Demographic and potential biological removal models identify raptor species sensitive to current and future wind energy


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Abstract. A central challenge in applied ecology is understanding the effect of anthropogenic fatalities on wildlife populations and predicting which populations may be particularly vulnerable and in greatest need of management attention. We used three approaches to investigate the potential effects of fatalities from collisions with wind turbines on 14 raptor species for both current (106 GW) and anticipated future (241 GW) levels of installed wind energy capacity in the United States. Our goals were to identify species at relatively high vs low risk of experiencing population declines from turbine collisions and to also compare results generated from these approaches. Two of the approaches used a calculated turbine-caused mortality rate to decrement population growth, where population trends were derived either from the North American Breeding Bird Survey or from a matrix model parameterized from literature-derived demographic values. The third approach was potential biological removal, which estimates the number of fatalities that allow a population to reach and maintain its optimal sustainable population set by management objectives. Different results among the methods reveal substantial gaps in knowledge and uncertainty in both demographic parameters and species-specific estimates of fatalities from wind turbines. Our results suggest that, of the 14 species studied, those with relatively higher potential of population-level impacts from wind turbine collisions included barn owl, ferruginous hawk, golden eagle, American kestrel, and red-tailed hawk. Burrowing owl, Cooper’s hawk, great horned owl, northern harrier, turkey vulture, and osprey had a relatively lower potential for population impacts, and results were not easily interpretable for merlin, prairie falcon, and Swainson’s hawk. Projections of current levels of fatalities to future wind energy scenarios at 241 GW of installed capacity suggest some species could experience population declines because of turbine collisions. Populations of those species may benefit from research to identify tools to prevent or reduce raptor collisions with wind turbines.

Key words: Breeding Bird Survey; matrix model; mixture distribution; population-level effects; potential biological removal; raptors; wind energy; wind turbine collisions.

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INTRODUCTION

Energy is required for modern human societies to prosper, but the extraction, generation, and use of energy can have negative effects on humans and natural systems. Wind energy is rapidly growing because it has reduced air pollution, water use, and CO₂ production relative to fossil fuels, and technological advances make it commercially viable (Sovacool and Enevoldsen 2015). Despite these benefits, wildlife fatalities from wind energy extraction cause concern among natural resource managers, conservation organizations, and the public (Katzner et al. 2019). A fundamental question is whether the fatalities occurring at wind facilities alter the status or trends of populations (Beston et al. 2016, Cook and Robinson 2017, May et al. 2019). If they do, then avoidance, minimization, and mitigation may be necessary to reduce wildlife fatalities or offset their impacts (U.S. Fish and Wildlife Service 2012). Such practices may increase the cost of electricity produced by wind and restrict where wind turbines can be located.

Understanding the population-level effects of turbine-caused mortality on species such as birds is difficult. The species (and turbines) are widely distributed, requiring range-wide estimates of demographic parameters such as population size, survival, and fatality from turbines. In addition, many species are migratory, so their populations may be impacted in regions distant from the location of turbine-caused mortality (Erickson et al. 2016, Katzner et al. 2017, 2020) or they may interact with wind facilities only during brief periods of the year, such as migration. Further, within the United States, fatalities caused by collisions with turbine blades are not sampled in a geographically representative manner (Erickson et al. 2014, Huso and Dalthorp 2014), and the methods, timing, and effort of fatality surveys vary across facilities (Erickson et al. 2002, Loss et al. 2013, Beston et al. 2015, Conkling et al. 2021).

Despite information gaps and issues with data quality, wind energy facilities will continue to be installed and decisions regarding wind energy and wildlife management will continue to be made. Machtans and Thogmartin (2014) and May et al. (2019) suggested attempts to understand and measure the population-level effects of wind energy on birds and bats are necessary despite limitations associated with the available data. In some cases, data have allowed some confidence in conclusions about population-level consequences, for example, hoary bats (Aeorestes cinereus; Frick et al. 2017) and golden eagles (Aquila chrysaetos; Katzner et al. 2017) in the United States, common buzzards (Buteo buteo) and red kites (Milvus milvus) in Germany (Grünkorn et al. 2016), and Egyptian vultures (Neophron percnopterus) in Spain (Carrete et al. 2009). Even if these previous studies produce uncertain results or only provide a qualitative understanding of which species are more or less likely to be affected by wind energy, they are informative because they can differentiate species likely requiring attention from those with lesser need of further research and management intervention. Furthermore, these efforts help define quantitative frameworks and methodologies, uncover problems with implementation, suggest improvements, and point out key data gaps that can be filled in the future.

Raptors are a focus of considerable attention in wind–wildlife research and management. Relative to most passerines, raptors reproduce at a lower rate, delay sexual maturation, are longer-lived, and generally have smaller population sizes. These traits mean that variation in survival, particularly of adults, is usually a key driver of population dynamics (Sæther and Bakke 2000, Oli 2004, Tack et al. 2017). Furthermore, some studies suggest fatalities from wind energy could have population-level impacts for raptors at both local and regional scales (Carrete et al. 2009, Schaub 2012, Grünkorn et al. 2016, Katzner et al. 2017).

In this paper, we describe investigations of the potential for population-level impacts of wind energy on 14 raptor species in the conterminous United States and Alaska, with the goal of identifying those species that may experience higher potential impacts as candidates for more intensive study and conservation attention. Secondary, we compare three different approaches to assess population-level impacts and discuss data needs to increase the future utility of these methods. Two approaches decremented estimated population growth rates by turbine mortality rates: One of these used observed population growth rates from the North American breeding
bird survey (BBS) and the other used matrix models parameterized from published demographic data. The third approach estimated potential biological removal (PBR; Wade 1998) and compared it to estimates of fatalities. PBR differs from the other two methods primarily in assuming density dependence and estimating a limit on fatalities rather than a change in population trend.

