Because WNS advances spring emergence times (Norquay and Willis 2014), even bats with low infection loads and fat reserves sufficient to initiate pregnancy may be negatively affected by the cold temperatures and low insect availability of early spring. Alternatively, the severity of initial WNS mortality may have triggered an increase in juvenile reproductive rates, as has been observed at some maternity sites (C. Dobony, *unpublished data*) and demonstrated for some populations of Tasmanian devils (*Sarcophilus harrisii*; Jones et al. 2008). The lingering effects of WNS on individuals that survive initial infection may prove profound, and continued research focused on reproductive females at maternity colonies should be a priority.

Considering the population structure of a remnant colony is important when defining short-term management objectives because population dynamics over the first few years following initial WNS mortality vary based upon the distribution of age classes. Stable populations exhibit decreasing annual growth rates, but a heavily adult-skewed population will show a temporary pulse in abundance before measurable declines reestablish (Fig. 3). Although successful management intervention of any population can increase the probability of its persistence in the long term, capitalizing on the temporary pulse in growth of an adult-skewed population by increasing survival results in a higher return on management efforts, in this case with a net gain of 395 individuals (Table 2, Fig. 3). If bats are adaptively responding to WNS infection, boosting colony size in the short term may reduce the negative stochastic impacts and Allee effects until the colony can recover on its own.

#### *Conclusions*

Our analysis demonstrates the first empirical evidence that annual survival rates can improve markedly in remnant little brown bat colonies infected with WNS and may result in lengthened colony persistence. Our results suggest that there exists either a strong selection pressure for genetically resistant little brown bats or an adaptive immunological response to WNS infection. However, despite the marked increase in survival relative to initial mortality from WNS at individual hibernating colonies, current survival rates are not sufficient to support long-term recovery. These data, combined with the increased vulnerability of small populations to stochastic processes,

raise serious concerns regarding the long-term regional persistence of this species. Timely, active management targeting increased survival is likely to improve the recovery potential of little brown bats. However, the continued ability of this species to respond adaptively to WNS infection through continued amelioration of survival and reproduction will ultimately determine their probability of persistence for the long term.

#### ACKNOWLEDGMENTS

We thank N. H. Fefferman, J. L. Lockwood, and A. M. Kilpatrick for helpful insights and constructive comments on this analysis. M. Hall, M. Kitchell, M. Kaiura, K. Kerwin, K. Leu, E. Buenaventura, and several other field assistants volunteered during mark–recapture activities. W. F. Frick was supported by NSF DEB-1115895.

