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White-nose syndrome is likely to extirpate the endangered Indiana bat over large parts of its range

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ABSTRACT

White-nose syndrome, a novel fungal pathogen spreading quickly through cave-hibernating bat species in east and central North America, is responsible for killing millions of bats. We developed a stochastic, stage-based population model to forecast the population dynamics of the endangered Indiana bat (*Myotis sodalis*) subject to white-nose syndrome. Our population model explicitly incorporated environmentally imposed annual variability in survival and reproductive rates and demographic stochasticity in predictions of extinction. With observed rates of disease spread, >90% of wintering populations were predicted to experience white-nose syndrome within 20 years, causing the proportion of populations at the quasi-extinction threshold of less than 250 females to increase by 33.9% over 50 years. At the species' lowest median population level, ca. year 2022, we predicted 13.7% of the initial population to remain, totaling 28,958 females (95% CI = 13,330; 92,335). By 2022, only 12 of the initial 52 wintering populations were expected to possess wintering populations of >250 females. If the species can acquire immunity to the disease, we predict 3.7% of wintering populations to be above 250 females after 50 years (year 2057) after a 69% decline in abundance (from 210,741 to 64,768 [95% CI = 49,386; 85,360] females). At the nadir of projections, we predicted regional quasi-extirpation of wintering populations in 2 of 4 Recovery Units while in a third region, where the species is currently most abundant, >95% of the wintering populations were predicted to be below 250 females. Our modeling suggests white-nose syndrome is capable of bringing about severe numerical reduction in population size and local and regional extirpation of the Indiana bat.

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1. Introduction

Species extinction and collapse of biotic systems is one of the most pressing problems facing humanity (Sala et al., 2000). Preventing extinction for many species is difficult, however, because of a fundamental lack of information regarding the dynamics of their populations and the multifarious threats they face (Lande, 1993; Wake, 2012). Over the last quarter century, considerable attention has been paid to the role pathogens play in determining population dynamics and the risk faced by species (May, 1988; Scott, 1988; Daszak et al., 2000; Dobson and Foufopoulos, 2001; Cleaveland et al., 2002; Lafferty and Gerber, 2002; Smith et al., 2006). Infectious diseases, such as chytridiomycosis (Skerratt et al., 2007), West Nile virus (LaDeau et al., 2007), and rinderpest (de Castro and Bolker, 2005), are capable of causing massive and rapid die-offs.

Fungal diseases pose an emerging worldwide threat (Fisher et al., 2012), with much concern in North America paid to the conservation of hibernating bats because of the risk these taxa face from the fungal disease white-nose syndrome (Blehert et al., 2009, 2011; Foley et al., 2011). White-nose syndrome, caused by the psychrophilic fungus *Geomyces destructans* (Lorch et al., 2011), is characterized by the presence of profuse but delicate hyphae and conidia on the muzzles, wing membranes, and pinnae of infected bats; the fungal hyphae pervade the tissue surrounding hair follicles and sebaceous glands (Gargas et al., 2009; Meteyer

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et al., 2009). The disease results in increased frequency of arousal during hibernation, depleted fat reserves, and severe wing damage (Meteyer et al., 2009; Cryan et al., 2010). As a consequence, more than 75% of bats die in some WNS-affected wintering populations (Blehert et al., 2009; Foley et al., 2011; Turner et al., 2011).

White-nose syndrome (WNS) was first documented in North America at Howe's Cave near Albany, NY, USA, during winter 2006 (Blehert et al., 2009). Since that sighting, the disease has rapidly spread throughout the eastern US and Canada (Blehert et al., 2011; Foley et al., 2011; Thogmartin et al., 2012a; USFWS, 2012); as of spring 2012, WNS was confirmed in wintering populations in 19 US states and four Canadian provinces and is believed to have killed as many as 6 million bats (USFWS, 2012). The disease is believed to be spread through physical contact among individual bats (Frick et al., 2010a; Lorch et al., 2011; Hallam and McCracken, 2011) but may also be spread to novel locations anthropogenically (Turner et al., 2011).

As of spring 2012, *G. destructans* was observed to cause mortality in six species of bats, the Indiana bat (*Myotis sodalis*), little brown (*Myotis lucifugus*), northern long-eared (*Myotis septentrionalis*), eastern small-footed (*Myotis leibii*), big brown (*Eptesicus fuscus*), and tricolored bats (*Perimyotis subflavus*) (Blehert et al., 2009; Cryan et al., 2010; Turner et al., 2011). Genetic material consistent with *G. destructans* has been identified on three additional *Myotis* species (*Myotis grisescens*, *Myotis velifer*, and *Myotis austroriparius*) in Missouri, Oklahoma and Virginia, respectively (Turner et al., 2011).

The Indiana bat is of particular concern because of its status as endangered under the U.S. Endangered Species Act of 1973, as amended (16 U.S.C. 1531 et seq.). The Indiana bat is also a redlisted species according to the International Union for the Conservation of Nature (Arroyo-Cabrales and Ticul Alvarez Castaneda, 2008). This animal lives primarily in eastern, midwestern, and parts of the southern United States. Estimates of trend from hibernacula count data suggested that the species declined in abundance by 57% from 1965–2001 though recent evidence indicated no appreciable change in abundance between 1983 and 2009 (Thogmartin et al., 2012b). Reasons for the species' decline and subsequent listing included alteration of hibernacula (USFWS, 2007), disturbance of colonies by humans (Johnson et al., 1998), pesticide use (Schmidt et al., 2001), and loss of summer habitat resulting from the clearing of forest cover (Menzel et al., 2001; Carter and Feldhamer, 2005; Sparks et al., 2005).

The emergence of WNS poses a threat of extinction. Fungal pathogens such as *G. destructans* are uniquely capable of driving host populations extinct because of their ability to survive in a host-free environment (Casadevall, 2005). The loss of ≥40,000 Indiana bats since emergence of WNS (Turner et al., 2011) represents nearly 10% of the 2006 population (Thogmartin et al., 2012b). This novel threat increases the urgency for understanding the population dynamics of the endangered Indiana bat. Unfortunately, there is little demographic information for the Indiana bat, no models have been devised for characterizing the demographic processes of this species, and indeed few demographic modeling efforts exist for bats of any species (Federico et al., 2008; Frick et al., 2010a; O'Shea et al., 2011). Our modeling effort fills this information gap for Indiana bats following the recommendations of a 2008 structured decision-making exercise hosted by the U.S. Fish and Wildlife Service (Szymanski et al., 2009). The purpose of this study was to develop a stage-based demographic model for Indiana bats, derive parameter values from empirical data on trends at hibernacula, and project population trends at hibernacula, Recovery Unit (management regions designated in the draft Recovery Plan [USFWS, 2007]), and species-wide levels in the face of the rapidly evolving threat from WNS. The model and results are needed as decision-support tools to assess the status of the species and evaluate potential management actions.

