Assessing local population vulnerability with branching process models: an application to wind energy development

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Abstract.   Quantifying the impact of anthropogenic development on local populations is important for conservation biology and wildlife management. However, these local populations are often subject to demographic stochasticity because of their small population size. Traditional modeling efforts such as population projection matrices do not consider this source of variation whereas individual-based models, which include demographic stochasticity, are computationally intense and lack analytical tractability. One compromise between approaches is branching process models because they accommodate demographic stochasticity and are easily calculated. These models are known within some sub-fields of probability and mathematical ecology but are not often applied in conservation biology and applied ecology. We applied branching process models to quantitatively compare and prioritize species locally vulnerable to the development of wind energy facilities. Specifically, we examined species vulnerability using branching process models for four representative species: A cave bat (a long-lived, low fecundity species), a tree bat (short-lived, moderate fecundity species), a grassland songbird (a short-lived, high fecundity species), and an eagle (a long-lived, slow maturation species). Wind turbine-induced mortality has been observed for all of these species types, raising conservation concerns. We simulated different mortality rates from wind farms while calculating local extinction probabilities. The longer-lived species types (e.g., cave bats and eagles) had much more pronounced transitions from low extinction risk to high extinction risk than short-lived species types (e.g., tree bats and grassland songbirds). High-offspring-producing species types had a much greater variability in baseline risk of extinction than the lower-offspring-producing species types. Long-lived species types may appear stable until a critical level of incidental mortality occurs. After this threshold, the risk of extirpation for a local population may rapidly increase with only minimal increases in wind mortality. Conservation biologists and wildlife managers may need to consider this mortality pattern when issuing take permits and developing monitoring protocols for wind facilities. We also describe how our branching process models may be generalized across a wider range of species for a larger assessment project and then describe how our methods may be applied to other stressors in addition to wind.

Key words: endangered species assessment; population assessment; wind turbine mortality.

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Introduction

Conservation biology and applied ecology often make decisions about stressors that adversely affect populations. These stressors may affect populations that range from local to global scale. Populations models are a tool to quantify these risks and different models are appropriate for different scales (Caswell 2001, Morris and Doak 2002, Gotelli 2008). Two of the most common approaches that are currently used include matrix models and individual-based models (IBMs). Matrix population models are commonly used to model population-level dynamics through the study of aggregate groups or stages of individuals (Cushing 1995, Caswell 2001). Simulation-heavy IBMs are increasingly used to study how individuals influence population-level dynamics by tracking and specifying the actions and interactions of specific organisms through time (Grimm et al. 1999, Grimm and Railsback 2005). Both modeling approaches have advantages and disadvantages. Population-level models such as population projection matrices have a long history of application, are relatively easy to construct, program and parameterize, and often have analytical solutions (Cushing 1995, Caswell 2001, Allen 2007). Theses models work best when used with large, homogeneous populations where individual variability tends to not be important. An example with wind energy development would be conducting a national- or regional-level assessment such as Diffendorfer et al. (2015). Conversely, IBMs focus on using rules to describe individuals and then examine the emergent properties of the system, including population-level dynamics (Grimm et al. 1999, Grimm and Railsback 2005). Developing IBMs require more programming than either branching processes models or matrix models. The resources needed to develop IBMs are not always be available to conduct assessments for many species. However, when examining the risk to a single ecologically or economically important species, an IBM may offer insight not found with other approaches.

Branching process models (Caswell 2001), on the other hand, use the analyticity of population-level models and the individuality of IBMs to approach the problem of assessing risk of population extinction with recursive formulas from probability theory. This recursive formula incorporates individual variability (Caswell 2001, Haccou et al. 2005, Allen 2011, Meli et al. 2013) and Caswell (2001) recommends that branching process models be used to complement matrix population models as means to include demographic stochasticity. Branching process models are well known in probability theory (Haccou et al. 2005) and some subdisciplines of mathematical biology, theoretical ecology, and epidemiology (Allen 2011), but are rarely used in applied ecology and conservation biology (Caswell 2001). Branching process models align well with the conservation needs of assessing the impacts of stressors on wildlife at a local scale. One such stressor is the development of wind energy facilities.

Alternative energy sources such as solar and wind hold the potential to decrease greenhouse gas emissions and other types of pollution when compared to energy produced from fossil fuels (Turner 1999). The United States (US) has placed a high priority on increasing electricity generation from wind turbines (Obama, State of the Union Address, 2013). The US capacity for wind power production was 61,108 megawatts at the end of 2013 (AWEA 2014), accounting for approximately 4% of all US electricity generation for 2013 (USEIA 2014).

Wind power production varies greatly across the US both temporally and spatially. For example, on 28 March 2014, the Electric Reliability Council of Texas (ERCOT) reported that 10,296 megawatts were produced at 8:48pm, accounting for 29% of the electricity on ERCOT's grid (http://www.ercot.com/news/press_releases/show/26611). Conversely, many areas of the US have little to no power generated from wind energy (Diffendorfer et al. 2014). Despite the benefits of decreased pollution, wind energy development may incur environmental costs such as wildlife mortality (Kunz et al. 2007a, Kuvlesky et al. 2007, Loss et al. 2013a).

Conservation planning efforts in locations where wind energy development has occurred or will occur requires an understanding and prioritizing of vulnerable species. Different species of wildlife appear to be more vulnerable to wind energy development and understanding this vulnerability is critical to successful conservation and management of wildlife (Kunz et al.
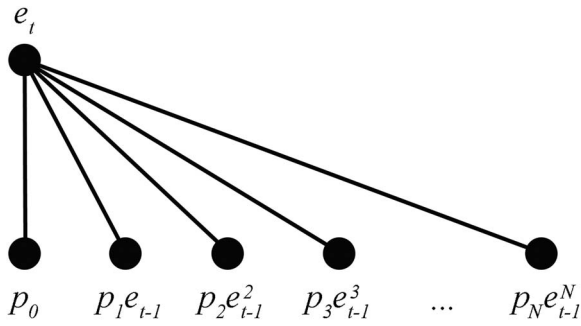
Fig. 1. A graphical illustration of the branching structure in the model (Eq. 2), where the probability of population extinction by time t is the sum of the probabilities of various reproductive outcomes, p_i, multiplied by the probability that every of the individuals reproduced elicits a population that goes extinct by time $t - 1$, e_{t-1}^i. For overlapping generations one can think of survival from one time-period to the next as an organism reproducing itself.