#### LITERATURE CITED

- Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics* 53:666–677.
- Barker, R. J., and G. C. White. 2001. Joint analysis of live and dead encounters of marked animals. Pages 361–367 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century*. Proceedings of the Second International Wildlife Congress. The Wildlife Society, Bethesda, Maryland, USA.
- Boyles, J. G., and C. K. R. Willis. 2010. Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? *Frontiers in Ecology and the Environment* 8:92–98.
- Brunet-Rossini, A. K., and G. S. Wilkinson. 2009. Methods for age estimation and the study of senescence in bats. Pages 315–325 in T. H. Kunz and S. Parsons, editors. *Ecological and behavioral methods for the study of bats*. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- Caswell, H. 2001. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. J. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: implications for wildlife welfare and research. *Journal of Mammalogy* 89:973–990.
- Cornelison, C. T., K. T. Gabriel, C. Barlament, and S. A. Crow, Jr. 2014. Inhibition of *Pseudogymnoascus destructans* growth from conidia and mycelial extension by bacterially produced volatile organic compounds. *Mycopathologia* 177:1–10.
- Cryan, P. M., C. U. Meteyer, D. S. Blehert, J. M. Lorch, D. M. Reeder, G. G. Turner, J. Webb, M. Behr, M. Verant, and R. E. Russell. 2013a. Electrolyte depletion in white-nose syndrome bats. *Journal of Wildlife Diseases* 49:398–402.
- Cryan, P. M., et al. 2013b. Electrolyte depletion in white-nose syndrome bats. *Journal of Wildlife Diseases* 49:398–402.
- Fefferman, N. H., and J. M. Reed. 2006. A vital rate sensitivity analysis for nonstable age distributions and short-term planning. *Journal of Wildlife Management* 70:649–656.
- Field, K. J., C. R. Tracy, P. A. Medica, R. W. Marlow, and P. S. Corn. 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). *Biological Conservation* 136:232–245.
- Flajnik, M. F., and M. Kasahara. 2010. Origin and evolution of the adaptive immune system: genetic events and selective pressures. *Nature Reviews Genetics* 11:47–59.
- Flory, A. R., S. Kumar, T. J. Stohlgren, and P. M. Cryan. 2012. Environmental conditions associated with bat white-nose syndrome mortality in the northeastern United States. *Journal of Applied Ecology* 49:680–689.
- Foley, J., D. Clifford, K. Castle, P. Cryan, and R. S. Ostfeld. 2011. Investigating and managing the rapid emergence of white-nose syndrome, a novel, fatal, infectious disease of hibernating bats. *Conservation Biology* 25:223–231.
- Frick, W. F., J. F. Pollock, A. C. Hicks, K. E. Langwig, D. S. Reynolds, G. G. Turner, C. M. Butchkoski, and T. H. Kunz. 2010a. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682.
- Frick, W. F., et al. 2015. Disease alters macroecological patterns of North American bats. *Global Ecology and Biogeography*. <http://dx.doi.org/10.1111/geb.12290>
- Frick, W. F., D. S. Reynolds, and T. H. Kunz. 2010b. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *Journal of Animal Ecology* 79:128–136.
- Gargas, A., M. Trest, M. Christensen, T. J. Volk, and D. Blehert. 2009. *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. *Mycotaxon* 108:147–154.
- Harvell, D., S. Altizer, I. M. Cattadori, L. Harrington, and E. Weil. 2009. Climate change and wildlife diseases: when does the host matter the most? *Ecology* 90:912–920.
- Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* 17:20–29.
- Humphrey, S. R. 1971. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. Dissertation. Oklahoma State University, Stillwater, Oklahoma, USA.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.
- Jones, M. E., A. Cockburn, R. Hamede, C. Hawkins, H. Hesterman, S. Lachish, D. Mann, H. McCallum, and D. Pemberton. 2008. Life-history change in disease-ravaged Tasmanian devil populations. *Proceedings of the National Academy of Sciences USA* 105:10023–10027.
- Langwig, K. E., W. F. Frick, J. T. Bried, A. C. Hicks, T. H. Kunz, and A. M. Kilpatrick. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology Letters* 15:1050–1057.
- Langwig, K. E., W. F. Frick, R. Reynolds, K. L. Parise, K. P. Drees, J. R. Hoyt, T. L. Cheng, T. H. Kunz, J. T. Foster, and A. M. Kilpatrick. 2015. Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proceedings of the Royal Society of London B* 282:20142335.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latto, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease? *Trends in Ecology and Evolution* 20:511–519.
- Loehle, C. 1995. Social barriers to pathogen transmission in wild animal populations. *Ecology* 76:326–335.
- Maslo, B., and N. H. Fefferman. 2015. A case study of bats and white-nose syndrome demonstrating how to model population viability with evolutionary effects. *Conservation Biology* 29:1176–1185.
- Matthews, J. H., W. C. Funk, and C. K. Ghalambor. 2013. Demographic approaches to assessing climate change impact: an application to pond-breeding frogs and shifting hydro-patterns. Pages 58–85 in J. F. Brodie, E. S. Post, and D. F. Doak, editors. *Wildlife conservation in a changing climate*. University of Chicago Press, Chicago, Illinois, USA.
- Mills, L. S. 2012. *Conservation of wildlife populations: demography, genetics, and management*. John Wiley, Chichester, West Sussex, UK.