**METHODS**

To parameterize models used to estimate impacts of wind energy on raptor populations, we conducted literature searches that identified 186 studies reporting any combination of survival, reproduction, nesting success, age structure, and population growth rates of raptors occurring in North America. These data and associated R scripts are available at Diffendorfer et al. (2021). Studies included any geographic scope or location, including outside of the United States. Parameter estimates were extracted from the studies and screened by our raptor and avian specialists (TK and SL) to exclude unlikely values or those whose results were judged to be unduly affected by regionally or temporally anomalous conditions such as exposure to the pesticide DDT (dichlorodiphenyltrichloroethane). We searched for data on any North American raptor species and found 14 species with adequate demographic information (i.e., estimates of maternity, survival, and age at reproduction) for analyses. We did not weight studies in any way, for example, based on sample size. For each species, we used the approaches described below to understand the potential impacts of fatalities from wind energy on population status and trend at both current (106 GW) and future (241 GW) levels of installed electricity generation capacity.

Our approach is best described as a series of steps, each described in detail below. First, we estimated species-specific turbine-caused mortality rates. Second, we estimated the observed population growth rate in the absence of wind turbines using historical BBS data and then calculated the effect of current and future turbine mortality on population growth. Third, we also estimated population growth rates with matrix models, based on published demographic data and an allometric scaling filter, and assessed the effect of adding turbine mortality to population rates of change calculated with the matrix model. Fourth, we estimated the PBR for each species and compared it to estimated turbine-caused fatalities.

**Turbine-caused mortality rates**

To estimate species-specific turbine-caused mortality rates, we first estimated an all-species fatality rate for the United States (birds killed/MW of installed capacity/year) using finite mixture distribution modeling to combine the distributions of three fatality rate estimates from previous studies (Appendix S1: Table S1 for details). In the mixture distributions, we gave equal weighting to the three estimates because each estimate derives from different assumptions and methods (Johnson et al. 2016), and whether one approach was superior to the others is unclear. We used the mean fatality rate from the mixed distribution as an estimate of a national all-bird fatality rate.

We then multiplied the mean all-species fatality rate from the mixture distribution by the installed capacity of wind energy in the United States in 2019 (105.583 GW [105,583 MW]; American Wind Energy Association 2018), and also by an estimate of potential future installed capacity (241 GW [240,605 MW]), to coarsely estimate the total number of birds of all species killed per year presently and in the future, respectively. The estimate of future installed capacity is based on the National Renewable Energy Laboratories mid-scenario projection for installed wind capacity in 2040 (Wesley et al. 2019), which is similar to a linear extrapolation of the growth in installed wind capacity from 2006 to 2019 (7.33 GW added per year; 260 GW by 2040). Together, these values suggest ~240–250 GW is a reasonable estimate for installed, onshore wind capacity in the United States within the next 20–30 yr.

We used the estimate of the total number of birds killed per year to estimate the number of fatalities for each raptor species in our study. Limitations in existing fatality studies do not allow direct estimates of the number of individuals killed annually by turbines for any species (Conkling et al. 2021). Alternatively, Zimmerling et al. (2013) and Erickson et al. (2014) coarsely estimated species-specific fatalities from wind turbine collisions by multiplying an estimate of
the total fatalities across all species by the proportion of fatalities accounted for by each species. We used a similar approach modified to account for differences in detection rates for differently sized species.

We began with a list of the numbers of observed fatalities by species based on 68 publications and reports describing fatalities at wind facilities (Loss et al. 2013). To adjust species-specific fatalities \( (n_i) \) by body size, we used published data in Barrientos et al. (2018), to fit a model describing the relationship between bird body mass and searcher efficiency (i.e., the proportion of birds detected by observers during fatality surveys). The data included 171 unique searcher efficiency trials of birds (ranging in body mass from 4 to 4000 g) with the estimated searcher efficiency and sample size reported. We fit a binomial generalized linear model describing the relationship between searcher efficiency and body mass of birds, with sample size as the weighting factor. A Hosmer and Lemeshow goodness-of-fit test indicated the model.

\[
\text{efficiency} = \left(1 + e^{-0.3224 + 0.004(Mass)}\right)^{-1}
\]

fit the data \( (\chi^2 = 6.29, \text{df} = 8, P = 0.61, \text{data separated into 10 bins}) \). We used the modeled equation and the average mass of each of the 14 raptor species to estimate a species-specific value of searcher efficiency, which we used to adjust raw counts of fatalities to account for imperfect detection. Given the data available, we could not adjust species-specific numbers of fatalities by other sources of bias such as persistence times (i.e., how long carcasses remain available for detection in the survey area before being removed by scavengers or decomposing beyond recognition). This lack of further adjustment to potential biases is a limitation of the approach given the data available. Finally, the estimated annual number of fatalities for each raptor species was the total bird fatality rate multiplied by the proportion of the adjusted fatalities attributed to that species.

We next converted the annual fatalities to a turbine-caused mortality rate, \( c \), for each species. The turbine-caused mortality rate is the number of individuals killed each year divided by the U.S. population size estimate from Partners in Flight (Partners in Flight 2019). This approach to estimating species-specific fatalities and mortality rates assumes the sampled wind facilities are representative of all facilities across the United States. Although this assumption is likely violated (Huso and Dalthorp 2014), as no other alternative currently exists, we believe this approach provides a reasonable starting point for comparing the potential impacts of wind energy on raptors.