2007a, Arnett et al. 2010).

Species may be vulnerable because of both collision risk (e.g., some species suffer disproportionate mortality) and their life history (e.g., some species may be more vulnerable to increased mortality rates). Species producing many offspring and having short lifespans should be less vulnerable than species producing few offspring and having long lifespans. This risk needs to be understood for hundreds of species of both birds and bats across the United States.

Wind energy development may have a localized effect on wildlife populations. These small populations are subject to demographic stochasticity, a central attribute modeled by branching process models (Caswell 2001, Allen 2011). The size of local populations affected by wind energy can range from just a few individuals for organisms with a large home range such as eagles to hundreds or possibly even a thousand individuals for colonial species such as bats or birds. Based upon these considerations, we used branching process to model four generic life history strategies to examine extinction probabilities caused by vulnerabilities to wind energy development. These four species types included (1) a cave bat (e.g., *Myotis* spp.), (2) a tree bat (e.g., *Lasiurus* spp.), (3) a grassland song bird (e.g., *Passeriformes*), and (4) an eagle (e.g.,

Accipitridae). We also compared branching process models to population projection matrices to facilitate a comparison between the two methods.

MATERIALS AND METHODS

Branching process models

Branching process models are individual-based models for the growth or decline of populations (Haccou et al. 2005) that, instead of using simulations to track populations in time, use a generating function f. This function is similar to those used in population-level models, and hence the overlap and relationship between the two modeling approaches.

In the simplest case of a population with one stage, we denote with X_t the size of the population at time t. Unlike many population-level models, X_t is only allowed to take on integer values. We are initially concerned with the probability of population extinction by time t, given the population initially starts with one individual. Mathematically, this is denoted as

$$e_t = P(X_t = 0 | X_0 = 1). \tag{1}$$

If the probabilities of life events (e.g., survival, growth and reproduction) for an individual are independent, e_t is given recursively by

$$e_t = p_0 + p_1 e_{t-1} + p_2 e_{t-1}^2 + p_3 e_{t-1}^3 + \ldots = f(e_{t-1}) \tag{2}$$

where e_{t-1} is the probability of extinction in $t - 1$ time-steps, and p_i is the probability of an individual producing i individuals (including possibly itself) during a given time period (Fig. 1). For example, if survival happens before reproduction and individuals produce one offspring with probability p and zero with probability $1 - p$, then $p_0 = 1 - s$ (the individual dies), $p_1 = s(1 - p)$ (the individual survives but does not reproduce) and $p_2 = sp$ (the individual survives and reproduces). The term $p_i e_{t-1}^i$ can be thought of as the probability of going from one individual to i individuals in one time-step, only to have the populations elicited by each of the offspring all go extinct in $t - 1$ subsequent time steps. Summing up all of these possibilities yields the probability of extinction in t time-steps or fewer (see Fig. 1).

The function f is often called the probability

generating function for the probability distribution p_0, p_1, p_2, ..., which all sum to 1. Since $e_0 = 0$ (the population is not extinct initially), one can compute e_t simply by iterating (2) forward in time, using $e_1 = f(0)$, $e_2 = f(e_1) = f(f(0))$, etc., to see that

$$e_t = f^t(0) \qquad (3)$$

where $f^t(\cdot)$ is the function f composed with itself t times (Caswell 2001, Haccou et al. 2005, Bacaër and Dads 2014). Since $0 \le e_1 \le e_2 \le \ldots \le 1$, we know that e_t has a limit e^*, which is the asymptotic probability of population extinction, starting with one member. This limit can be found by solving the fixed point equation

$$e^* = f(e^*). \qquad (4)$$

It follows that $e^* = 1$ (the population is sure to go extinct in the long run) if $\lambda = f'(1) \le 1$ (where λ is the expected population growth rate), while $e^* < 1$ (there is a positive probability that the population with persist) if $\lambda = f'(1) > 1$, where $f'(\cdot)$ is the first derivative of the function f. It is not difficult to show that

$$\lambda = p_1 + 2p_2 + 3p_3 + ..., \qquad (5)$$

which is the expected growth rate of the population.

For species types with n discrete stages the process of creating the probability generating function for the (multitype) branching process is analogous to the process above, with an increase in dimension and complexity due to the fact that individuals can change stages and create new individuals throughout the range of stages. In this multi-stage case extinction probability is modeled with an n-dimensional vector $\vec{e}$, where the ith element of $\vec{e}$ is the probability of the entire population going extinct by time-step t given that it started with 1 individual in stage i. The probability generating function f in this case is a non-linear vector-valued function, which can be best summarized using matrix notation. The order and structure of the matrices for a given model will depend on what one assumes for the order of the various life history events. If one assumes, as we do in this paper, that the order of life history events is survival, followed by growth, followed by reproduction and recruit-

ment into the newborn stage, then one can see that $\vec{e}$ is given recursively by

$$\vec{e}_t = (I - S)\mathbf{1} + (STE_{t-1}^d PE_{t-1}^r J), \qquad (6)$$

where $\mathbf{1}$ is a vector of n ones, I is the $n \times n$ identity matrix

$$I = \begin{pmatrix} 1 & 0 & \ldots & 0 \\ 0 & 1 & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & 1 \end{pmatrix}.$$