2. Materials and methods

We developed a stage-structured matrix model to describe Indiana bat demography. Parameters of this model were back-calculated from historically observed population rates of change determined from trend analyses. Projections for individual wintering populations were based upon these observed trends and three sources of annual variation – environmental and demographic stochasticity and uncertainty in the parameter values contributing to the population rate of change. To examine the potential consequences of WNS given uncertainty in how it operates, we examined two scenarios likely bounding the possible effects of the disease; an 'acquired immunity' scenario allowed populations to resume their pre-WNS demography after a period of 7 years, whereas a 'persistent influence' scenario applied a perpetual consequence to winter survival. We varied the magnitude of environmental stochasticity and minimum viable population sizes to assess consequences to our estimates of risk. Details of these methods follow below.

2.1. Stage-structured model

We focused our stage-structured matrix model (Lefkovitch, 1965; Caswell, 2001) on 2 age-dependent stages in winter: first-year females (females born the previous summer) and adult females (after-first year females) (Fig. 1); this winter period is coincident with long-term population surveys of the species (Thogmartin et al., 2012b). Over the rest of the year, the population is also divided by reproductive status, resulting in four groups: reproductive adult, non-reproductive adult, first-year breeders, and non-reproductive first-year individuals. In the summer, another stage is added for the offspring (pups). The primary sex ratio of offspring born each summer was assumed to be 1:1; thus, all reproductive effort was halved to account for this ratio. This model included neither explicit spatial structure nor males, and assumed individual wintering populations constituted a closed population. We further assumed that first-year individuals perform demographically no better than adults (Schowalter and Gunson, 1979, for instance, reported lowered reproductive effort by juveniles compared to adults). We concentrated on describing the female segment of the population because of the polygynous nature of this species (McCracken and Wilkinson, 2000).

Survival and reproductive parameters delineate transitions between the classes (Table 1). Transitions from winter to summer included overwinter survival (φ^W) and the proportion of females
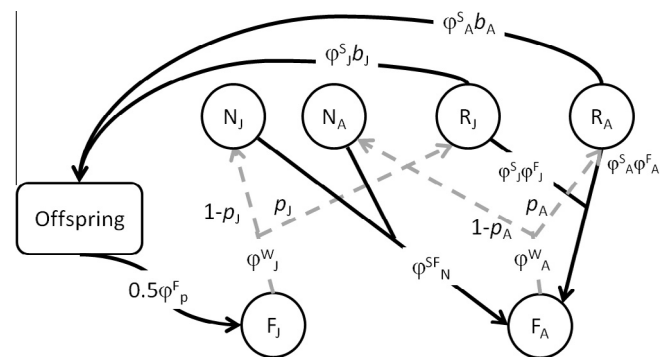

Fig. 1. Life-cycle graph for the Indiana bat population model, female segment only. The state variables are measured in November, at the beginning of hibernation. Offspring is an intermediate state variable, measured at volancy. Transitions are stage-specific – adults, A and juveniles, J. The transition from winter to spring is overwinter survival (φ^W). Transitions from spring to winter include summer survival (φ^S), fall survival (φ^F), propensity to reproduce (p), and birthing success (b). In summer, individuals are either breeders (R) or non-breeders (N). See Table 1 for definitions.

becoming pregnant (p). The transitions from summer to winter included summer survival (φ^S) and fall survival (φ^F). The reproductive transitions included summer survival of reproductive females (φ^S), proportion of pregnant females successfully birthing one offspring (b), and fall offspring survival (φ_P^F). The summer survival transition (φ^S) was applied before determining whether a female was a successful breeder; this assumption prevented a pup surviving summer without maternal care.

The model can be described with a matrix equation describing the transition from the winter population structure in year t to the winter population structure in year $t + 1$:

$$\begin{bmatrix} F_J \\ F_A \end{bmatrix}_{t+1} = \begin{bmatrix} 0.5\varphi_J^W p_J \varphi_J^S b_J \varphi_P^F & 0.5\varphi_A^W p_A \varphi_A^S b_A \varphi_P^F \\ \varphi_J^W p_J \varphi_J^S \varphi_J^F \varphi_J^W (1-p_J)\varphi_N^{SF} & \varphi_A^W p_A \varphi_A^S \varphi_A^F \varphi_A^W (1-p_A)\varphi_N^{SF} \end{bmatrix} \begin{bmatrix} F_J \\ F_A \end{bmatrix}_t ,$$

with age-classes subscripted and seasons superscripted. Subscripts are A for adults, J for first-year individuals (juveniles), P for offspring (pups), and N for non-breeding adult and first-year individuals. The superscripts W, S, and F denote winter, summer, and fall, respectively.

We set the initial stage distribution to the stable stage distribution calculated from the projection matrix. The starting population for each wintering population was identified according to results of hibernaculum-specific hierarchical log-linear models of winter counts (Thogmartin et al., 2012b). When considering the consequences of WNS, we ran scenarios in parallel, using the same values for each parameter for each run except for those parameters differing between scenarios (McGowan et al., 2011). All demographic projections were conducted in MATLAB R2010 (Mathworks, Natick, Massachusetts, USA).

2.2. Parameter derivation

All model parameters for survival and reproduction are probabilities on the interval [0,1]. For each wintering population, we used the mean population rate of change identified through hibernaculum-specific trend analyses (Thogmartin et al., 2012b) to point to relevant parameter combinations capable of returning the observed trend. These trends (r) were estimated for the period 1983–2003 for 222 wintering populations (Thogmartin et al., 2012b). These trend estimates characterized Indiana bat populations before the onset of WNS, which was first noticed in 2006.

Once we obtained trend estimates for each wintering population, where $r = \ln\lambda$, we created a lookup table comprised of random parameter combinations and the λ resulting from those combinations to identify sets of parameters compatible with the observed trends. This lookup table (available from the first author) was created from 10,000 Monte Carlo simulations of 100,000 random parameter combinations with most parameters drawn with replacement from the interval [0,1]. Parameters were drawn independently, assuming no correlation among survival or reproductive rates. To obtain greater representation of positive rates of population change (which require correlation among demographic parameters, i.e., a growing population can only occur when all seasonal survival rates are high), we calculated λ for random parameter combinations after setting adult and first-year female winter

survival to every 0.05-point increment between 0.7 and 1.0. For every random combination of parameters, we estimated the average annual growth rate with our matrix equation, creating the lookup table. These additional 50,000 systematically drawn parameter combinations were added to the 100,000 randomly drawn parameter combinations to produce a lookup table linking observed λ over the interval 0 to 1.417 to 150,000 combinations of parameters potentially causing those rates of change.

We used these parameter combinations in the lookup table in subsequent population projections. We assumed individual estimates of population change persisted throughout the period of the simulation, i.e., populations either increased or decreased at the same rate for each year of the model as determined by their population-specific pre-WNS dynamic and as amended by environmental and demographic stochasticity, unless under the influence of disease.

Differing combinations of parameters may yield the same population rate of change; for instance, in our lookup table, there were 108 combinations for $\lambda = 1.000$. We used random draws (with replacement) from this set of parameter combinations for a particular λ (to three decimal places) to characterize the dynamics of a wintering population and to determine the consequences of parameter uncertainty (i.e., not knowing the exact combination of parameter values causing a particular λ) on subsequent inferences.