The preceding methods describe how we estimated the number of fatalities for each species and the turbine mortality rate. These two variables were subsequently used in the simulations described below to model species-specific impacts. Accurately estimating uncertainty around these variables is currently not possible given the unrepresentative sampling of fatalities and methodological differences across facilities (Conkling et al. 2021). Because we could not estimate the uncertainty around \( c \), we used an order of magnitude error \( (c/10 \text{ to } c \times 10) \) in our simulations. We considered using the uncertainty in the mixture distribution to generate bounds on total fatalities, and then carrying this into species-specific fatality rates and turbine mortality rates. However, doing so generated levels of uncertainty around \( c \) smaller than the order of magnitude approach. Partners in Flight population estimates (Partners in Flight 2019) are now reported with uncertainty bounds estimated using the Monte Carlo methods (Stanton et al. 2019, Will et al. 2019). We did not use these and took a more conservative approach to encompass the unreported uncertainty in the numerator (fatalities) and the denominator (population size) of \( c \). For species-specific fatalities, we approximated upper and lower bounds by adding and subtracting 40%, based on 95% confidence interval of the cumulative fatality estimate from Loss et al (2013; 234,012 birds, 95% CI: 140,438–327,586).

**Observed population rate of change**

To estimate the observed population growth rate in the absence of wind turbines, \( \lambda_b \), we derived national trend estimates from the North American Breeding Bird Survey (BBS, Link and Sauer 2002, Sauer et al. 2017). As a baseline no-wind scenario, we used the annual U.S. abundance indices for each species from 1970 to 1990...
to estimate growth rate in the absence of wind energy generation. We selected the end date of 1990 because wind turbines were still rare across the United States at that time (with only 1.2 GW of generating capacity installed). For each species, we calculated the baseline growth rate $\lambda_b$ as the geometric mean, with uncertainty described as the geometric standard deviation of the annual year-to-year ratio of the BBS indices of annual abundance from 1970 to 1990.

We estimated the change in $\lambda_b$ attributed to wind energy-caused fatalities as $(1 - c) \lambda_b$ (see derivation below). We simulated $\lambda_b$ values using the log of the geometric mean and geometric standard deviation of the BBS trend estimate to parameterize a log-normal distribution (rnorm function in R), and we simulated the order of magnitude uncertainty around $c$ (the adjusted number of annual fatalities/Partners in Flight population size) using a triangular distribution with ($c/10$ to $c \times 10$).

This approach makes several simplifying assumptions. First, it assumes fatalities from wind turbines affect all individuals equally, regardless of age, sex, condition, or other factors. Second, it assumes the absence of density dependence, that fatalities are additive, and that populations grow exponentially. While this is not a realistic model of population dynamics, it is arguably a reasonable approach for comparing across species because the lack of density dependence essentially estimates an upper bound on impacts, given that there is no demographic compensation for fatalities.

Under these assumptions, the population dynamics can be described as $N_{t+1} = \lambda N_t$, where $N_t$ is the population size in year $t$ and $\lambda$ is the population growth rate. Including fatalities using $c$, $N_{t+1} = \lambda N_t - c\lambda N_t$, where $c\lambda N_t$ is the number of individuals killed by wind energy from $t$ to $t + 1$. Rearranging this formula to $N_{t+1} = (1 - c)\lambda N_t$, the growth rate of a population with a turbine-caused mortality rate of $c$ is equal to the population growth rate without fatalities from wind turbines, $\lambda_b$ (our baseline scenario), multiplied by $(1 - c)$. Thus, $\lambda_w = (1 - c)\lambda_b$, where $\lambda_w$ is the growth rate of a population including the turbine-caused mortality rate. Given this formulation, declines in $\lambda$ with increasing wind energy depend only upon the magnitude of $c$, and the population will decline when $c > (\lambda_w - 1)/\lambda_b$.

### Matrix models with an allometric scaling filter

We used stage-structured, postbreeding matrix models to simulate population growth rates with and without the added fatalities from collisions with wind turbines. For all raptor species, the age of first reproduction determined the shift from juvenile to adult and the size of the matrix (e.g., a 2 × 2 matrix for species breeding their first year of life, a 4 × 4 matrix if reproduction begins at year 3). The first row of the matrix described recruitment, and subsequent rows described survival after hatching and each following year. The second-to-last column described juveniles surviving into reproductive age and reproducing before the next year.

$$
\begin{pmatrix}
0 & 0 & \ldots & s_{j,m} & s_{a,m} \\
0 & s_j & \ldots & 0 & 0 \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \ldots & s_j & s_a
\end{pmatrix}
$$

In the matrix, $s_j$ represents female survival (juvenile = $s_j$, or adult = $s_a$), and $m$ is the number of female offspring per female per year. In our application, the matrix assumes no density dependence, no senescence, and no age-related variation in reproduction. Survival varied between juveniles and adults.

We parameterized the matrix with estimates of $s_j$, $s_a$, and $m$ from the literature. However, combining random draws from distributions of observed life-history traits may create unrealistic combinations of parameter values. Life-history trade-offs result in correlations between life-history parameters (e.g., negative correlation between fecundity and juvenile or adult survival) and using literature searches to compile ranges of observed life-history parameters from multiple populations over time, space, and wide-ranging environmental conditions, which can result in the correlations between the observed vital rates being lost. To constrain our population matrices to more realistic parameter combinations, we applied a filter based on allometric scaling relationships similar to Dillingham et al. (2016). The approach used the allometric relationship between generation time and maximum intrinsic growth rate ($r_{\text{max}}$, Niel and Lebreton 2005, described in Appendix S2) to generate a multivariate normal distribution
Potential biological removal

The previous methods ignore potential density-dependent responses to novel mortality sources, such as increased reproductive rates or decreased rates of mortality from other mortality sources or age/stage classes. Therefore, we also considered the potential biological removal (PBR) approach, which allows for density dependence and was originally developed for the management of marine mammals impacted by fishing bycatch (Wade 1998). As with raptors, marine mammal populations are difficult to assess, fatality from fishing bycatch is variable across species ranges and incompletely reported, some species are migratory, and mitigation is often expensive and difficult to employ and enforce. The PBR is a mortality limit, defined in the Marine Mammal Protection Act as “the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimal sustainable population.”