S is the $n \times n$ survival matrix

$$S = \begin{pmatrix} s_1 & 0 & \ldots & 0 \\ 0 & s_2 & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & s_n \end{pmatrix},$$

where s_i is the probability of survival by an individual of stage i in a given time-step, T is the $n \times n$ transition matrix

$$T = \begin{pmatrix} t_{11} & t_{12} & \ldots & t_{1n} \\ t_{21} & t_{22} & \ldots & t_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ t_{n1} & t_{n2} & \ldots & t_{nn} \end{pmatrix},$$

where t_{ij} is the probability of transitioning from stage i to stage j (conditioned on survival) in a given time-step, E_{t-1}^d is the $n \times n$ time-varying matrix

$$E_{t-1}^d = \begin{pmatrix} e_{1;t-1} & 0 & \ldots & 0 \\ 0 & e_{2;t-1} & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & e_{n;t-1} \end{pmatrix}$$

denoting the distribution of individuals after they stage transition, P is the $n \times N$ reproduction matrix

$$P = \begin{pmatrix} p_{11} & p_{12} & \ldots & p_{1N} \\ p_{21} & p_{22} & \ldots & p_{2N} \\ \vdots & \vdots & \ddots & \vdots \\ p_{n1} & p_{n2} & \ldots & p_{nN} \end{pmatrix}$$

where $p_{i,j}$ is the probability of an individual in stage i producing j newborns (conditioned on survival) in a given time-step (where N can be theoretically unbounded), E_{t-1} the $N \times n$ time-varying matrix

$$E^r_{t-1} = \begin{pmatrix} 1 & 1 & \cdots & 1 \\ e_{1;t-1} & e_{2;t-1} & \cdots & e_{n;t-1} \\ e^2_{1;t-1} & e^2_{2;t-1} & \cdots & e^2_{n;t-1} \\ \vdots & \vdots & \ddots & \vdots \\ e^N_{1;t-1} & e^N_{2;t-1} & \cdots & e^N_{n;t-1} \end{pmatrix},$$

tracking the extinction probability of populations elicited by the various possible reproductive events, and J the juvenile distribution vector

$$J = [j_1 \cdot j_2 \cdots j_n]^T, \tag{7}$$

where j_i is the probability that a newborn ends up in stage i during their first time-step (the superscript T denotes matrix/vector transposition).

For a two-stage model where all newborns are placed in the first stage, and individuals can grow from the first stage to the second with probability g and one can have at most one newborn each time-step (but both stages can reproduce), the model (6) can be written as

$$\begin{aligned} e_{1,t} = 1 - s_1 \\ + s_2((1-g)e_{1,t-1}(p_{10} + p_{11}e_{1,t-1}) \\ + ge_{2,t-1}(p_{20} + p_{21}e_{1,t-1})) \end{aligned} \tag{8}$$

$$e_{2,t} = 1 - s_2 + s_2 e_{2,t-1}(p_{20} + p_{21}e_{1,t-1}),$$

where

$$S = \begin{pmatrix} s_1 & 0 \\ 0 & s_2 \end{pmatrix}$$

$$T = \begin{pmatrix} 1-g & g \\ 0 & 1 \end{pmatrix}$$

$$E^d_{t-1} = \begin{pmatrix} e_{1;t-1} & 0 \\ 0 & e_{2;t-1} \end{pmatrix}$$

$$P = \begin{pmatrix} p_{10} & p_{11} \\ p_{20} & p_{21} \end{pmatrix}$$

$$E^r_{t-1} = \begin{pmatrix} 1 & 1 \\ e_{1;t-1} & e_{2;t-1} \end{pmatrix}$$

and $J = [1\ 0]^T$.

To find the expected growth rate of the population modeled by (6) one takes the transpose of the Jacobian (n-dimensional derivative) matrix for f evaluated at the vector 1 of ones and then finds the leading eigenvalue. Provided that the population model is primitive (there is a positive probability that each stage can contribute to each stage in a finite number of time-steps) this leading eigenvalue is the growth rate λ of the population (Caswell 2001, Allen 2011). Additionally, the matrix for which we take the leading eigenvalue ends up being what one would use for the projection matrices of the population if we ignored stochasticity. As with the one-dimensional model, if $\lambda \leq 1$ the entire population is predicted to go extinct with probability 1, regardless of initial population distribution, and if $\lambda > 1$ there exists a vector $\vec{e}^*$ that is a fixed point for the model (6), where the ith element of $\vec{e}^*$ is the long-term probability of population extinction given the population started with one individual in stage i.

In this paper we are concerned with the probability of population extinction starting from various initial populations sizes, not just initial populations with one individual. We investigated extinction probabilities across a range of initial population sizes based upon targets for population management. These sizes are described in the next section. If we assume that individuals and their offspring are independent, then we can find the probability of total population extinction by time t, ε_t, starting with an initial population distribution $X_0 = [x_{1,0}, x_{2,0}, \ldots, x_{n,0}]^T$ by using

$$\varepsilon_t = e_{1,t}{}^{x_{1,0}} e_{2,t}{}^{x_{2,0}} e_{n,t}{}^{x_{n,0}}. \tag{9}$$

Representative species types

To investigate how the effects of wind turbine mortality might impact species with different life histories, we studied 4 species types: A short-lived, high fecundity species (grassland song bird); a long-lived, slow maturation species (eagle); a long-lived, low fecundity species (cave bat); and a short-lived, moderate fecundity species (tree bat). We only modeled females from each species because males are less important from a population-level perspective (Caswell 2001). Additional details about these species are provided in the following paragraphs and Fig. 2.

We compared different aspects of the branching process model in addition to life history strategy. We explored the importance of population size on the risk of local extinction from demographic stochasticity by comparing different population sizes. We examined population
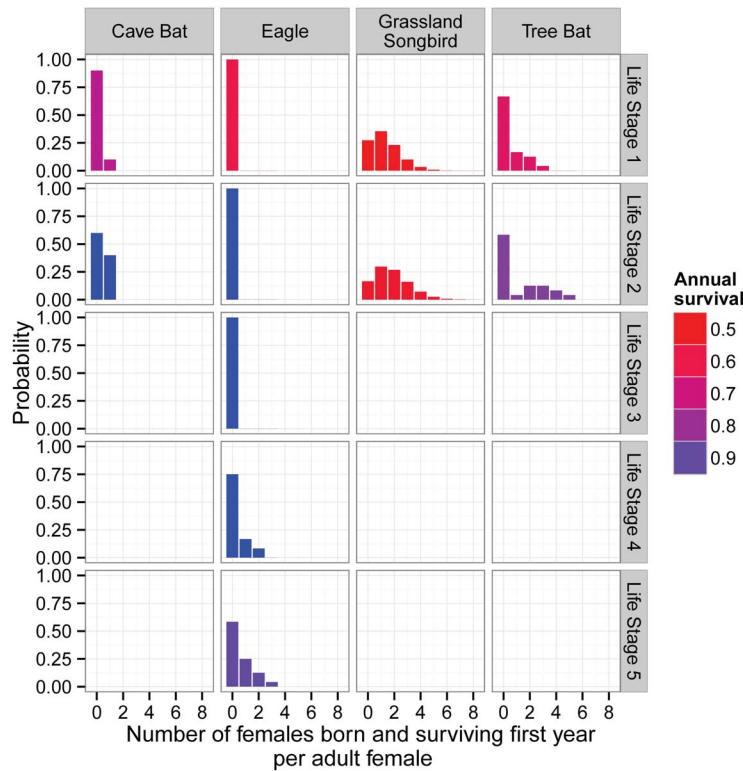
Fig. 2. Branching process model inputs. Each column is a different species and each row is a different life stage.