2.3. Spatial structure

The temporal and spatial patterns of movement of individuals among hibernacula is poorly known. This limited our ability to embed our population dynamics model in a spatial framework. As a consequence, we did not allow individuals occurring in one wintering population to migrate to other hibernacula; our model, therefore, assumes wintering populations are independent, closed populations without capability for rescue at low population sizes. A few wintering populations did, however, exhibit prior to the onset of WNS a rate of change exceeding biological possibility under this closed population assumption (i.e., $\lambda \geqslant 1.417$), suggestive of immigration (Thogmartin et al., 2012b). For those populations, we chose a λ from a higher level (the complex of neighboring wintering populations or Recovery Unit) in our hierarchy of trends in partial recognition of inter-hibernaculum movement. This hierarchical structure was also important in determining spread of WNS across hibernacula; wintering populations occurring in a complex of other wintering populations were at greater risk of the disease once a neighboring hibernaculum experienced the disease (see below). For reporting, dynamics of individual wintering populations were summed to Recovery Units, which were summed to the species level.

2.4. Environmental stochasticity

Environmental stochasticity is variation in vital rates caused by annual differences in environmental conditions (May, 1973). Combining randomly selected parameter values to simulate stochastic temporal variability is a long-standing practice in projection

Table 1
Definition of age-specific parameters for demographic model of single hibernaculum Indiana bats.

Parameter	Definition
φ^W	Survival from hibernation to beginning of breeding season (winter)
φ_N^{SF}	Survival from time of parturition (summer) to hibernation for non-reproductive individuals
φ^S	Survival from time of parturition to time of volancy of pups (summer)
φ^F	Survival from time of volancy of pups to hibernation (fall)
p	Propensity to reproduce: proportion of females becoming pregnant
b	Reproductive success: proportion of pregnant females giving birth to one offspring

matrix models (Bierzychudek, 1982; Paton, 1986; van Groenendael and Slim, 1988). For the congeneric little brown bat, typical variation in adult reproductive rate (most akin to our estimate of adult breeding propensity) was equivalent to ±0.04 units of the mean value (Frick et al., 2010b). Conversely, considerable differences in annual survival of 0.2–0.3 across the range of years were reported (Frick et al., 2010b) ($\varphi_{\text{First-year}}$ = 0.23–0.46, φ_{Adult} = 0.63–0.90). However, much of this variation could be explained by a deterministic trend in annual precipitation; taking this environmental trend into account, stochastic variation in annual survival was also on the order of ±0.04. Thus, we drew randomly from a uniform distribution within ±0.04 units centered on the randomly drawn parameter value (Section 2.2) to identify the stochastically influenced values used in the simulations.

2.5. Demographic stochasticity

Seasonal survival, proportion of breeding females, and proportion of successful breeding females are Bernoulli processes in the sense that each female can be considered a trial with a binary outcome (live or die, breed or not breed, successfully breed or fail). Demographic stochasticity is the temporal variation caused by differences in the fate of each animal. In this Indiana bat model, a binomial random variable with success probability equal to the parameter value was used to determine the vital rate. Demographic stochasticity was applied to the class in the model which is the same as applying stochasticity to each individual (Runge et al., 2007).

2.6. Ceiling mechanisms and absorbing limits

We accommodated density dependence with a ceiling mechanism (Morris and Doak, 2002) using 150% of the historical maximum number of bats observed in the particular hibernaculum, divided by 2 to represent the female segment of the population. Failure to implement this ceiling mechanism would allow some projections to reach unrealistically large population sizes.

Indiana bats are a gregarious species. We set the quasi-extirpation level (Ginzburg et al., 1982) for most of our analyses to 250 females (500 total bats), a management-relevant population size. This quasi-extirpation level is an absorbing lower boundary, below which a population would not be expected to recover because of Allee effects (Allee et al., 1949), inbreeding depression (Soulé, 1980), and other consequences of small population size (Soulé, 1987; Remmert, 1994; Morris and Doak, 2002). Because a quasi-extirpation level of 250 females is arbitrary (necessarily so given the lack of data; Williams et al., 2002), we assessed the consequences of this quasi-extirpation level through sensitivity analyses.

2.7. Sensitivity and elasticity

Sensitivity and elasticity analysis can be used to measure the relative effect on λ of small changes to particular transitions in the life cycle (Jørgenson, 1986; Caswell, 2001; Morris and Doak, 2002; Thogmartin, 2010). The sensitivity s_i of the growth rate λ to a vital rate r_i is:

$$s_i = \frac{\Delta \lambda}{\Delta r_i},$$

Because the range of parameter estimates over which we evaluated model sensitivity varied among parameters, we also calculated the proportional effect, i.e., model elasticity e_i (de Kroon et al., 1986, 2000; Caswell, 2001; Morris and Doak, 2002):

$$e_i = \frac{r_i}{\lambda} \frac{\Delta \lambda}{\Delta r_i}.$$

Elasticities indicate relative importance of stage transitions to population growth.

To calculate sensitivity and elasticity, we conducted 150 simulations of the Indiana bat model, each with a random set of parameter values drawn in a stratified manner across the entire 90% confidence interval of the complex hibernacula trends (i.e., λ = 0.815–1.248). This interval for the parameters avoided rates of change obviously influenced by emigration and immigration, allowing us to analyze sensitivity over a biologically realistic range of values (Table 2). We regressed λ against each vital rate to measure the relative value of different rates in determining λ (Morris and Doak, 2002). This sensitivity analysis did not include variation associated with demographic or environmental stochasticity nor density dependence, all of which could exacerbate quasi-extirpation and therefore estimates of parameter sensitivity.

Global sensitivity, unlike local sensitivity, measures the influence of each parameter averaged over all possible values of the other parameters (Saltelli et al., 1999; Fieberg and Jenkins, 2005; Cariboni et al., 2007). We conducted a Fourier amplitude sensitivity test (FAST), a variance-based measure, to assess global model sensitivity (Chan et al., 2000). The FAST method yields partial variances, which are the fractions of the variance of the output function resulting from variation of one input parameter when the output function is averaged over the variation of all other parameters. Thus, the partial variance is a measure of the sensitivity of the output variable to the variation of one input parameter.

The FAST approach entails a transformation converting a multidimensional integral of the model inputs into a one-dimensional integral. In this case, the dimensions equate to the 12 demographic parameters. This transformation occurs via a search curve spanning the entire parameter space, with scanning of each axis of the parameter space explored with a different frequency. The extended-FAST method is useful because it is independent of assumptions about model structure, accommodates interactions between parameters, and works for monotonic and non-monotonic models. First-order and total global sensitivities were calculated for each parameter with the 'sensitivity' library (version 1.4) in R (Pujol and Iooss, 2009). In this application, 120,000 model evaluations were calculated.

We also examined the relative importance of the main sources of annual variability: demographic stochasticity, environmental stochasticity, and parameter uncertainty. We conducted three 50-year simulations for the Ozark-Central Recovery Unit with one simulation individually devoted to each source of annual variability (each simulation was the mean of n = 500 runs). These simulations were then compared to results when these sources of variance were combined.