PBR is calculated as

\[
PBR = F \frac{r_{\text{max}}}{2} N_{\text{min}},
\]

where \(r_{\text{max}}\) is the maximum annual population growth rate under optimal conditions, \(N_{\text{min}}\) is a lower bound on the current population size, and \(F\) is a recovery factor. Assuming density-dependent logistic growth, \(r_{\text{max}}/2\) generates a rate of take (in our case, rate killed by wind turbines) that maximizes the net productivity of a population. \(F\) ranges from 0 to 2 (0 = no allowed take, 2 = maximum take) and is set by decision-makers to adjust the value of the PBR for the specific demographic and conservation situation of the species. In the United States, guidelines for marine mammals based on numerical simulations suggest 0.1 as the default value of \(F\) for endangered species and 0.5 for depleted or threatened populations (Barlow et al. 1995, Wade 1998).

We present our results in terms of a risk ratio, the number of anthropogenic-caused fatalities/PBR (Richard and Abraham 2013), but call it the “PBR ratio” because it is not a true measure of risk. The PBR ratio represents the proportion of the total take limit represented by fatalities from wind energy. For example, if 30 birds are killed by wind energy and the species has a PBR of 100, the PBR ratio is 0.30, indicating 30% of the total take limit is caused by fatalities from wind energy. PBR ratios >1 occur when fatalities are greater than the PBR and suggest the population will decline below what managers consider optimal.

We estimated PBR and the associated PBR ratio for each species while incorporating uncertainty in parameter estimates by simulating variation in \(F\) from 0.5 to 1 (this range follows guidelines for non-endangered marine mammals; Barlow et al. 1995, Wade 1998). We varied \(N_{\text{min}}\) from 20% to 50% (National Marine Fisheries Service 2016) of the U.S. continental population size for each species (Partners in Flight 2019). We used the allometric scaling filter process (described above and in Appendix S2) to simulate \(r_{\text{max}}\) where the product of \(r_{\text{max}}\) and generation time is roughly equivalent to 1 (Niel and Lebreton 2005). As described above, we included uncertainty around species-specific fatalities using the 95% confidence interval of the cumulative fatality estimate from Loss et al. (2013). We simulated 5000 estimates of PBR and associated PBR ratio for each species.

We emphasize that none of the three modeling approaches incorporates efforts to reduce raptor fatalities at turbines (e.g., deterrents or turbine
shUTDOWN), nor mitigation activities attempting to offset fatalities from wind facilities by preventing fatalities from other sources (e.g., retrofitting power lines to prevent electrocutions) or increasing vital rates through habitat improvements. As such, these approaches are meant to identify those species where mitigation is more likely to be necessary if the goal is to sustain populations while increasing wind energy production. Finally, we used scatterplots and correlations to make comparisons across all species for the three different approaches described above. All simulations were developed and run in R (R Core Team, 2019) and are available at Diffendorfer et al. (2021).

RESULTS

Turbine-caused mortality rates

Estimates of national fatality rates from the literature included means ranging from 2.42 to 10.52 birds-MW\(^{-1}\)-yr\(^{-1}\) (Table 1). The mixture distribution (Appendix S1: Fig. S1) was skewed with a mean and standard deviation of 5.26 ± 8.52 birds-MW\(^{-1}\)-yr\(^{-1}\), and median of 2.32, suggesting an estimated 554,000 birds of all species were killed by turbines in 2019.

Estimated raptor-specific, turbine-caused mortality rates ranged from <0.001 up to 0.016 individuals per year (Table 2). Barn owl (Tyto alba), American kestrel (Falco sparverius), ferruginous hawk (Buteo regalis), and Golden eagle (Aquila chrysaetos) had the highest turbine-caused mortality rates, while great horned owl (Bubo virginianus) had the lowest mortality rates followed by Cooper’s hawk (Accipiter cooperii) and turkey vulture (Cathartes aura). Burrowing owl (Athene cunicularia), prairie falcon (Falco mexicanus), and merlin (Falco columbarius) had intermediate to low mortality rates.

Observed population rate of change

From 1970 to 1990, BBS national trend estimates varied around a mean of 1 (representing a stationary population) for most species (Fig. 1, no-wind scenario, Table 2), while means for American kestrel, barn owl, golden eagle, great horned owl, and northern harrier (Circus hudsonius) were <1 and the remaining species were >1. For turkey vulture and osprey, the interquartile range of the BBS trend estimate did not include 1.

Species with higher turbine-caused mortality rates (Table 2) showed higher predicted declines in population growth rate as future installed wind capacity increased (Fig. 1). Burrowing owl, ferruginous hawk, merlin, osprey, prairie falcon, red-tailed hawk (Buteo jamaicensis), and Swainson’s hawk (Buteo swainsoni) all had means or medians of \(\lambda\) decline from >1 to <1 as future installed wind energy capacity increased. The 75th percentile of the data dropped below 1, though 1.5× the interquartile range (IQR) did not, for American kestrel, barn owl, ferruginous hawk, golden eagle, and red-tailed hawk at either 106 or 241 GW of installed capacity (Fig. 1).

