

# Direct human-caused mortality of birds: improving quantification of magnitude and assessment of population impact

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Hundreds of millions to greater than one billion North American birds are directly killed each year by human stressors, including collisions with man-made structures, predation by feral and pet cats, intentional and accidental poisoning, and pollution. Because these causes of mortality are increasingly abundant and because some result in large bird die-offs, they have received both increased scientific attention and general media coverage. However, quantifying bird mortality remains imprecise and methods to assess whether these losses cause important biological impacts remain underdeveloped. If local mortality studies followed rigorous design and sampling schemes, allowing comparison of data and scaling up of mortality estimates to broad regions, this could lead to improved analyses. Several analytical techniques – including hierarchical and population models – show potential for improving quantification of anthropogenic mortality of birds and inference of population-level effects. Results arising from improved study designs and analytical techniques will more effectively inform decision making about policies and regulations aimed at reducing avian mortality and minimizing population impacts.

*Front Ecol Environ* 2012; 10(7): 357–364, doi:10.1890/110251 (published online 15 Jun 2012)

Birds are killed as a result of numerous direct and indirect threats. Well-documented indirect threats to birds include the effects of climate change and habitat loss and degradation. A substantial proportion of bird mortality results from direct anthropogenic sources, including collisions with buildings, communication towers, wind turbines, electrical infrastructure, automobiles, and aircraft (collectively “birdstrikes”), predation by free-roaming feral and pet cats, poisoning, pollution, and invasive pathogens (Figure 1). In particular, collisions with man-made structures and cat predation are thought to rank among the top threats to North American birds in terms

of number of individuals killed (Banks 1979; Stallcup 1991; Erickson *et al.* 2005; Manville 2005).

Many North American bird species are experiencing substantial population declines (Sauer *et al.* 2011). Determining whether direct mortality sources contribute to these declines is crucial for developing conservation and management objectives. Because direct threats often result in mortality that can be traced to a specific structure or activity, substantial mortality reductions may be possible if targeted regulations are enacted. Decision making to prioritize among alternative mortality sources requires accurate estimation of the magnitude of mortality caused by each source as well as assessment of population-level impacts. Furthermore, because unauthorized killing of individuals of nearly all North American bird species, whether deliberate or incidental, is illegal under the Migratory Bird Treaty Act, accurate mortality quantification and population assessment is essential to informing policy decisions.

Quantification of direct anthropogenic mortality, although critical for conservation efforts, remains imprecise. National mortality estimates are often based on extrapolation from a limited sample of small-scale studies, and estimates of uncertainty are ignored or only superficially assessed. For example, Klem’s (1990) estimate of 100 million to 1 billion annual bird deaths from window strikes in the US was informed primarily by a study at two buildings; many later studies repeated this estimate without the associated qualifications and assumptions. Erickson *et al.* (2005) used an estimate of 8 million to 219 million birds killed annually by free-roaming cats in Wisconsin (Coleman and Temple 1996) to reach a con-

## In a nutshell:

- Human activities combine to directly kill millions to more than one billion North American birds each year, but there is tremendous uncertainty about the magnitude of this mortality and the relative importance of different mortality sources
- Prioritization of measures to reduce these deaths requires accurate estimates of numbers of birds killed by each threat and impacts of losses on bird populations
- Systematic use of statistical approaches shows promise for improving quantification of bird mortality estimates and their uncertainty
- Population impact assessment can be improved by incorporating mortality estimates into population models

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servative US estimate of 100 million bird kills per year. These values are presumed to represent relative magnitudes of mortality; however, they are of limited use for decision making about the introduction of mortality reduction measures. Such estimates may appear arbitrary to non-scientists, a viewpoint that can result in apathy or resistance to regulations, such as that seen for efforts to control free-roaming cat colonies (Winter 2004).