An underlying premise of our projections is that the environment will continue over the projection interval to be as variable (no more, no less) as it is today. Climate conditions can influence bat population dynamics; warmer and drier weather, for example, was associated with decreased adult female little brown bat survival (Frick et al., 2010b). Climate variability is expected to increase in the face of changing climate (IPCC, 2001), potentially influencing our estimates of extinction risk. Because of the importance of environmental stochasticity on our estimates of quasi-extirpation probability, we examined the sensitivity of our inferences to increases in environmental stochasticity; we compared our baseline level of environmental stochasticity (±0.04) to uniform random draws from the intervals ±0.08 and ±0.12 and applied these more widely drawn values to our originally drawn parameter values. Our current quasi-extirpation level of 250 females is also ad hoc; we examined the sensitivity of our inferences by considering a quasi-extirpation level of 25 females (50 total bats).

2.8. White-nose syndrome scenarios

Fully parameterizing a host-pathogen model is particularly difficult for a novel, rapidly spreading pathogen affecting an endangered species (Gerber et al., 2005). We incorporated WNS into

Table 2
Local sensitivity (s) and elasticity (e) for parameters of a stage-based matrix model of Indiana bat demography relative to the population rate of change (λ); median and 90% confidence interval values of the parameters are provided.

Parameter[a]	λ		5th Percentile	Median	95th Percentile
	s	e			
Adult winter survival	0.915	0.834	0.905	0.951	0.995
Adult summer survival	0.747	0.669	0.901	0.948	0.995
Adult fall survival	0.582	0.524	0.901	0.948	0.995
Non-repro summer/fall survival	0.255	0.225	0.724	0.922	0.993
First-year winter survival	0.206	0.158	0.705	0.902	0.965
Pup fall survival	0.217	0.146	0.505	0.898	0.962
Adult breeding success	0.196	0.135	0.519	0.847	0.985
Adult breeding propensity	0.190	0.110	0.451	0.843	0.985
First-year summer survival	0.126	0.087	0.587	0.905	0.966
First-year fall survival	0.104	0.072	0.591	0.902	0.964
First-year breeding success	0.035	0.009	0.057	0.558	0.874
First-year breeding propensity	0.017	0.004	0.034	0.555	0.872

[a] The parameters are ordered from most to least influential to λ, according to e.

our population viability analyses as a catastrophe (Simberloff, 1988; Lande, 1993; Gerber and Hilborn, 2001; Gerber et al., 2005); to do so, we addressed four questions, drawn directly from Gerber and Hilborn (2001):

(1) What is the likelihood of pathogen arrival into the population under consideration?

Recent evidence suggests transmission of WNS is frequency-dependent (Langwig et al., 2012), such that the number of newly infected bats is $\beta SI/N$, where S is the number of susceptible individuals, I is the number of infected individuals, β is the transmission coefficient, and N is the total number of bats (McCallum et al., 2001). S, I, and β are rapidly evolving unknowns, and N is known but imprecisely for only one of the six afflicted species, the Indiana bat, and not at all (outside of the northeastern US) for the other, generally more numerous species co-habiting Indiana bat hibernacula. Because of the lack of an alternative or default disease transmission model for novel diseases (McCallum and Dobson, 1995), to provide a mechanism for distributing this disease among hibernacula, we modeled the observed hibernaculum-level occurrence of infection among Indiana bat wintering populations as a random intercept and random slope mixed-effects regression (described in Thogmartin et al. (2012a)). Among hibernacula, larger wintering populations closer to infected sources were found to be at greatest risk (Wilder et al., 2011; Thogmartin et al., 2012a). This analysis provided a rate of infection of 9.6% per year for hibernacula within complexes not yet experiencing WNS and 19.1% per year for those in which ⩾1 hibernaculum within a complex of interacting hibernacula was already infected. We used these rates, as a random Bernoulli draw, to project disease among unaffected wintering locations.

(2) Given that infection has arrived, what is the likelihood that an epizootic will become established in the population?

Diseases transmitted via frequency-dependent mechanisms are spread proportional to the frequency of infected individuals. Because WNS appears to be transmitted among Indiana bats in a frequency-dependent manner (Langwig et al., 2012), given one infected individual (of any of the afflicted species) in a hibernaculum, we assumed all individuals of an Indiana bat wintering population were at risk of infection. This premise seems particularly sound given the gregarious nature of Indiana bats and the high observed losses from this disease. We had insufficient information among our set of wintering populations to amend risk according to the climatic conditions of the hibernaculum or the sociality of individuals (which appears to change as WNS progresses in a wintering population; Langwig et al., 2012). Further, we did not impose a host-threshold density below which the disease did not operate (Lafferty and Gerber, 2002; Tompkins et al., 2002).

(3) Once it has become established, what will be the impact of the pathogen on the host population? Identifying how WNS is likely to affect the population is crucial to estimating species risk. We have a growing amount of information on the magnitude of mortality expected from WNS (Turner et al., 2011); information for a congener, the little brown bat (Frick et al., 2010a), also provided guidance for how to proceed. Initial-year population loss resulting from WNS for little brown bat ranged from 30% to 99% ($\bar{x}_{\text{regional}} = 73\%$) (Frick et al., 2010a). Further, results for one hibernacula complex, Ulster County, New York, suggested loss rates by Indiana bats of ~84% after 3 years (Thogmartin et al., 2012b), within the bounds of this mortality rate for little brown bats. Frick et al. (2010a) suggested mortality from WNS ameliorated over time. We replicated their scenario to characterize the year-specific consequences of WNS in Indiana bats. Once a wintering population within a hibernaculum was infected, we drew a proportion of the population surviving in the year since infection from a year-specific beta distribution that we based on mortality estimates described in Frick et al. (2010a) (Fig. A1).

(4) How long will the pathogen persist in the population, once it has become established?

Having characterized the magnitude of the disease effect, we then examined two scenarios characterizing the temporal extent or persistence of the disease. Our first scenario was akin to an acquisition of immunity whereby WNS was precluded from re-occurring in areas that were already affected ('acquired immunity' scenario); we further assumed with this scenario that after 7 years of the disease, a population returned to its pre-disease estimated rate of population change. Our second scenario described a persistent influence of the disease ('persistent influence' scenario); for this scenario we applied the year-6 mortality pattern ($\varphi = 0.82$–0.90) for the remaining years of the projection interval. The former scenario (akin to a Susceptible–Infective–Resistant model) may be considered a best-case situation, whereas the latter (akin to a Susceptible–Infective model) is considerably more pessimistic because it lacks recovery and indicates a perpetually endemic infection; therefore, these two scenarios bound the potential responses Indiana bats are likely to exhibit in the face of this disease.

We calculated for the two scenarios the proportion of wintering populations dropping at any time during the projection below a management-relevant quasi-extirpation threshold of 250 females. The U.S. Fish and Wildlife Service partitions Indiana bats among four categories of wintering population size (U.S. Fish and Wildlife Service, 2007); we also calculated the proportion of Priority 1 wintering populations (the largest and deemed most important populations) dropping below a threshold of 10,000 individuals (5000 females).