Matrix model with an allometric scaling filter

The matrix method used the observed allometric relationship between maximum population growth rate and generation time (Niel and Lebreton 2005) to reduce variation around estimates of \(\lambda\) while maintaining central measures (median and mean) nearly identical to the original estimates (Appendix S2: Fig. S1). Despite efforts to filter the models for allometrically possible correlations between vital rates, the matrix-generated population growth rates appeared biologically unreasonable for most species, suggesting declines or increases in population size from 10% to 20% a year (Fig. 2, Matrix). In addition, the literature-based estimates of \(\lambda\) were substantially different from the BBS observed \(\lambda\) with no consistent bias in the direction of the difference. For 11 of the 14

<table>
<thead>
<tr>
<th>Study</th>
<th>Sample size</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erickson (Table 2)</td>
<td>35</td>
<td>1.67</td>
<td>2.42</td>
<td>2.09</td>
</tr>
<tr>
<td>Loss (Appendix)</td>
<td>58</td>
<td>2.16</td>
<td>2.78</td>
<td>2.57</td>
</tr>
<tr>
<td>Smallwood (Appendix)</td>
<td>70</td>
<td>5.65</td>
<td>10.52</td>
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<tr>
<td>Mixture</td>
<td>100,000</td>
<td>2.32</td>
<td>5.26</td>
<td>8.52</td>
</tr>
</tbody>
</table>

Notes: Sample size refers to the number of fatality monitoring field studies used in each estimate or the number of model iterations. For Smallwood, data from Altamont Pass, Calif., were not included in the calculations. Studies included are Smallwood (2013), Loss et al. (2013), and Erickson et al. (2014).
species, one of the point estimates of $\lambda$ predicted population decline, while the other predicted population increase (Fig. 2).

For all species, decrementing population growth rates by the turbine-caused mortality rate did not change the underlying direction of population change (Fig. 3); species with growing populations remained growing, albeit at a slower rate, while species with declining populations declined faster.

**Potential biological removal**

Mean PBR values varied with values of the recovery factor ($F$; Table 3). At $F = 0.5$, the proportion of the population accounted for by PBR was small across all species (0.006–0.016).

PBR ratios were skewed such that mean values were higher than medians (Fig. 4A,B). At current levels of wind energy generation (106 GW, Fig. 4A), the mean PBR ratio exceeded 1, meaning that 100% of the PBR was accounted for by fatalities from wind turbines for ferruginous hawk, golden eagle, and barn owl when $F = 0.5$, the most precautionary $F$ value we tested. At $F = 0.75$, the 75th percentile of the PBR ratio was greater than 1 for golden eagle and barn owl. At $F = 1$, the least precautionary value tested, mean PBR ratios and IQRs were below 1 for all species. American kestrel, barn owl, ferruginous hawk, golden eagle, and red-tailed hawk had mean PBR ratios between ~0.3 and 0.7 at $F = 1$, suggesting 30–70% of an estimated sustainable take limit for these species may be accounted for solely by fatalities from current wind energy generation. Burrowing owl, Cooper’s hawk, great horned owl, northern harrier, merlin, prairie falcon, and turkey vulture had low mean PBR ratios at all levels of $F$.

In the future scenario (241 GW, Fig. 4B), the mean or median PBR ratio exceeded 1 for barn owl, golden eagle, ferruginous hawk, and red-tailed hawk regardless of the value of $F$. At $F = 1$, the mean PBR ratio was 1.64 for golden eagle, 1.45 for barn owl, 1.26 for ferruginous hawk, 1.09 for red-tailed hawk, and 0.76 for American kestrel. As seen with current levels of wind energy generation, burrowing owl, Cooper’s hawk, great horned owl, merlin, and prairie falcon experienced smaller contributions toward their take limits of fatalities from wind energy generation (PBR ratio ~0.05–0.15 at $F = 1$, ~0.08–0.3 at $F = 0.5$).

The turbine-caused mortality rate was mathematically related to the magnitude of declines simulated in the observed $\lambda$ approach ($(1 - c)\lambda_{\text{obs}}$) and the matrix approach, and the PBR ratio incorporated the estimated species-specific turbine fatalities. Thus, there were positive correlations between the PBR ratios and the magnitude of the decline in $\lambda$ across species (Fig. 5A–C).

### Table 2. Turbine-caused mortality rate ($c$) and demographic variables used as input parameters for the modeling approaches.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>$c$</th>
<th>AFR (yr)</th>
<th>Juvenile survival</th>
<th>Adult survival</th>
<th>Maternity</th>
<th>BBS observed $\lambda$</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>Variance</td>
<td>Mean</td>
<td>Variance</td>
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<td>American kestrel</td>
<td>120</td>
<td>0.0091</td>
<td>1</td>
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<tr>
<td>Golden eagle</td>
<td>4800</td>
<td>0.0078</td>
<td>4</td>
<td>0.84</td>
<td>0.001</td>
<td>0.94</td>
<td>0.001</td>
</tr>
<tr>
<td>Great horned owl</td>
<td>1191</td>
<td>0.0003</td>
<td>2</td>
<td>0.68</td>
<td>0.002</td>
<td>0.88</td>
<td>0.002</td>
</tr>
<tr>
<td>Merlin</td>
<td>195</td>
<td>0.0019</td>
<td>1</td>
<td>0.23</td>
<td>0.001</td>
<td>0.67</td>
<td>0.012</td>
</tr>
<tr>
<td>Northern harrier</td>
<td>392</td>
<td>0.0023</td>
<td>1</td>
<td>0.41</td>
<td>0.003</td>
<td>0.70</td>
<td>0.001</td>
</tr>
<tr>
<td>Osprey</td>
<td>1362</td>
<td>0.0022</td>
<td>3</td>
<td>0.47</td>
<td>0.003</td>
<td>0.86</td>
<td>0.0004</td>
</tr>
<tr>
<td>Prairie falcon</td>
<td>750</td>
<td>0.0015</td>
<td>1</td>
<td>0.31</td>
<td>0.003</td>
<td>0.87</td>
<td>0.002</td>
</tr>
<tr>
<td>Red-tailed hawk</td>
<td>1362</td>
<td>0.0066</td>
<td>2</td>
<td>0.36</td>
<td>0.003</td>
<td>0.78</td>
<td>0.001</td>
</tr>
<tr>
<td>Swainson’s hawk</td>
<td>981</td>
<td>0.0026</td>
<td>3</td>
<td>0.44</td>
<td>0.003</td>
<td>0.86</td>
<td>0.001</td>
</tr>
<tr>
<td>Turkey vulture</td>
<td>1500</td>
<td>0.0011</td>
<td>6</td>
<td>0.79</td>
<td>0.003</td>
<td>0.78</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Notes: BBS observed $\lambda$ and its variance were calculated from the period 1970–1990. AFR, age at first reproduction.
**DISCUSSION**