sizes of 30 individuals because it is often viewed as a minimum viable population size for short-term survival (Morris and Doak 2002), 100 individuals because it would be the population size found in many different colonial species of summer maternity roosts for bats, and 1,000 individuals because some colonial species such as cave bats may live in groups this large (Kunz and Fenton 2006). We used the stable-stage distribution for each species as our initial population condition. The stable-stage distribution was calculated using the popbio Package for R (Stubben and Milligan 2007, R Core Team 2013).

We examined the risk of extinction at 10 years, 30 years, and 100 years based upon current policy and management. Ten years was chosen because many field ecology studies are only conducted for short time periods (Pickett 1989). Thirty years was chosen because the USFWS may issue take permits for a 30-year period as is currently being done for the Golden Eagle (USFWS 2013) and Indiana bat (Erickson et al.

2014). "Take" is defined to include "harass, harm, pursue, hunt, shoot, wound, kill trap, capture, or collect, or to attempt to engage in any such conduct" under the Endangered Species Act of 1973. When issuing permits for incidental take from wind energy, the USFWS focuses on mortality and we focused on lethal take within this manuscript. Additionally, both 10 and 30 years are part of the extinction risk criteria used by the International Union for Conservation of Nature (http://www.iucnredlist.org/). One hundred years was chosen to examine the dynamics over a longer time period and allow the solution to reach convergence.

For all species types, we assumed no density effects (e.g., density dependency or Allee effects), independence between individuals, and a positive growth rate. These assumptions would be suited to a small, source population that is growing. While not realistic assumptions, the assumptions allows us to compare which species types (life history strategy) may be more vulnerable relative to other species. We were also

interested in examining relative vulnerability, not absolute risk. Fewer model inputs also allow the model to be used with many different species if this framework were to be applied for a wide variety of locations and species. We assumed mortality affects all life stages other than the first-year life stage.

The distribution of female offspring produced and surviving one year was selected based upon values found in the literature. Survival rates were adjusted to give growth rates λ commensurate with an increasing population (λ = 1.09). These rates of increase would be high for a wild population, but recovering species such as the Bald Eagle (USFWS; http://www.fws.gov/Midwest/eagle/population/chtofprs.html) and Whooping Crane (Allen 2007) have demonstrated exponential growth. These λ values were calculated using the leading eigenvalue of the population projection matrix for each species type. We also calculated generation time using the popbio Package for R (Stubben and Milligan 2007, R Core Team 2013).

Cave bats.—We modeled our long-lived, low fecundity species type after cave bats. Cave bats are found throughout the United States and we chose to focus on *Myotis* spp. found in the eastern United States (i.e., those east of the 100th Meridian). Example *Myotis* bats include the Indiana Bat (*M. sodalis*) and Little Brown Bat (*M. lucifugus*). The Indiana Bat was in the first group listed under the Endangered Species Act of 1973 (32 FR4001, March 11, 1967) whereas the Little Brown Bat was the most common bat in the eastern United States until the arrival of White-nose Syndrome (Froschauer et al. 2011). *Myotis* bats produce only one pup per year. Cave bats reproduce during their first-year, but younger individuals are less likely to produce a pup and are less likely to survive (Thogmartin et al. 2013, Erickson et al. 2014). Assuming an even sex distribution, this implies a maximum production of 0.5 female pups per year. Based upon these considerations, we used a two-stage population model with an annual survival rate of 0.747 for first-year cave bats and 0.855 for adults. The first year breeders produced 0.16 female bats per year that survived until the next year and the adults produced 0.36 (Thogmartin et al. 2013). This has a generation time of 6.71 years.

Tree bats.—We based our short-lived, moderate fecundity species on tree bats, primarily the Hoary Bat (*Lasiurus cinereus*). This species is found throughout North and South America. The Hawaiian subspecies was one of the first species listed under the Endangered Species Act of 1973 (35 FR16047, October 13, 1970), but elsewhere the species is common and has an ICUN Conservation Status of least concern (http://www.iucnredlist.org/details/11345/0). This species is the most commonly killed bat species at wind turbines in United States although uncertainty exists as to why (Cryan and Barclay 2009, Cryan et al. 2014). This mortality may occur because the species is highly abundant or may occur because the species is attracted to wind turbines owing to its mating strategy (Cryan and Barclay 2009). First-year tree bats had an annual survival of 0.25 and adults had an annual survival of 0.65. The distribution of births were assumed to come from a binomial distribution with a maximum of 6 surviving female offspring and an average of 0.75 females produced per first year reproducing female and 1.25 per adult (Koehler and Barclay 2000, Kunz and Fenton 2006, Hallam and Federico 2009, Altringham 2011). This matrix has a generation time of 4.09 years.

Grassland songbird.—We modeled a short-lived, high-fecundity species after the Horned Lark (*Eremorphila alpestris*). The Horned Lark is an abundant and wide-ranging species of barren land, scrubby grasslands, and shrublands (Beason 1995). It is also one of the most common species discovered during bird mortality surveys at wind turbines (Loss et al. 2013a). Although still relatively common and abundant, sharp declines have been noted over most of this species' North American range (Sauer et al. 2013). Additionally, the Streaked Horned Lark, a subspecies endemic to Oregon, USA, was listed as a threatened species in 2013 (78 FR61505, October 3, 2013) Horned Lark reproduce annually typically beginning the first year after hatching (Beason 1995). From a study of a stable population of a subspecies of Horned Lark, survival was estimated at 0.20 the first year and 0.65 thereafter and the number of female offspring per female successfully fledging per year was 1.75 (Camfield et al. 2010). To simulate an increasing population (λ = 1.09), we increased the first year survival rate to 0.22 and estimated the average annual number of female offspring as 2.0. This produces a matrix

Table 1. Parameter distributions used branching processes model.