Beyond the direct effects of mortality from this disease, WNS could reduce breeding success resulting from the reduced physiological condition of surviving adults (Jonasson and Willis, 2011). We assessed the sensitivity of our extirpation risk estimates by decreasing the randomly drawn parameter value for adult winter survival or the probability of successfully birthing a pup by (a) 5%, (b) 15%, (c) 25%, and (d) 35%, and evaluated the consequence of this reduced parameter to the probability of quasi-extirpation (where quasi-extirpation = 25 female bats) for each of four starting population sizes: 40,700 bats (default; 2008 population of Magazine Mine, Illinois, a typical Priority 1 hibernaculum), 5000 bats, 1000 bats, and 500 bats.

3. Results

From 1983 through 2005, Indiana bat populations exhibited a stationary dynamic (Thogmartin et al., 2012b). Survival and reproductive rates consistent with this stationary trend (defined as ranging in mean growth rate, λ, between 0.99 and 1.01) consisted of high adult fall survival and relatively high adult survival in winter and summer. Thus, mean annual adult survival for a stationary population was $\varphi_{annual} = 0.867$ (Fig. 2). Given these annual survival rates, the mean lifespan for Indiana bats (calculated following Sendor and Simon (2003)) was 5.7 years; 7% of individuals would be expected to live 14 years, with more than 25% living $\geqslant 4$ years. Adult females in a stationary population would be expected to breed (p) at least 3 out of 4 years (more typically closer to 9 out of 10 years) with a success rate (b) of 3 out of 4 births. The stable age ratio in winter was 0.82 first-year females per adult female (95% CI = 0.76, 0.86).

3.1. Sensitivity and elasticity

The population rate of change (λ) was most sensitive to adult seasonal survival rates (Table 2). A 1% increase in adult winter survival, for instance, led to a 0.83% increase in population growth. Conversely, first-year female measures of demography were generally negligibly influential, except when first-year female winter survival interacted with the other parameters (Table A1). Environmental stochasticity was the principal source of variability in projections of Indiana bat population size, accounting for >90% of annual variation (Fig. A2). We found the consequences of an increased magnitude of environmental stochasticity to the risk of quasi-extirpation were most pronounced as population size decreased (Fig. A3); environmental variability in parameter values of ±12% for a 1000 bat wintering population was roughly equivalent (~5% risk of quasi-extirpation) to a ±4% or ±8% annual variability in parameter values incurred by a 500 bat wintering population.

3.2. Population projections in the absence of WNS

As of 2011, 22.6% of known hibernacula (51 of 226) maintained wintering populations of >250 females and 10 maintained wintering populations >5000 females (10,000 individuals is a U.S. Fish and Wildlife Service criterion for a Priority 1 hibernaculum). Using 250 females as a management-relevant quasi-extirpation threshold at the hibernaculum level, this suggests 77.4% of populations are currently quasi-extirpated. Absent WNS, the proportion of quasi-extirpated wintering populations was expected to increase 10.1% over 50 years (from 71.9% quasi-extirpated in 2008 to 79.2% in 2058) with quasi-extirpations of wintering populations occurring in 2 of the 4 Recovery Units (Appendix 1). All but 2 overwintering populations in the Ozark-Central Recovery Unit were expected to be quasi-extirpated after 50 years; because of their underlying positive rate of population change, the Northeast and
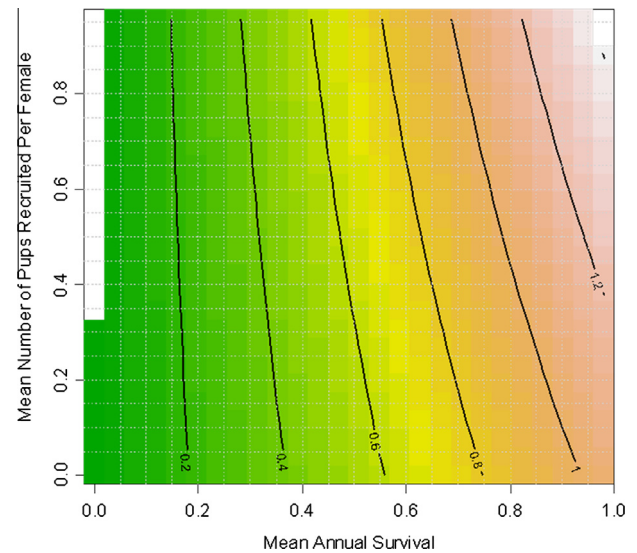

Fig. 2. Population rate of change (λ) as a function of annual reproduction (mean number of offspring recruited per female) and mean annual survival in Indiana bats.

Appalachian Recovery Units were expected to maintain the same proportion of extant wintering locations. For the Midwest Recovery Unit, while the proportion of quasi-extirpated populations increased 28.3%, the total population size in the unit increased as well (+160%), an increased concentration of the population in fewer locations resulting strictly from our closed population assumption. Because of the prominence of the Midwest Recovery Unit to the species, this pattern of increasing concentration was observed at the species-level as well; in the absence of WNS, the population of female Indiana bats would be expected to increase from 210,741 in 2008 to 323,807 (95% CI = 300,389; 345,358) in 50 years as the proportion of viable wintering populations declined.

3.3. Population projections in the presence of WNS

According to the parameters of our WNS scenarios, >90% of wintering populations were expected to face the disease within 20 years, causing the proportion of quasi-extirpated wintering populations to increase from 71.9% to $\geqslant 96\%$ over 50 years irrespective of the scenario considered, an increase in quasi-extirpated populations of 33.5% (Fig. 3).

For the "acquired immunity" scenario, at the species' lowest median population level, ca. 2022, 13.7% of the initial population was expected to remain, totaling 28,958 females (95% CI = 13,330; 92,335) (Fig. 4). By 2022, only 12 hibernacula were expected to possess wintering populations exceeding 250 females (7 in the Midwest, 2 in the Ozark-Central, 1 in the Appalachians, and 2 in the Northeast Recovery Unit). Over the entirety of the 50-year simulation period, all wintering populations dropped below 2500 females (half of the Priority 1 classification criterion). After 50 years, 3.7% of wintering populations were expected to be above 250 female bats after a 69% decline in abundance (from 210,741 to 64,768 [95% CI = 49,386; 85,360] females).