We applied three approaches to compare the potential consequences of collisions with wind turbines across raptor species in the United States with the goal of drawing inferences about the relative impacts of wind energy generation on population status and draw two main conclusions. First, some raptor species appear to be much more vulnerable to fatalities from wind energy than others. Though definitive estimates of population-level effects of wind energy generation on raptors are not currently possible, our results, when considered alongside population trends and additional information on the species assessed, suggest we should consider more detailed studies of wind energy generation impacts on those species our models indicate are most likely to be affected. Second, methodological differences among the three approaches identified key gaps in knowledge and associated levels of uncertainty in many of the parameter estimates needed to make inferences about population-level impacts from wind energy generation.

The inconsistent outcomes estimated by the three methods (observed population rate of change, matrix model with allometric scaling, and PBR) have implications for studies attempting to understand the impacts of wind energy on population dynamics. Had we used the BBS-based, observed population rate of change approach, we would have predicted seven species may switch from growing or stationary population trends to declining in future build-out scenarios. The matrix models, which our results suggested were poorly parameterized, predicted no species would experience a change from increasing to declining population growth solely as a result of fatalities from wind energy generation.
wind energy generation. Finally, PBR indicated current levels of wind energy generation, in isolation from other human-caused fatalities, may be affecting populations of four species with a fifth also affected in future scenarios.

Our approach to using values from previously published field studies to parameterize demographic models is common practice in the absence of data collected in situ. Although often the only option, this can lead to biases in several ways. First, field-based demographic rates vary within and across a species’ range (Weins 1989, Dixon Hamil et al. 2016), and if this heterogeneity is not accommodated, it can skew model outputs. Second, field studies often occur where species are abundant. While appropriate for the original study’s aims, when combined across studies, this can lead to biased depictions of species’ vital rates (Fournier et al. 2019). Finally, demographic rates vary over time, a factor rarely accounted for in most short-term field studies (Doak et al. 2005).

Our matrix results, particularly when compared to the observed trends from BBS (Fig. 2), suggest these types of biases may exist in the collective literature on demographics of U.S. raptor populations. One solution might be estimating survival over broad geographic ranges using banding data, as was done for bald and golden eagles (U.S. Fish and Wildlife Service 2016).

Ideally, models will be parameterized by demographic data representative of population-wide processes. Methods tuning the initial parameterization to an observed population trend, for example, integrated population models (Schaub and Abadi 2011, Thogmartin et al. 2013), may improve estimates of demographic parameters and thus the utility of this approach. In the absence of this more involved treatment of literature-derived vital rates, we have the least confidence in the matrix model results.

Inferences regarding population-level effects

Given the differences across the approaches we used and potential biases in the data associated with underlying parameters, what inferences can we make regarding the impacts of current and future wind energy generation on raptor populations? First, our analyses suggest, given the available data, the current methods will not provide highly accurate estimates of changes in population trends caused by fatalities from wind energy generation. The lack of consistent results across methods and the inherent uncertainty in nearly all steps of the workflow suggest we cannot confidently measure the absolute impact that fatalities caused by wind turbines have on U.S.-wide raptor populations. However, our results, when combined with the conservation status and natural history of the raptor species we assessed, can help categorize species according to the level of risk our models predict they face in current and future wind energy scenarios.

Of the 14 species in our study, those with a relatively higher potential for impacts included barn owl, ferruginous hawk, golden eagle, American kestrel, and red-tailed hawk. These species showed relatively larger estimated declines in population growth rates with increasing levels of wind energy. For example, the barn owl is
Table 3. Mean matrix-based $r_{\text{max}}$, mean (with upper [97.5%] and lower [2.5%] in parentheses), potential biological removal (PBR) estimates at $F = 0.5$ and $F = 1$, population size, and the proportion of the population accounted for by the PBR at $F = 0.5$; PBR estimates for each species were generated from 5000 simulations.