Parameter	Symbol	Distribution	Representative species type
Survival	s	beta	all
Offspring produced	p	binomial	cave bat, tree bat, and eagle
Mean offspring produced	NA	beta	cave bat, tree bat, and eagle
Offspring produced	p	poisson	grassland songbird
Mean offspring produced	NA	normal	grassland songbird

with a generation time of 4.38 years, which is similar to reported generation times for this species (BirdLife International 2014*b*).

Eagle.—We modeled a low fecundity, long-lived species after the golden eagle (*Aquila chrysaetos*) and the bald eagle (*Haliaeetus leucocephalus*). The Bald and Golden Eagle Protection Act of 1940 (16 U.S.C. 668-668d) prevents the incidental take of eagles without permitting. Eagle mortalities have been documented at wind energy facilities (Smallwood and Thelander 2008, Loss et al. 2013*a*). In 2014 the United States Fish and Wildlife Service revised the regulations for the take of eagles to allow permits for up to 30 years (78 FR73704, April 13, 2013). Neither species is considered to be at immediate risk of extinction (BirdLife International 2014*a*), however wind turbines have the potential to impact local populations where the probability of collisions are unusually high (Smallwood and Thelander 2008). Both species are wide ranging across North America and have similar life-history characteristics. Bald and Golden Eagles do not reproduce until at least age 4 and in dense populations, reproduction may not occur until age 6 or 7 (Buehler 2000, Kochert et al. 2002). Both species have estimated generation lengths of approximately 17 years (BirdLife International 2014*a*). Probabilities of survival from fledging to adulthood in bald eagles has been measured to vary from 0.3 to 0.6 (Buehler 2000), with similar numbers reported for golden eagles (Harmata 2002). For both species, breeding pairs normally attempt one clutch per year of 1–3 eggs (Buehler 2000, Kochert et al. 2002). For this analysis, we constructed an eagle model with the following mean survival parameters for each age stage: 0.68, 0.7, 0.8, 0.9, 0.955. Assuming that a lower proportion of 4-year-old eagles attempt breeding and are likely less successful than older birds, we set the mean number of female offspring produced per female at 0.135. We set the mean fecundity for eagles 5 years or greater at 0.525 female offspring/female.

Numerical methods and uncertainty quantification

All simulations were conducted using R (R Core Team 2013) and our source code is included as a Supplement. We examined the risk of extinction by decreasing the probability of survival by a value μ, μ∈[0, 1]. For example, the probability of survival for stage 2 would become $s_2(1 - \mu)$. We first examined the effect of population size on the cave bat species and compared the results to a population projection matrix. We compared the 4 different life history types using simulations of 30, 100, and 1,000 individuals. We used the stable age distribution used for the initial population distribution. We calculated the probability of extinction after 10, 30, and 100 years. Note that extinction probability was a state variable within our model rather than an emergent property (Eq. 1). Parameter uncertainty was incorporated into the model by replacing parameters with distributions (Table 1). Survival parameters were drawn from a beta distribution. The probability parameter in the binomial distribution (used to model births for the cave bat, tree bat, and eagle) was drawn from a beta distribution (i.e., statistically the beta distribution was a hyperparameter for the binomial distribution or mathematically the beta distribution was mapped to the binomial distribution). A normal distribution was used for the hyperparameter for Poisson birth distribution (used to model the grassland songbird births). The normal distribution had sufficiently small standard deviation so that all draws were positive. Parameters for the beta distributions were scaled by a factor of a 1,000 times the mean (e.g., if the survival probability was 0.6, the beta distribution would be $B(\alpha=600, \beta=400)$). We ran 5,000 simulations to quantify uncertainty.
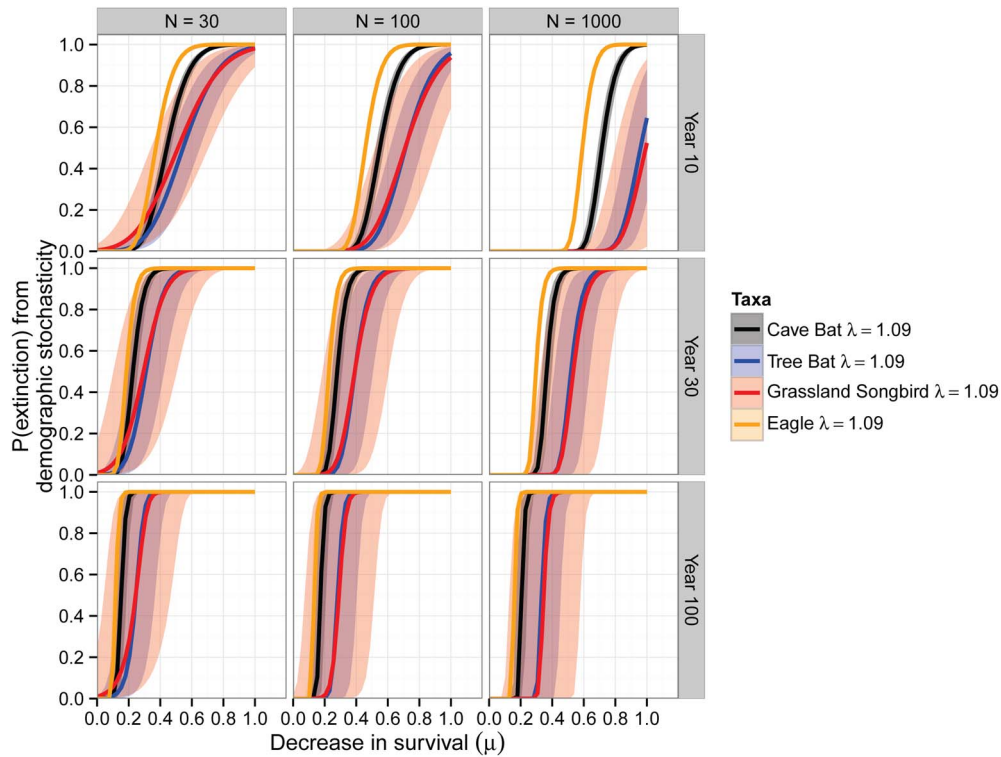
Fig. 3. Probability of extinction from demographic stochasticity (y-axis) for different populations sizes (columns) at different times (rows) under different levels of take (x-axis) for different representative species (line and shaded region colors). The branching process model considers females only and assumes each individual is independent. The eagle population included uncertainty, but was not great enough to appear on the figure.