Under a "persistent mortality" scenario positing a persistent influence of WNS through the projection interval, Indiana bats continued to decline after 2022 and reached their nadir by 2035, resulting in a remaining population of 43,000 bats; after that point in time, the underlying positive population dynamic in 3 of the 4 Recovery Units pre-WNS led to a 4% increase over the year 2035 population size (Fig. 3). The "persistent mortality" scenario led to 297,000 fewer bats at the end of the projection interval compared to the "acquired immunity" scenario (10,000 fewer bats in the
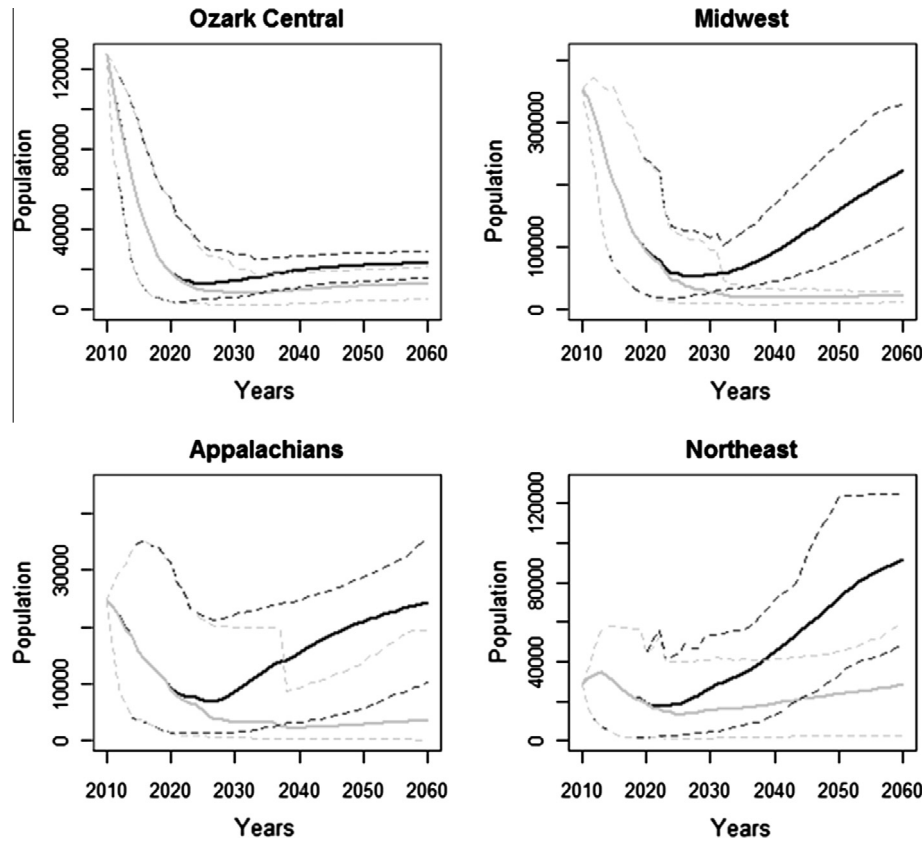
Fig. 3. Fifty-year population trajectories for Indiana bats disrupted by white-nose syndrome, in each of four Recovery Units. Two scenarios describing the effect of white-nose syndrome were assessed, "acquired immunity" (black) and "persistent influence" (gray). Dashed lines represent 95% confidence intervals.

Ozark-Central, 203,000 fewer in the Midwest, 21,000 fewer in the Appalachians, and 63,000 fewer in the Northeast).

We explored the sensitivity of the projections to assumptions about the magnitude and mechanism of WNS persistence. For these scenarios we defined quasi-extirpation as <25 bats because many wintering populations currently exist with fewer than 250 bats. We found an increasing risk of quasi-extirpation when mortality of ⩾10% beyond the background rate of survival persisted for all years beyond the initial 6 years of the scenario (Fig. A4). When populations were small because of WNS and posited to have an effect on subsequent winter survival (an Allee effect on survival), we found risk of quasi-extirpation was a function of the magnitude of the survival consequences of WNS. For instance, for survival of 95% and 85% that of the background survival rate, populations exhibited a maximum increased risk of ~8% and 18%, respectively. For survival rates 75% and 65% that of the background rate, risk of quasi-extirpation continued to increase with each passing year of the scenario (Fig. 5a). We also examined a persistent effect of WNS on breeding success and found few consequences to risk except when the wintering population was small; for populations starting at 500 bats and experiencing reduced breeding success from the background rate of 95%, 85%, 75%, and 65%, risk of quasi-extirpation was 6%, 8%, 10%, and 14%, respectively, by year 25. These rates of quasi-extirpation increased by less than 1% between year 10 and year 25 (Fig. 5b). For a starting population of 40,700 (a large Priority 1 hibernaculum) there was no risk of quasi-extirpation over a 25-year time span under any of the scenarios we examined.

4. Discussion

Novel pathogens are important drivers of population extirpation for naïve species (van Riper et al., 1986; de Castro and Bolker,
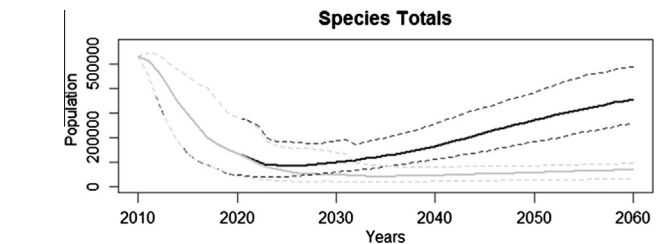

Fig. 4. Species-level consequences of two scenarios, "acquired immunity" (black) and "persistent influence" (gray), depicting the effect of white-nose syndrome on populations of Indiana bats. Dashed lines represent 95% confidence intervals.

2005; Lips et al., 2006; Smith et al., 2006; Skerratt et al., 2007), especially when species are predisposed by population status or life history characteristics (McCallum and Dobson, 1995; Cleaveland et al., 2002; Tompkins et al., 2002; de Castro and Bolker, 2005; Pedersen et al., 2007). Our modeling suggests the high-impact and fast-spreading nature of WNS will likely result in severe reduction in population size of the endangered Indiana bat; local and regional extirpation of wintering populations may be expected to lead to a contraction in range unless immigration from unaffected areas is sufficient to overcome local population declines (Grenfell and Harwood, 1997). Numerical losses in the face of this disease are expected to be >86%; the proportion of extant wintering populations were predicted to be no more than 4% after 50 years, with no wintering populations above 250 females expected in the Ozark-Central and Appalachian Recovery Units. Less than 5% of historical wintering populations were expected to persist above our quasi-extirpation level where the species is currently most abundant, the Midwest Recovery Unit.
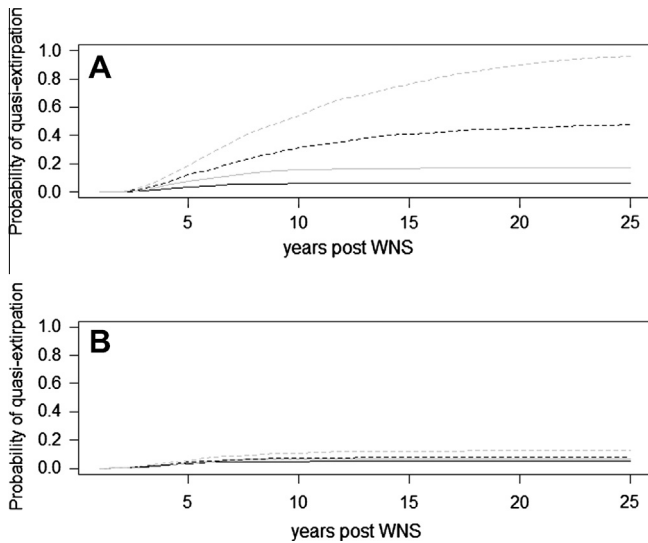
Fig. 5. Probability of quasi-extirpation risk (where quasi-extirpation = 25 female bats) for starting populations of 500 bats under scenarios where (a) adult winter survival was decreased from the background rate by 0.95 (solid black line), 0.85 (solid gray line), 0.75 (dotted black line), and 0.65 (dotted gray line) and (b) where adult breeding success was decreased from the background rate by 0.95 (solid black line), 0.85 (solid gray line), 0.75 (dotted black line), and 0.65 (dotted gray lines).