The use of mortality estimates to assess whether a threat has biologically important population impacts is also critical for conservation; however, this exercise is imprecise in the absence of data on other population parameters (eg survival and fecundity). Analyses of population impacts are conducted for endangered species in risk assessments required by the US Endangered Species Act (eg Biological Assessments and Habitat Conservation Plans), but they are rarely subjected to rigorous external review and have yet to proliferate within the broader scientific community. Recently, researchers have shown a more systematic usage of statistical methods, including an analysis of bird population trends relative to collision vulnerability (Arnold and Zink 2011) and analyses that incorporate mortality estimates into population models (eg Runge *et al.* 2009; van Heezik *et al.* 2010). These studies improve the standard of population-level inference; however, further development and adoption of rigorous statistical approaches is required.

Our goal here is to outline a path toward more accurate and precise estimates of avian mortality and more reliable assessment of its population effects. Specifically, we (1) highlight limitations that prevent accurate quantification of mortality and confident conclusions about population effects, and (2) propose methods that, if widely adopted, will lead to improved quantification and inference, and

therefore to more informed decision making and policy development to reduce bird mortality. Since direct mortality sources kill large numbers of birds and uncertainty is inherent in even the most sophisticated analytical approaches, we conclude by proposing that those making policy decisions based on mortality estimates and population assessments should consider adopting a precautionary approach (Foster *et al.* 2000). Although our focus is on birds, we believe that many of the concepts presented in this paper are transferable to studies of direct anthropogenic mortality among other animal taxa.

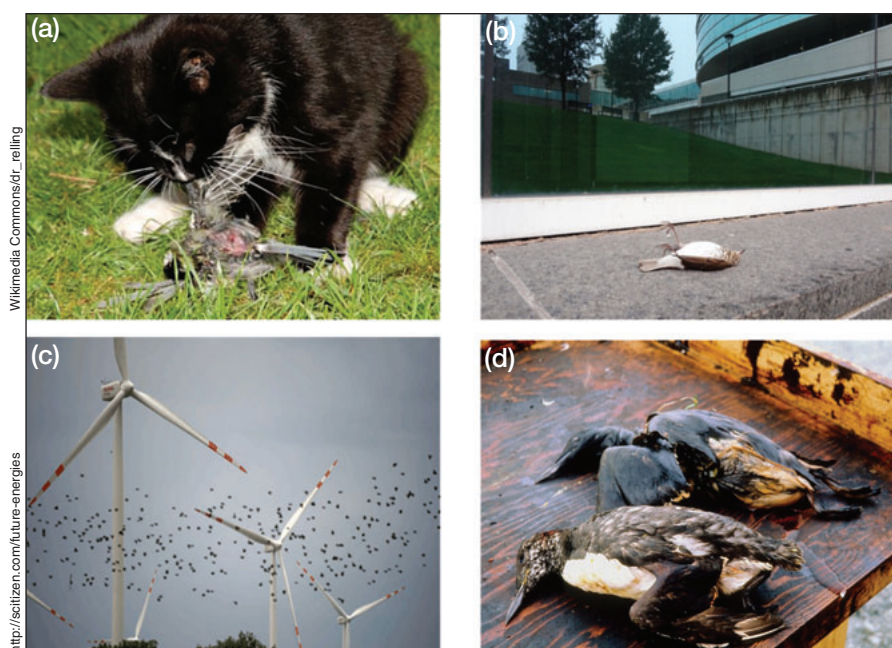
## ■ Limitations affecting quantification of mortality and population impacts

### *Sources of bias in syntheses of multiple studies*

Currently, there is no systematic and comprehensive data source for animal mortality in the US. Consequently, data-driven methods of mortality quantification require synthesis of multiple studies (eg Longcore *et al.* 2008, 2012; Arnold and Zink 2011). Data synthesis allows analysis of the regional and taxonomic variations associated with mortality estimates, but differences exist among studies in terms of temporal and spatial sampling schemes, and not all studies account for the probability of detecting bird carcasses. Failure to consider these differences may bias mortality estimates when scaling up from a sample of survey locations to the scales at which populations might be impacted.