RESULTS

The risk of extinction relative to declines in survival followed a general sigmoid curve for all life history traits (Fig. 3). All four representative species had overlapping vulnerabilities. In general, the eagle and cave bats, with the longest generation times, were the most vulnerable species. These two species types also had the least amount of uncertainty with their curves and their distribution is barely visible in Fig. 3. The tree bats and grasslands songbird both had similar and often overlapping curves though these differed with regard to their variability and uncertainty. The grassland songbird had a wider distribution that covered a ≈30% points decrease in survival whereas the widest tree bat distribution only spanned ≈20% points.

Both initial population size and magnitude of loss from wind at a given time changed the extinction curves (Fig. 3). Regardless of life

history, populations became more extinction prone (i.e., the curve's inflection point shifted left) as initial population sizes became smaller and time increased. The transition between low probability of extinction and high probability of extinction (i.e., the steepness or slope of the curve) increased as both population size and time increased. Both the changes in slope and inflection point occurred across all species types, although the changes in the slope and inflection points were more pronounced for the grassland songbirds and tree bats than the cave bats and the eagles. Another trend emerged from the model where increasing population size decreased the risk of extinction from demographic stochasticity. Overall, these model behaviors agree with our expectation for the system.

The probability of extinction decreased as population size increased until the branching process model converged to the matrix model (Fig. 4). The branching process model also
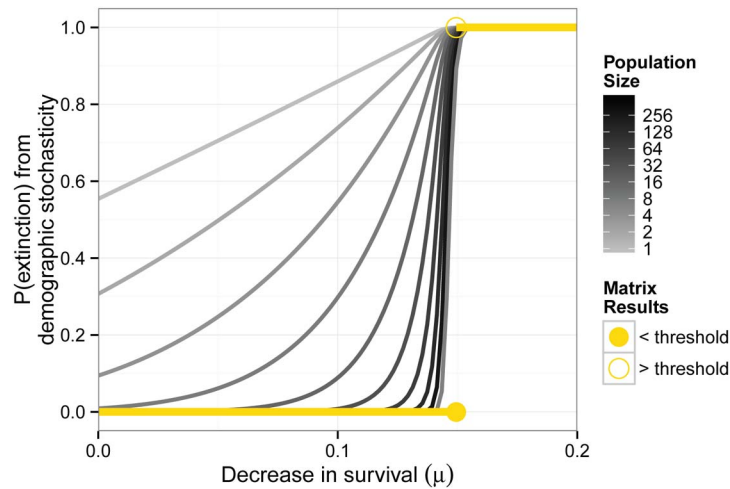
Fig. 4. Probability of extinction from demographic stochasticity for a cave bat population with different population sizes and different levels of take. The model only considers females and is a two-stage branching process model. The branching process model and matrix model results are the equilibrium results. We ran population sizes up to 1,000 individuals but truncated the results because the solution converges as the population size increases.

produced a probability of extinction whereas the matrix model produced a binary threshold for extinction, which was expected given underlying assumptions and construction of both models. This convergence occurred around 200–300 individuals and is in agreement with previous research on demographic stochasticity (Melbourne and Hastings 2008). The branching process model indicated a risk of extinction at lower mortality levels than the matrix model, with small populations (16) having a non-trivial risk of extinction even without a decrease in survivorship. This difference became less important for larger populations and would be less important ecologically given uncertainty in parameter estimates.

DISCUSSION

We found that representative species differed not only in their vulnerability to wind energy, but also varied with respect to the amount of variability and uncertainty associated with the vulnerability. The eagles and cave bats were more vulnerable than tree bats and grassland songbirds over shorter time periods, but some overlap in vulnerabilities occurred by year 100. However, the variability of vulnerability was greatest for the grassland songbird. This was due to the wide range of possible offspring production. This range of variability may result in local extinctions due to chance alone, even without wind energy development. In reality, this risk would likely be mitigated by metapopulation dynamics or diffusion and dispersion processes played out over a larger landscape. Conversely, the eagle had almost no variability in its vulnerability because of its delay between birth and reproduction.

The sharp rate at which extinction was predicted for both the eagle and tree bat raises concerns. A population may appear to be healthy until mortality increases slightly beyond a critical threshold, shifting the trajectory toward a sudden decline. This represents the possibility for a critical transition (Scheffer 2009) after which a local population may either be extirpated or become a sink. Either of these outcomes may impact regional or range-wide dynamics for the species (Runge et al. 2006). For local populations, a critical transition may be masked by demographic stochasticity and variability within the system.

Our findings inform wind energy monitoring. Currently, many different approaches are being used to monitor mortality at wind energy

facilities, although standardized methods have been developed (Kunz et al. 2007a, b, Kuvlesky et al. 2007, Huso 2013, Loss et al. 2013a). Increases in mortality rates caused by wind energy development may be difficult to detect due to natural variability and stochasticity. This "noise" may obscure wind energy mortality because the trend would be lost within the background variability. To statistically observe the mortality trends through this background noise, more sampling effort (e.g., more sampling sites, sampling time) would be required to robustly detect the impact of wind energy development. Future research incorporating branching processes could help to optimize sampling design.

Wind energy development is one of many factors causing avian and bat fatality (Loss et al. 2013a). All development is potentially threatening to wildlife (Sovacool 2009, Loss et al. 2012). Other major mortality sources, at least for birds, include free-ranging domestic cats (Coleman and Temple 1993, Loss et al. 2013b), vehicle traffic (Loss et al. 2014b), power lines (Loss et al. 2014c), and buildings (Klem Jr et al. 2004, Loss et al. 2014a). Bats face additional threats including white-nose syndrome (Frick et al. 2010, Thogmartin et al. 2012), and hibernaculum vandalism (Crimmins et al. 2014). Both avian and chiropteran taxa also face broad threats from climate change, habitat loss, and land use changes. Branching process models may provide insight into the impact these stressors may cause on local populations. However, these assessments would need to focus on different parameter estimates. For example, cats might decrease first-year songbird survival more if they prey on nests and fledglings whereas turbine collisions would be more likely to affect older individuals that migrate.