Because of the unusual nature of this disease, our near-term projections of Indiana bat demography come with a number of important limitations and sources of uncertainty. We are quickly accumulating evidence of the magnitude of loss resulting from this disease as it progresses through eastern North American populations of hibernating bats (Turner et al., 2011). Disease transmission, a key process in host-pathogen interactions (McCallum et al., 2001), is however only slowly being elucidated (Wilder et al., 2011; Langwig et al., 2012; Maher et al., 2012). Whereas most losses at hibernacula are believed to be a result of death, some number of infected individuals may be lost from the wintering population because of emigration, and in the process propagating this disease to new locations (Turner et al., 2011).

Possibly the most important unresolved uncertainty lies in the notion of whether Indiana bats can resume the population dynamic exhibited prior to the onset of the disease. Pre-WNS, the species exhibited stationary population dynamics across its range, but populations in 3 of the 4 Recovery Units (all but the Ozark-Central) were increasing in abundance (Thogmartin et al., 2012b). In our "acquired immunity" scenario, this increasing dynamic was responsible for recovery of abundance after its predicted nadir in 2022. Our "persistent influence" scenario largely forbade resumption of former dynamics except for the fastest growing populations, and as a consequence led to perpetually depressed abundance in each region except for the Northeast; in the Northeast, the expected persistence of WNS was less influential because of the underlying strongly growing dynamic (8% annual growth rate; Langwig et al., 2012). Our sensitivity analyses suggested that if WNS annually succeeded in killing 10% of the population, the species would not be able to persist despite the rates of growth we observed pre-WNS (Fig. A4). The extent to which the species can grow in abundance and fill depleted portions of its range after WNS passes through the population will dictate the fate of this endangered species. Research to determine whether *Myotis* species are developing a genetic resistance or behavioral tolerance to this disease is critical to determining which of these paths the species is on.

Poorly known is what happens to Indiana bats when their populations become small (Barbour and Davis, 1969; Gregory and

Jones, 2010; Wilder et al., 2011; Langwig et al., 2012). Indiana bats are an obligate colonial roosting species (Barbour and Davis, 1969; Thomson, 1982); dense clusters of individuals in winter hibernacula provide thermal protection and increased individual survival (Clawson et al., 1980; Boyles and Brack, 2009). We assumed a quasi-extirpation level of 250 females for most scenarios (by implication, a wintering population of 500 bats given an equal sex ratio) but whether 500 bats is a viable long-term population size for a wintering population is unclear (Gregory and Jones, 2010); our sensitivity analyses indicated increased risk of extirpation as population size declined and environmental stochasticity increased, coincident with a considerable body of empirical and theoretical study (e.g., Lande, 1993; Lafferty and Gerber, 2002; de Castro and Bolker, 2005).

The results of Langwig et al. (2012) suggested that WNS is altering patterns of sociality leaving hibernacula with a much greater proportion of single-roosting bats. At some threshold population size, possibly varying by hibernaculum, the protective advantage
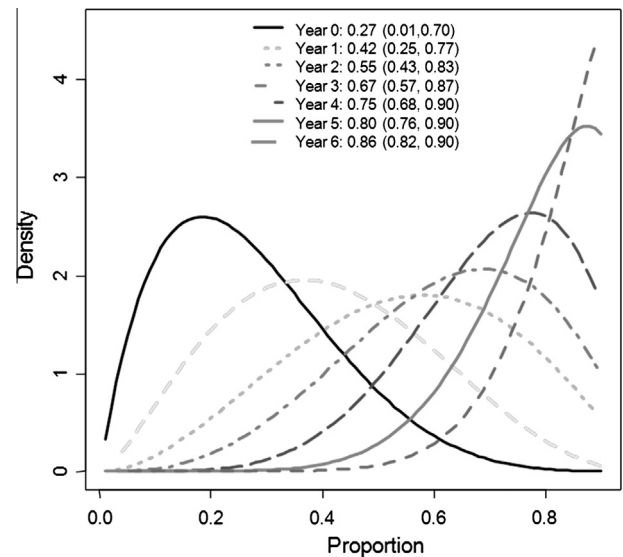

Fig. A1. Beta distributions describing proportion of surviving population of Indiana bats for each year since initial infection with white-nose syndrome. Annual values drawn from the distributions were centered on the mean and truncated to the interval described in the legend. This amelioration of mortality from white-nose syndrome follows from Frick et al. (2010a).
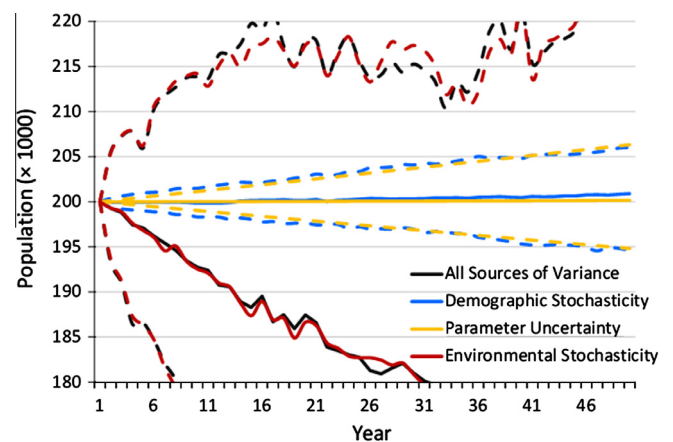

Fig. A2. Comparative influence of annual sources of variation imposed on projections of Indiana bat population size. Dashed lines represent 95% confidence intervals.

of clustering is likely to be lost. Thus, a population could be extant, but not viable over the long-term below some threshold. Further, our models suggest none of the most abundant populations were expected to stay above a threshold of 2500 females; the loss of these wintering populations in Priority 1 hibernacula is worrisome because these super-abundant populations likely act as critical nexuses for social interaction, including rescuing smaller neighboring overwintering sites (Gotelli, 1991; Hanski, 1999).