Mortality studies vary in terms of spatial and temporal data collection. Study locations are often non-random, chosen for ease of sampling or because they are known to experience major mortality events. For example, many communication tower studies (reviewed by Longcore *et al.* 2008) documented mass mortality events (Figure 2) or were conducted at towers known to kill large numbers of birds. Duration of data collection is also variable; for instance, a review of mortality at 47 communication towers (Shire *et al.* 2000) included studies ranging in length from a single night to more than three decades. Short-duration studies typically occur during peak periods of migration and can therefore provide only a non-random snapshot of mortality and species composition. Excluding these studies from analyses may be necessary to ensure unbiased mortality estimates.

Quantification bias can also arise because the number of carcasses found is nearly always less than the true number of birds killed, and the rate of carcass detection is variable among loca-



**Figure 1.** Sources of direct human-caused mortality of birds include (a) predation by domestic cats, (b) collision with building windows, (c) collision with wind turbines, and (d) pollution, in this case by oil spill.

tions. Factors contributing to variable detectability include vegetation cover, carcass size and coloration, scavenger removal, and carcass decomposition. Analyses of factors affecting detection have been conducted for many mortality sources, including wind turbines (Smallwood 2007), agricultural poisoning (reviewed by Prosser *et al.* 2008), power lines (Ponce *et al.* 2010), and automobiles (Santos *et al.* 2011). Nonetheless, many studies only tally unadjusted carcass counts without correcting for imperfect detection.

Reducing the biases associated with synthesis of multiple datasets may be possible with statistical adjustments to existing data. For example, mortality counts can be weighted by study duration using monitoring effort, mortalities recorded, and mortalities recorded per unit effort. Number of species recorded has been proposed as a surrogate for mortalities per unit effort (Roberts *et al.* 2007; Szabo *et al.* 2010) because species richness generally increases with greater study duration and a higher number of observations before reaching an asymptote. However, this adjustment may be valid only when data do not span a geographic gradient of species richness that leads to sites in high-richness areas being strongly weighted regardless of effort (eg due to many species being recorded even with short study duration or little effort). For detection probability, if most studies do not correct for reduced detectability, raw carcass counts can be adjusted based on the results of other studies. For example, only one study has formally quantified detection bias associated with pet cats not bringing prey to their owners (Kays and DeWan 2004). An estimate of the number of birds killed by free-roaming house cats could be produced by adjusting the raw counts by the Kays and DeWan (2004) multiplier of 3.3 birds killed for every mortality observation. Because detection probability varies among locations, observers, and sampling periods, this type of blanket adjustment provides only an approximation of numbers of birds killed. If possible, it is better to adjust each dataset according to detection rates at unique sites.

### **Spatial-scale matching and regional analyses**

When synthesizing mortality studies to assess population impacts, the spatial scales of mortality and population data must be accurately matched, and regional population responses to such losses should be assessed. Whereas studies of avian mortality are typically conducted across a small area or at specific locations associated with man-made obstacles, population monitoring programs, such as the North American Breeding Bird Survey (BBS; Sauer *et al.* 2011), cover regional and/or continental scales. Spatial-scale mismatches between the two data types could obscure how mortality impacts populations. Furthermore, analyses that assess population responses only at coarse spatial scales do not account for the possibility that mortality could affect populations at the regional level.