We used branching process models to examine potential vulnerability for abstract, generic species types. Branching process models could also be applied to actual site assessments for particular species of interest. Annual survivorship rates, calculated with mark-recapture methods for instance (Krebs 1999, Kéry and Schaub 2012), and local population sizes could be used with our approach to inform site-specific risk. Alternatively, multiple datasets could be used to parameterize the model (Kéry and Schaub 2012) in an integrated-modeling approach (Abadi et al. 2010).

Despite, or possibly in light of, these theoretical underpinnings, known limitations of branching process models exist. Our model assumed independence for each individual. Similarly, we did not consider the effects of density dependence. Addressing this assumption as part of the branching process model would also address the assumption of individual independence. This approach would require incorporating a density term similar to how one might incorporate density in a population projection matrix model by including a density function such as Ricker function or logistic growth function. Incorporating density dependence would also require individual cohorts be tracked through time, something our current formulation does not do. Our approach was also limited because we do not usually know mortality rates from a wind energy facility, only observed counts. For example, we often know how many birds or bats carcasses were found at a turbine but do not know what fraction this would be of the total population, nor how many individuals were killed but not observed because they were outside of the search radius, obscured by ground vegetation, or removed by scavengers. We also ignored the spatial structure of our system. Even with these limitations, branching process models may be useful for high-level screenings when other, more parameter-intense methods may not be feasible due to limited resources or other considerations.

Branching process models have a well developed theoretical underpinning both in the probability literature and biological literature but have yet to be applied to conservation settings (Karlson and Taylor 1992, Haccou and Iwasa 1996, Caswell 2001, Allen 2011). We have demonstrated how branching process models may be applied to wind energy risk assessment. Branching process models may also be used for other types of assessments ranging from ecotoxicology to population vulnerability analysis (Caswell 2001, Morris and Doak 2002, Forbes et al. 2008). Branching processes models would be well suited for laboratory ecotoxicology studies because of the independence of the individuals and a desire to estimate a risk of extinction. Population vulnerability and viability analysis would benefit from branching processes models

as well if demographic stochasticity is important but the processes of an IBM are not required.

Literature Cited

32 FR4001. March 11. 1967. Notices. Federal Register 32:48:4001.

35 FR16047. October 13. 1970. Notices. Federal Register 35:199:16047.

78 FR61505. October 3. 2013. Rules and Regulations. Federal Register 78:192:61505–61589.

78 FR73704. April 13. 2013. Rules and Regulations. Federal Register 78:236:73704–73725.

Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology 91:7–14.

Allen, L. 2007. An introduction to mathematical biology. Pearson/Prentice Hall, Upper Saddle River, New Jersey, USA.

Allen, L. 2011. An introduction to stochastic processes with applications to biology. Second edition. CRC Press, Boca Raton, Florida, USA.

Altringham, J. D. 2011. Bats: from evolution to conservation. Oxford University Press, Oxford, UK.

American Wind Energy Association. 2014. AWEA U.S. Wind industry fourth quarter 2013 market report. Technical report. American Wind Energy Association, Washington, D.C., USA.

Arnett, E. B., M. M. Huso, M. R. Schirmacher, and J. P. Hayes. 2010. Altering turbine speed reduces bat mortality at wind-energy facilities. Frontiers in Ecology and the Environment 9:209–214.

Bacaër, N., and E. Dads. 2014. On the probability of extinction in a periodic environment. Journal of Mathematical Biology 68:533–548.

Beason, R. C. 1995. Horned Lark (*Eremophila alpestris*). *In* The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/195

BirdLife International. 2014*a*. IUCN Red List for birds. Technical report. BirdLife International, Cambridge, UK.

BirdLife International. 2014*b*. Species factsheet: *Eremophila alpestirs*. Technical report. BirdLife International, Cambridge, UK.

Buehler, D. A. 2000. Bald Eagle (*Haliaeetus leucocephalus*). *In* The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/506

Camfield, A. F., S. F. Pearson, and K. Martin. 2010. Life history variation between high and low elevation subspecies of horned larks Eremophila spp. Journal of Avian Biology 41:273–281.

Caswell, H. 2001. Matrix populations models. Sinauer, Sunderland, Massachusetts, USA.

Coleman, J. S., and S. A. Temple. 1993. Rural residents' free-ranging domestic cats: a survey. Wildlife Society Bulletin 21:381–390.

Crimmins, S. M., P. C. McKann, J. A. Szymanski, and W. E. Thogmartin. 2014. Effects of cave gating on population trends at individual hibernacula of the Indiana bat (*Myotis sodalis*). Acta Chiropterologica 16:129–137.

Cryan, P. M., and R. M. Barclay. 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. Journal of Mammalogy 90:1330–1340.

Cryan, P. M., et al. 2014. Behavior of bats at wind turbines. Proceedings of the National Academy of Sciences USA 111:15126–15131.

Cushing, J. 1995. Systems of difference equations and structured population dynamics. Pages 123–132 *in* Proceedings of the First International Conference on Difference Equations. Gordon and Breach, London, UK.

Diffendorfer, J. E., J. A. Beston, M. D. Merrill, J. C. Stanton, M. D. Corum, S. R. Loss, W. E. Thogmartin, D. H. Johnson, R. A. Erickson, and K. W. Heist. 2015. Preliminary methodology to assess the national and regional impact of U.S. wind energy development on birds and bats: U.S. Geological Survey Scientific Investigations Report 2015-506. http://dx.doi.org/10.3133/sir20155066

Diffendorfer, J., R. Compton, L. Kramer, Z. Ancona, and D. Norton. 2014. Onshore industrial wind turbine locations for the United States through July, 2013: data series 817. Technical report. United States Geological Survey, Denver, Colorado, USA. http://dx.doi.org/10.3133/ds817

Erickson, R. A., W. E. Thogmartin, and J. A. Szymanski. 2014. BatTool: an R package with GUI for assessing the effect of White-nose syndrome and other take events on Myotis spp. of bats. Source Code for Biology and Medicine 9:9.

Forbes, V. E., P. Calow, and R. M. Sibly. 2008. The extrapolation problem and how population modeling can help. Environmental Toxicology and Chemistry 27:1987–1994.