<table>
<thead>
<tr>
<th>Species</th>
<th>$r_{\text{max}}$</th>
<th>$F = 0.5$</th>
<th>$F = 1$</th>
<th>Population size</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>American kestrel</td>
<td>0.177</td>
<td>30,558 (13,155–51,426)</td>
<td>61,116 (26,310–102,852)</td>
<td>2,000,000</td>
<td>0.015</td>
</tr>
<tr>
<td>Barn owl</td>
<td>0.164</td>
<td>1858 (845–3296)</td>
<td>3715 (1698–6591)</td>
<td>130,000</td>
<td>0.014</td>
</tr>
<tr>
<td>Burrowing owl</td>
<td>0.187</td>
<td>16,069 (7004–29,348)</td>
<td>32,137 (14,008–58,696)</td>
<td>980,000</td>
<td>0.016</td>
</tr>
<tr>
<td>Cooper’s hawk</td>
<td>0.161</td>
<td>11,006 (5494–18,702)</td>
<td>24,550 (11,810–41,543)</td>
<td>790,000</td>
<td>0.013</td>
</tr>
<tr>
<td>Ferruginous hawk</td>
<td>0.101</td>
<td>771 (337–1362)</td>
<td>1543 (506–2044)</td>
<td>87,000</td>
<td>0.009</td>
</tr>
<tr>
<td>Golden eagle</td>
<td>0.068</td>
<td>248 (123–413)</td>
<td>494 (246–826)</td>
<td>40,000</td>
<td>0.006</td>
</tr>
<tr>
<td>Great horned owl</td>
<td>0.106</td>
<td>27,681 (12,462–46,969)</td>
<td>55,363 (24,924–93,937)</td>
<td>3,000,000</td>
<td>0.009</td>
</tr>
<tr>
<td>Merlin</td>
<td>0.163</td>
<td>3305 (1411–5953)</td>
<td>6612 (2824–11,905)</td>
<td>240,000</td>
<td>0.014</td>
</tr>
<tr>
<td>Northern harrier</td>
<td>0.125</td>
<td>5728 (2491–10,185)</td>
<td>11,455 (4982–20,371)</td>
<td>520,000</td>
<td>0.011</td>
</tr>
<tr>
<td>Osprey</td>
<td>0.085</td>
<td>1708 (780–2837)</td>
<td>3416 (1561–5873)</td>
<td>230,000</td>
<td>0.007</td>
</tr>
<tr>
<td>Prairie falcon</td>
<td>0.168</td>
<td>1362 (616–2308)</td>
<td>2723 (1232–4615)</td>
<td>95,000</td>
<td>0.014</td>
</tr>
<tr>
<td>Red-tailed hawk</td>
<td>0.096</td>
<td>17,979 (7429–32,007)</td>
<td>35,958 (14,859–64,014)</td>
<td>2,100,000</td>
<td>0.009</td>
</tr>
<tr>
<td>Swainson’s hawk</td>
<td>0.100</td>
<td>5583 (2637–9458)</td>
<td>11,166 (5273–18,915)</td>
<td>640,000</td>
<td>0.009</td>
</tr>
<tr>
<td>Turkey vulture</td>
<td>0.080</td>
<td>58,808 (24,321–110,024)</td>
<td>117,617 (48,643–220,049)</td>
<td>8,200,000</td>
<td>0.007</td>
</tr>
</tbody>
</table>

Notes: We provide 95% confidence limits (CL) of the simulations.

considered a species of greatest conservation need (SGCN) in 57% of the U.S. states where it occurs. Our results suggested that for this species, fatalities from wind energy account for 50–100% of the total allowable PBR under both current and future levels of installed wind energy. Likewise, although BBS data suggest a stable population, ferruginous hawks are a SGCN in 53% of states where they occur, and our results suggest this species is also likely to be sensitive to additional fatalities from wind energy. However, both these species have somewhat specialized habitat associations, and our models assume future build-out will occur consistently in habitats they occupy. If that does not occur, the predictions from our models could be substantially biased.

The golden eagle, a species of high conservation concern compared with other raptor species, showed relatively large potential impacts from wind energy generation with the highest PBR ratios and relatively large change in observed population growth rates with increasing wind energy development. Previous studies suggest anthropogenic fatalities from all sources, including mortality at wind energy installations, electrocutions at power lines, and other causes, already exceed PBR for golden eagles by ~1200 fatalities a year (U.S. Fish and Wildlife Service 2016). Our PBR estimate (494 at $F = 1$, Table 3) is consistent with the USFWS finding that current anthropogenic fatalities exceed sustainable levels.

PBR ratios for American kestrel were smaller than those for golden eagle, but they showed somewhat larger decreases in population growth rates with fatalities from wind energy generation than did golden eagle. The American kestrel is still numerous, but is undergoing a long-term population decline, having lost an estimated 47% of its population size from 1966 to 2015 (Sauer et al. 2017; https://www.mbr-pwrc.usgs.gov/bbs/trend/tf15.shtml). Our results suggest fatalities from wind energy generation may make it more difficult to stabilize American kestrel populations.

We did not expect the abundant and continentally distributed red-tailed hawk to exhibit a greater potential for impacts of wind energy generation compared with other species. The turbine-caused mortality rate for this species was large enough to result in projected declining populations with increases in future wind energy, while the species’ relatively lower $r_{\text{max}}$ resulted in high PBR ratios. This example illustrates that abundance alone may not necessarily indicate the population-level vulnerability of a species to anthropogenic stressors.

Results were not easily interpretable for merlin, prairie falcon, and Swainson’s hawk. For these species, the observed population rate of change approach suggested populations may change from stationary or growing to declining as more wind turbines are installed. All species
Fig. 4. PBR ratio for unique values of $F$, by species for 106 GW (A) and 241 GW (B) of installed wind energy capacity. Boxplots describe the PBR ratio, and black dots represent mean values.

Fig. 5. Relationships between (A) the turbine mortality rate and the PBR ratio (at $F = 0.5$ and 241 MW), (B) the turbine mortality rate and the decrease in lambda between no wind and 140 GW using the matrix approach, and (C) the decrease in lambda between no wind and 140 GW using the matrix approach and the PBR ratio at 140 GW. In each graph, dots represent individual raptor species.
had pre-wind energy growth rates near 1, so even low turbine-caused mortality rates could result in a declining population. However, the PBR ratios were low, particularly for merlin and prairie falcon, suggesting relatively low impacts of wind energy generation on population size.

Species whose populations were estimated to have a low potential for impacts solely due to wind energy generation included burrowing owl, Cooper’s hawk, great horned owl, northern harrier, turkey vulture, and osprey. For all species except osprey, estimated fatalities were currently relatively low, and our models estimated small potential impacts of wind energy generation, even at 241 GW of future installed capacity.

Limited inferences regarding wind energy impacts on raptor populations

Uncertainty in input data and associated model outputs prevents us from generating definitive, quantitative estimates of wind energy impacts on species using widely accepted and commonly used approaches. The main sources of this uncertainty include estimates of species-specific fatalities and demographic variables, as well as a lack of clarity regarding how density-dependent compensatory mechanisms affect raptor populations.