A recent example illustrates accurate matching of scales for mortality and population data but incomplete regional



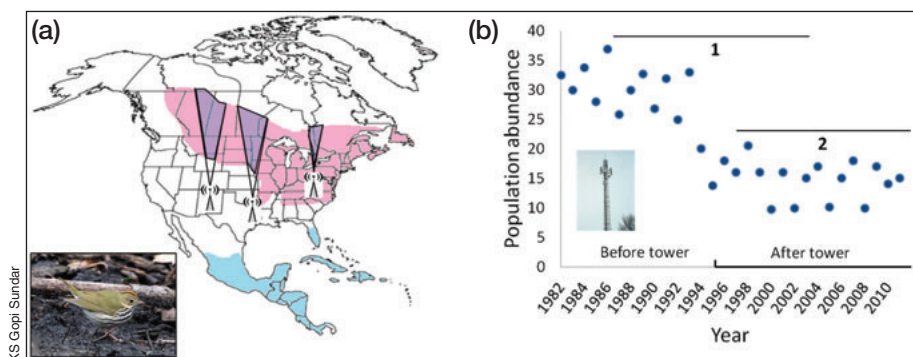
**Figure 2.** Songbirds killed in one night during fall migration at a communication tower in the northern Midwest US.

assessment of population trends. Arnold and Zink (2011) concluded that building and communication tower strikes have no effect on North American bird populations, based on a non-significant regression of BBS trends on estimates of species-specific collision vulnerability. The authors accurately matched the spatial scale of population data from which trends were estimated (east of the 100th meridian) with the scale of data used to estimate vulnerability (from the Great Plains eastward). However, except for an analysis of regional population trends at three window collision sites, the authors did not assess regional population responses to mortality. The authors justify this by stating that regional variation plus sampling error explained only 42% of trend variation. But given the uncertainty regarding the exact amount of trend variance attributable to regional variation, regional trends should be assessed for towers and a larger sample of window sites before conclusions can be extrapolated to the scale of North America.

For sources that affect migrating birds, including most man-made obstacles, it is difficult to match mortality data to population data that represent the migrants' affected population subset. This is because mortality counts during migration include both breeding residents and birds that are in transit to breeding grounds hundreds to thousands of kilometers away. Predicting how mortality sites are connected to breeding populations will improve inferences about impacts to migratory species. For each mortality source, researchers can consider a "region of catchment" – the portion of a species' breeding range that is represented by mortalities at a site, assuming straight north-to-south migration (Figure 3a). Regional subsets of population data can then be selected to match the catchment region, and survey data can be assessed relative to mortality from the sites of interest.

Identification of breeding locations for in-transit migrants and verification of the assumption regarding north-south migration can be supported by studies that document migratory connectivity (Marra *et al.* 2010). For example, geolocator and mark-recapture data indicate that gray catbirds (*Dumetella carolinensis*) breeding in the US mid-Atlantic region winter primarily in Florida and Cuba, while US Midwest populations winter in Central America (Ryder *et al.* 2011). Satellite transmitter data also





**Figure 3.** (a) Theoretical regions of catchment (shaded polygons) for ovenbirds (*Seiurus aurocapilla*; inset) during migration at three hypothetical communication towers, assuming straight north–south migration trajectories; pink and blue shading indicate ovenbird breeding and wintering ranges, respectively. (b) A possible pattern of population decline following construction of a communication tower; data from a before–after control–impact (BACI) study (line 1) allow detection of an initial population decline and subsequent stabilization at a lower level; data from after tower construction only (line 2) do not allow detection of this pattern.

indicate a migratory divide for double-crested cormorants (*Phalacrocorax auritus*) in the Great Lakes region, with western and eastern populations using Mississippi River and Atlantic migration routes, respectively (Guillaumet *et al.* 2011). These studies suggest that assessment of mortality impacts at sites along the western Gulf Coast should be based on population data from the Midwest (for catbirds) and from the western Great Lakes (for cormorants), rather than from each species' entire breeding range.

### Before–after control–impact designs

Before–after control–impact (BACI) designs use population and mortality data that are collected both before and after a threat is present, and at locations with and without the threat. BACI is ideal for testing multiple hypotheses about population responses to a threat, including sudden precipitous declines to lower population levels (Figure 3b) and steady linear or non-linear declines. LaDeau *et al.* (2007) used a BACI design to study bird abundance relative to West Nile virus (WNV) in North America. They used BBS data from the years before WNV emerged to predict post-emergence abundance and compared predicted and observed abundances. Species with observed post-WNV abundances lower than predicted were concluded to have declined due to WNV. The authors detected steady declines over several years for some species and sudden declines with subsequent stabilization at lower levels for others.