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. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682.

Froschauer, A., M. Racey, and C. Riley. 2011. Review finds endangered species protection may be warranted for two bat species. Technical report. U.S. Fish and Wildlife Service, Bloomington, Minnesota, USA.

Gotelli, N. J. 2008. A primer of ecology. Fourth edition. Sinauer, Sunderland, Massachusetts, USA.

Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton, Princeton, New Jersey, USA.

Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmański. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115:275–282.

Haccou, P., and Y. Iwasa. 1996. Establishment probability in fluctuating environments: a branching process model. Theoretical Population Biology 50:254–280.

Haccou, P., P. Jagers, and V. A. Vatutin. 2005. Branching processes: variation, growth, and extinction of populations. Cambridge University Press, Cambridge, UK.

Hallam, T. G., and P. Federico. 2009. Application of dynamic population models to bats. Pages 177–194 in T. H. Kunz and S. Parsons. Ecological and behavioral methods for the study of bats. Johns Hopkins University Press, Baltimore, Maryland, USA.

Harmata, A. R. 2002. Encounters of golden eagles banded in the Rocky Mountain West. Journal of Field Ornithology 73:23–32.

Huso, M. 2013. Estimating direct fatality impacts at wind farms: how far we've come, where we have yet to go. Page 175 in Proceedings of the Wind-Wildlife Research Meeting IX. , Broomfield, Colorado, November 28–30, 2012. American Wind Wildlife Institute, Washington, D.C., USA.

Karlson, R. H., and H. M. Taylor. 1992. Mixed dispersal strategies and clonal spreading of risk: predictions from a branching process model. Theoretical Population Biology 42:218–233.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts, USA.

Klem, D., Jr., D. C. Keck, K. L. Marty, A. J. Miller Ball, E. E. Niciu, and C. T. Platt. 2004. Effects of window angling, feeder placement, and scavengers on avian mortality at plate glass. Wilson Bulletin 116:69–73.

Kochert, M. N., K. Steenhof, C. L. Mcintyre, and E. H. Craig. 2002. Golden Eagle(*Aquila chrysaetos*). *In* The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/684

Koehler, C. E., and R. M. Barclay. 2000. Post-natal growth and breeding biology of the hoary bat (*Lasiurus cinereus*). Journal of Mammalogy 81:234–244.

Krebs, C. J. 1999. Ecological methodology. Benjamin/Cummings, Menlo Park, California, USA.

Kunz, T. H., E. B. Arnett, B. M. Cooper, W. P. Erickson, R. P. Larkin, T. Mabee, M. L. Morrison, M. Strickland, and J. M. Szewczak. 2007a. Assessing impacts of wind-energy development on nocturnally active birds and bats: a guidance document. Journal of Wildlife Management 71:2449–2486.

Kunz, T. H., E. B. Arnett, W. P. Erickson, A. R. Hoar, G. D. Johnson, R. P. Larkin, M. D. Strickland, R. W. Thresher, and M. D. Tuttle. 2007b. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Frontiers in Ecology and the Environment 5:315–324.

Kunz, T. H., and M. B. Fenton. 2006. Bat ecology. University of Chicago Press, Chicago, Illinois, USA.

Kuvlesky, W. P., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and opportunities. Journal of Wildlife Management 71:2487–2498.

Loss, S. R., T. Will, S. S. Loss, and P. P. Marra. 2014a. Bird-building collisions in the United States: estimates of annual mortality and species vulnerability. Condor 116:8–23.

Loss, S. R., T. Will, and P. P. Marra. 2012. Direct human-caused mortality of birds: improving quantification of magnitude and assessment of population impact. Frontiers in Ecology and the Environment 10:357–364.

Loss, S. R., T. Will, and P. P. Marra. 2013a. Estimates of bird collision mortality at wind facilities in the contiguous United States. Biological Conservation 168:201–209.

Loss, S. R., T. Will, and P. P. Marra. 2013b. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

Loss, S. R., T. Will, and P. P. Marra. 2014b. Estimation of bird-vehicle collision mortality on US roads. Journal of Wildlife Management pages 763–771.

Loss, S. R., T. Will, and P. P. Marra. 2014c. Refining estimates of bird collision and electrocution mortality at power lines in the United States. PLoS ONE 9:e101565.

Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454:100–103.

Meli, M., A. Palmqvist, V. E. Forbes, J. Groeneveld, and V. Grimm. 2013. Two pairs of eyes are better than one: combining individual-based and matrix models for ecological risk assessment of chemicals.

Ecological Modelling 280:40–52.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Pickett, S. T. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 *in* Long-term studies in ecology. Springer, Berlin, Germany.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. American Naturalist 167:925–938.

Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. J. Ziolkowski. 2013. The North American breeding bird survey 1966–2011: summary analysis and species accounts. North American Fauna 79:32.

Scheffer, M. 2009. Critical transitions in nature and society. Princeton University Press, Princeton, New Jersey, USA.

Smallwood, K. S., and C. Thelander. 2008. Bird mortality in the Altamont Pass wind resource area, California. Journal of Wildlife Management 72:215–223.

Sovacool, B. K. 2009. Contextualizing avian mortality: a preliminary appraisal of bird and bat fatalities from wind, fossil-fuel, and nuclear electricity. Energy Policy 37:2241–2248.

Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22.

Thogmartin, W. E., R. A. King, P. C. McKann, J. A. Szymanski, and L. Pruitt. 2012. Population-level impact of white-nose syndrome on the endangered Indiana bat. Journal of Mammalogy 93:1086–1098.

Thogmartin, W. E., C. A. Sanders-Reed, J. A. Szymanski, P. C. McKann, L. Pruitt, R. A. King, M. C. Runge, and R. E. Russell. 2013. White-nose syndrome is likely to extirpate the endangered Indiana bat over a large part of its range. Biological Conservation 160:162–172.

Turner, J. A. 1999. A realizable renewable energy future. Science 285:687–689.

United States Energy Information Administration. 2014. Electricity power monthly. Technical report. U.S. Energy Information Administration, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2013. Eagle conservation plan guidance: module 1–land-based wind energy. Version 2. Technical report. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Washington, D.C., USA. http://www.fws.gov/migratorybirds/Eagle_Conservation_Plan_Guidance-Module%201.pdf

SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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