- Minnis, A. M., and D. L. Lindner. 2013. Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans*, comb. nov., in bat hibernacula of eastern North America. *Fungal Biology* 117:638–649.
- Mörner, T., D. Obendorf, M. Artois, and M. Woodford. 2002. Surveillance and monitoring of wildlife diseases. *Revue Scientifique et Technique (International Office of Epizootics)* 21:67–76.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.
- Norquay, K. J. O., F. Martinez-Nunez, J. E. Dubois, K. M. Monson, and C. K. R. Willis. 2013. Long-distance movements of little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* 94:506–515.
- Norquay, K., and C. Willis. 2014. Hibernation phenology of *Myotis lucifugus*. *Journal of Zoology* 294:85–92.
- O'Shea, T. J., M. A. Bogan, and L. E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. *Wildlife Society Bulletin* 31:16–29.
- O'Shea, T. J., L. E. Ellison, and T. R. Stanley. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. Pages 297–336 in W. L. Thompson, editor. *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*. Island Press, Washington, D.C., USA.
- Rachowicz, L. J., J.-M. Hero, R. A. Alford, J. W. Taylor, J. A. T. Morgan, V. T. Vredenburg, J. P. Collins, and C. J. Briggs. 2005. The novel and endemic pathogen hypotheses: competing explanations for the origin of emerging infectious diseases of wildlife. *Conservation Biology* 19:1441–1448.
- Reed, J. M., N. Fefferman, and R. C. Averill-Murray. 2009. Vital rate sensitivity analysis as a tool for assessing management actions for the desert tortoise. *Biological Conservation* 142:2710–2717.
- Reichard, J. D., N. W. Fuller, A. B. Bennett, S. R. Darling, M. S. Moore, K. E. Langwig, E. D. Preston, S. von Oettingen, C. S. Richardson, and D. Scott Reynolds. 2014. Interannual survival of *Myotis lucifugus* (Chiroptera: Vespertilionidae) near the epicenter of white-nose syndrome. *Northeastern Naturalist* 21:N56–N59.
- Reichard, J. D., and T. H. Kunz. 2009. White-nose syndrome inflicts lasting injuries to the wings of little brown myotis (*Myotis lucifugus*). *Acta Chiropterologica* 11:457–464.
- Reynolds, D. S. 1999. Variation in life history traits in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Dissertation. Boston University, Boston, Massachusetts, USA.
- Richmond, J. Q., A. E. Savage, K. R. Zamudio, and E. B. Rosenblum. 2009. Toward immunogenetic studies of amphibian chytridiomycosis: linking innate and acquired immunity. *BioScience* 59:311–320.
- Slattery, S., and R. Alisauskas. 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): a case study. *Journal of Applied Statistics* 29:497–508.
- Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences USA* 99:15497–15500.
- Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 9:357–374.
- Thomas, C. D., et al. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Thompson, J. N. 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13:329–332.
- Verant, M. L., J. G. Boyles, W. Waldrep, Jr., G. Wibbelt, and D. S. Blehert. 2012. Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. *PLoS ONE* 7:e46280.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B* 365:2019–2024.
- Warnecke, L., J. M. Turner, T. K. Bollinger, J. M. Lorch, V. Misra, P. M. Cryan, G. Wibbelt, D. S. Blehert, and C. K. Willis. 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences USA* 109:6999–7003.
- Watt, E., and M. B. Fenton. 1995. DNA fingerprinting provides evidence of discriminate suckling and non-random mating in little brown bats *Myotis lucifugus*. *Molecular Ecology* 4:261–264.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Supplement):120–138.
- Willis, C. K., A. K. Menzies, J. G. Boyles, and M. S. Wojciechowski. 2011. Cutaneous water loss is a plausible explanation for mortality of bats from white-nose syndrome. *Integrative and Comparative Biology* 51:364–373.

#### SUPPLEMENTAL MATERIAL

##### Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-2472.1.sm>

##### Data Availability

Data associated with this paper are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.85709>