Limitations regarding U.S. wildlife fatality data from wind turbine collisions have been widely recognized and discussed (Arnett et al., 2008, Piorkowski et al. 2012, Huso and Dalthorp 2014, Conkling et al. 2021). While progress has been made in estimating fatalities based on field surveys (Simonis et al. 2018), utilizing BBS data to understand turbine effects on abundance (Miao et al. 2019), and accumulating fatality data from public and private sources (e.g., the document library at https://awwic.nacse.org/), we are not aware of efforts to strategically measure fatalities across wind facilities in the United States to generate robust and statistically defensible nationwide fatality estimates. In the only example of which we are aware, the prognosis and assessment of bird collision risks at wind turbines in northern Germany (PROGRESS) project measured fatality at 46 wind facilities using a systematic sampling design from 2012 to 2014 including carcass removal and searcher efficiency trials at all facilities. This sampling regime allowed robust extrapolations of total fatalities for individual species across the study extent and relatively high confidence in the resultant estimates of population impacts to common buzzard (Buteo buteo) and red kite (Milvus milvus; Grünkorn et al. 2016, 2017). Investigations comparing the costs (money spent on fatality surveys) and benefits (quality of information) of systematic fatality sampling across the United States at 5- to 10-yr intervals, instead of the current uncoordinated sampling efforts, would help determine whether more efficient approaches exist for gathering critical baseline information on fatalities caused by turbines.

The observed λ approach relied on BBS trend data, and analyses have found that BBS can detect trends in population dynamics for at least some raptor species (Farmer et al. 2007, Millsap et al. 2013). For red-tailed hawk, the observed λ, but not the matrix estimate, was similar to λ estimated using Christmas Bird Count and migration monitoring information (Paprocki et al. 2017).

The observed λ and matrix approach did not include density-dependent compensatory mechanisms. In fact, with only a few exceptions (Johnson et al. 2012, Stevens et al. 2017) compensatory responses have not been incorporated into data-based models of the effects of anthropogenic fatalities on populations. Research on avian life histories and population biology suggests longer-lived species have higher and less variable adult survival rates (Péron et al. 2016), and population dynamics of these species are more sensitive than shorter-lived species to changes in adult survival (Oli 2004). Thus, longer-lived species, including raptors, are hypothesized to have a lower ability to compensate for anthropogenic sources of fatality, and evidence supporting this hypothesis exists for birds and mammals (Péron 2013). This perspective leads to the expectation that raptors may be sensitive to changes in survival caused by fatalities from wind turbines. Tack et al. (2017) concluded that populations of golden eagles in Wyoming, for instance, are generally unable to compensate for reduced survival by increasing productivity.

Though it is possible to simulate a range of different forms of density dependence, it is logistically and quantitatively difficult to determine the degree to which compensation occurs in populations. Given these issues, our models assumed no compensation, so they tend to overestimate...
the impact of fatalities on population status and trend. A model with complete compensation, while unrealistic, would show no effects from additional fatalities, so our results may be considered an upper limit on the estimated magnitude of wind energy’s impact on raptor populations.

Our application of PBR as an indicator of the possible declines in populations at 241 GW has limitations. PBR was designed to be calculated regularly, in conjunction with continued monitoring of a population through time and together with estimates of all other anthropogenic mortality sources a species experiences (Wade 1998, Johnson et al. 2012, Moore et al. 2013). Thus, PBR will change as a population fluctuates and mortality from other sources varies. Since our PBR estimates are static, they are limited when projecting into the future. For example, had we assumed American kestrel populations would decline from 2019 to 2030 using current trends, the population would decline from 1.7 million to $1,700,000 \times 0.96^{11} = 1,085,000$ reducing PBR from ~43,000 to ~27,000 at ~241 GW. The approach we used only compared PBR to fatalities from wind energy generation, primarily because species-specific fatality rates from other mortality sources are unknown for virtually all bird species, including raptors. Accurately projecting PBR into the future requires understanding how the turbine fatality rate, $c$, will change with more turbines, how population size and other sources of fatality may change through time, and how managers may respond by setting a higher or lower value of the recovery factor $F$. Ultimately, we did not perform such detailed projections because our objective was a comparative analysis of relative impacts for different species with the goal of focusing further detailed research and we could not extrapolate confidently extrapolate into the future.

**CONCLUSIONS**

Our estimates of wind energy impacts suggest some raptor species could be experiencing population declines from turbine collisions. Our future projections suggest additional species that may not be declining now could eventually experience population declines within 20 yr as wind energy expands beyond 241 GW of installed generating capacity. Projections of wind energy development in the United States, however, are higher than 241 GW. For example, the mid-scenario projection of Wesley et al. (2019) forecasts >400 GW of install capacity in 2050. Our forecasting approaches assumed turbine fatality rates are not decreased in the future by technologies or improvements that reduce fatalities or mitigate them. They also assume turbine fatality rates do not increase as turbines expand to new geographic locations, potentially increasing exposure of species to fatality risk. The results highlight the vulnerability of certain raptor species, high levels of uncertainty, and the conservation value of ongoing efforts to continue developing collision deterrent technologies (May et al. 2020, Stokke et al. 2020), to implement automated shutdowns when raptors are in close proximity to wind turbines (Tomé et al. 2017, Hayes et al. 2019), and to site new turbines in locations that avoid raptors (de Lucas et al. 2012a, b, Hanssen et al. 2020).

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**LITERATURE CITED**


National Marine Fisheries Service. 2016. Guidelines for preparing stock assessment reports pursuant to the 1994 amendments to the MMPA. NMFS instruction 02-204-01.


**DATA AVAILABILITY**

Data are available from USGS ScienceBase: https://doi.org/10.5066/P952UAFD.

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3531/full