Except for newly emerging threats (eg wind turbines and diseases), most anthropogenic mortality sources pre-date reliable regional and continental sources of bird population data, and they comprise a growing collection of threats over time. In many cases, therefore, BACI designs cannot be implemented. Less powerful methods, based only on population data from the post-emergence period, can still be used to assess whether populations are affected

by a mortality source; however, these non-BACI designs do not allow for the full scope of hypotheses to be tested. For example, analysis of population trends relative to a mortality source that was present before population data were collected allows for assessment of whether populations experience continued declines after the threat's emergence (eg tower/window collision analysis of Arnold and Zink 2011), but not whether they underwent an initial sudden decline and then stabilized at a lower level, as observed for some species affected by WNV. The former hypothesis would be supported if per capita mortality risk is constant, while the latter would be supported if per

capita risk decreases with decreasing population size. These risk scenarios may not be equally likely for a given mortality source, and in some cases an argument could be made for testing one hypothesis over another. If both scenarios are possible, the absence of comprehensive BACI population data should not prevent evaluation of mortality impacts; however, in these cases, mortality estimates must be presented along with a clear statement of which hypotheses can and cannot be tested, given the data used.

### Advancing toward improved quantification and population inferences

#### Improving comparability and standardization of data

The most reliable information about mortality will be provided by analyzing data generated from well-designed sampling schemes. Rigorous study design improves comparability of mortality estimates and is essential for scaling up local estimates to spatial scales that are relevant for population analysis. In the future, more studies must sample appropriate temporal and spatial scales and account for rates of carcass detection. Focus on known mortality “hotspots” should be reduced, and data collection should be conducted at spatially random sites. Mortality studies at communication towers in Michigan illustrate how study sites can be randomly selected from a pool of locations (Gehring *et al.* 2009, 2011). For mortality sources that primarily affect migratory birds, studies should sample entire migratory periods. For sources that cause year-round mortality, sampling should extend across all seasons. Finally, studies should adopt accepted protocols to quantify carcass detection and scavenger removal rates, and developing such protocols should be a priority when few or none exist (eg for cat predation).

Even given sound local estimates of mortality generated with random sampling and detectability corrections, limitations still exist when estimates are scaled up from a sample

of locations to larger areas where population impacts may be occurring. With a large sample of discrete mortality sites, statistical models can be constructed that identify mortality correlates, and these correlates can be used to predict bird deaths across a broad area (Panel 2). Longcore *et al.* (2012) documented a significant relationship between tower height and bird mortality (corrected for sampling effort, search efficiency, and scavenging of carcasses) at 38 communication towers and then used the heights of > 80 000 towers to predict mortality across the US and Canada. This approach entails assumptions (eg that migrant density and tower height–mortality relationships are constant across regions), and upscaling exercises will be difficult for mortality sources that pose a spatially continuous threat (eg non-point poisoning). In all cases, the effect of simplifying assumptions on the accuracy and precision of mortality estimates should be explicitly considered.

Given that well-designed datasets are likely to provide better information, reduced bias in mortality estimates can be achieved by defining criteria that studies must meet to be included in analyses. For example, including only data generated from spatially and temporally rigorous sampling schemes reduces biases associated with non-random sampling. Similarly, bias can be reduced by only including studies that account for carcass detection rates. If there are numerous studies on a particular mortality source, definition of stringent inclusion criteria can still result in a large dataset. When less data are available, relaxation of inclusion criteria may be necessary to achieve a desired sample size. Further examples of inclusion criteria can be found for synthetic analyses of bird populations in relation to road effects (Benítez-López *et al.* 2010) and predators (Smith *et al.* 2011).