Connectedness of subpopulations is important in determining dynamics of species (Gotelli, 1991; Hanski, 1999), but from a disease perspective, the consequences of this population connectedness are mixed. Increased movement among disease-affected populations has been shown to both elevate (Hess, 1996) and depress (Gog et al., 2002; McCallum and Dobson, 2002) extinction risk. Recent theoretical findings suggested heightened risk is associated with the presence of alternative hosts (such as other, more abundant co-habiting species) and the extent of Allee effects (Lafferty and Gerber, 2002; Harding et al., 2012). To address the connectedness of populations in our modeling, we concentrated development of inferences at the hibernaculum-complex level and higher because dynamics at the level of the individual hibernaculum may be influenced by inter-hibernacula movements. Our development of hibernaculum complexes (clusters of interacting hibernacula) was a concession to this movement, but we do not believe this analytical shortcut makes our results immune to influence from immigration and emigration. There are potential mechanisms within the structure of our modeling process to allow for connectivity (e.g., Ozgul et al., 2009), namely by allowing growing populations to offset reductions in neighboring declining populations. To proceed in more than an ad hoc manner, however, requires robust information regarding the carrying capacity of hibernacula (and how the species responds to it) and the extent to which hibernacula are connected, information largely unknown at this time. As information on the geographic occurrence and environmental correlates of the fungus, *G. destructans*, become
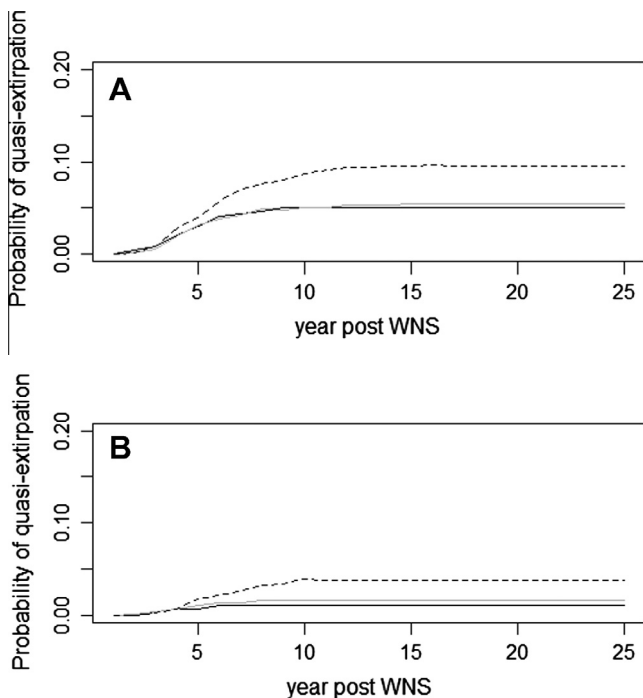

Fig. A4. Probability of quasi-extirpation risk (where quasi-extirpation = 25 female bats) under scenarios where adult winter survival was 30% (solid black line), 20% (solid gray line), and 10% (dotted gray line) of pre-white-nose syndrome conditions for years >7 post white-nose syndrome.

Table A1
Fourier amplitude sensitivity test indices computed for the 12-parameter stage-based matrix model predicting probability of quasi-extirpation for Indiana bats.

Model parameter	S^a	S_T	ΔS^b
Adult summer survival	0.057	0.499	0.441
Adult winter survival	0.027	0.320	0.293
Juvenile winter survival	0.017	0.302	0.285
Pup fall survival	0.016	0.263	0.247
Adult breeding success	0.008	0.157	0.149
Adult fall survival	0.008	0.119	0.111
Adult breeding propensity	0.004	0.092	0.088
Non-repro summer survival	0.004	0.061	0.057
Juvenile fall survival	0.003	0.115	0.112
Juvenile summer survival	0.001	0.057	0.056
Juvenile breeding success	0.000	0.037	0.037
Juvenile breeding propensity	0.000	0.008	0.008

[a] The first-order (S), or main effect, indices indicate impact of parameter i alone on population size whereas the overall impact of parameter i through its interactions with the other parameters is defined by total order (S_{Ti}).
[b] ΔS is the difference between the S and S_T indices, and indicates the importance of and proportion of variance attributed to parameter interactions.

Fig. A3. Probability of quasi-extirpation (where quasi-extirpation = 25 female bats) for simulated bat populations at environmental stochasticity rates of 4% (solid black line), 8% (solid gray line), and 12% (dotted black line) and (a) a starting population of 500 and (b) a starting population of 1000.
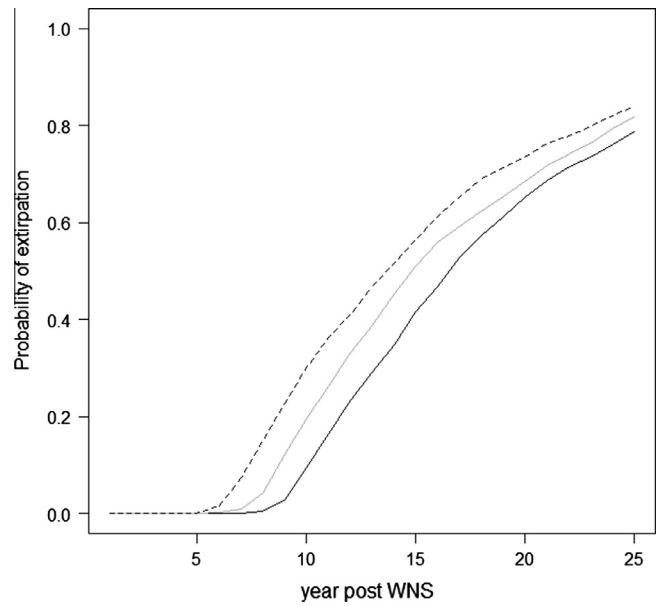
available (Flory et al., 2012; Hallam and Federico, 2012; Swezey and Garrity, 2012), spatially explicit modeling of host-pathogen relations may also be possible (e.g., Ferguson et al., 2001).

Another source of uncertainty is the inherent difficulty in estimating the current abundance and distribution of any bat species, including the Indiana bat (Thogmartin et al., 2012b). For example, the recent discovery of a large previously undocumented Indiana bat hibernaculum in Missouri (U.S. Fish and Wildlife Service, unpublished data) highlights this uncertainty. Unknown wintering populations of Indiana bats may continue to be found, but the ultimate projection of the disease is unlikely to be markedly changed. If the Indiana bat population is larger or more widely distributed than currently thought, this may slow the process of decline. However, the dynamics of the disease as we currently understand it suggest that eventually all populations of wintering Indiana bats (documented and undocumented) are likely to be subjected to the effect of WNS.

5. Conclusions

White-nose syndrome is disrupting the benign environment of the hibernaculum, leading to low winter survival rates. Therefore, it is no coincidence that WNS has the capability of causing population extirpation as it influences the most critical stage in the life cycle of Indiana bats, adult winter survival. Nevertheless, our predictions are that Indiana bats will persist for at least the next half-century, albeit at greatly reduced numbers (also see Dobony et al., 2011). Whether the species can recover from WNS is predicated upon whether populations can grow and fill in depleted portions of the range. Our sensitivity analyses indicated that management actions devoted to increasing, in order, winter, summer, and fall survival of breeding adult females would have the greatest potential for mitigating impacts of WNS on Indiana bat populations. Management actions for improving survival, however, may be difficult to achieve because these parameters are quite high (~95% seasonal survival) in the absence of WNS. Alternatively, increasing reproduction, while less efficient at addressing a declining population trajectory, has more room for improvement; further, if management actions on the breeding grounds to improve reproduction also improve adult female summer survival, our global sensitivity analyses suggest improved performance in the other parameters may occur as well. Because of the heightened risk faced by small, range-restricted populations (Terborgh and Winter, 1980; Gilpin and Soulé, 1986; Schoener and Spiller, 1987), it is also prudent in the face of this potential extinction agent to limit additive sources of mortality. Our model suggests a timeframe for action, for the species is expected to reach its lowest level of abundance by the early 2020s, no more than a decade hence.

Acknowledgements

Appendix A

See Figs. A1–A4 and Table A1.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.01.010.

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