An alternative to defining inclusion criteria is to conduct sensitivity analyses to assess whether mortality estimates are influenced by including suboptimal data. This approach entails comparison of mortality estimates calculated using the full dataset and a subset of higher-quality studies (eg those that sample randomly and model detectability). If these estimates are similar, it can be concluded that data quality has little effect on the estimate and the full dataset can be used. If estimates differ, it may be necessary to use the estimate from the high-quality data. Another way to account for variability in sampling among studies is to conduct random effects modeling (ie treating different sites as random effects) when upscaling local mortality estimates to larger spatial scales. If there are not enough studies to define inclusion criteria, conduct sensitivity analyses, or use random effects modeling, mortality estimates may have limited applicability and should be presented with qualifications.

To improve the accuracy and precision of mortality assessments and inferences about population effects, we suggest that a standardized database of avian mortality be developed. We envision a national dead-bird reporting system and a clearinghouse for mortality data that allows online submission of mortality observations from sources

such as birdstrikes, pollution, disease, and cat predation (Panel 1). Although there may be some bias associated with self-selected data reporting (ie individuals must decide whether a mortality event is worth reporting), data submission via a standardized system will reduce problems of data comparability and minimize biases associated with combining data from multiple sources. In addition, a comprehensive mortality database would allow diseases that present a potential risk to human health to be tracked.

### **Accounting for variability and estimate uncertainty**

Synthesizing datasets allows for assessment of the variability and uncertainty associated with mortality estimates. Estimates that account for variability and uncertainty are of greater use to managers and policy makers than simple point estimates. Given extensive data, a threat can be evaluated by region, season, and species. Mortality variation can also be investigated relative to characteristics of the threat itself; for example, a meta-analysis of communication-tower mortality found that birdstrike frequency increased with increasing tower height and at towers with guy-wires and steady-burning lights (Longcore *et al.* 2008).

Estimates of anthropogenic mortality are influenced by numerous sources of variability, including the previously discussed variations in study design and data collection, as well as randomness in biological and anthropogenic processes. Most current analytical approaches either fail to estimate uncertainty associated with mortality estimates or address this superficially (eg by providing upper or lower estimate bounds that are not statistically defensible). Incomplete quantification of uncertainty can lead to inaccurate conclusions about population impacts, misleading interpretations about best and worst case scenarios, and, ultimately, to ineffective policy decisions. Uncertainty estimates should therefore be brought to bear on the decision-making process, so that decisions are made in the context of the full potential range of mortality caused by a particular threat.

Hierarchical statistical models provide an opportunity to incorporate multiple uncertainty sources into mortality estimates, and therefore into policy decisions. As discussed above, under a hierarchical modeling framework,

#### **Panel 1. Features of envisioned standardized database of avian mortality**

- Online submission of mortalities from birdstrikes with man-made structures, pollution, poisoning, disease, and cat predation
- Core data collected: number, species, geographic location, source (if known) of mortalities
- Additional data collected: observer effort, bird's age (to inform population models requiring age-specific parameters)
- Cataloging, analysis, and prediction of bird mortality, including mortality sources affecting human safety and bird populations
- User-friendly interface modeled after successful "live sighting" eBird database ([www.ebird.org](http://www.ebird.org)) facilitating data submission by professional and citizen scientists

## Panel 2. Hypothetical example of mortality analysis (for illustrative purposes only; such high levels of bird mortality have not been documented at wind turbines)

**Objective:** to quantify the mortality rates of the bay-breasted warbler (*Setophaga castanea*) caused by wind turbines in the Piedmont Bird Conservation Region (BCR) of the eastern US (Figure 4). The bay-breasted warbler, a long-distance migrant that passes through the Piedmont en route to breeding grounds in southern Canada, was previously identified as experiencing a communication tower collision rate much greater than that expected by chance (Arnold and Zink 2011), and is an Audubon Society “Watch List” species.

**Data availability:** assume there are 70 wind farms in the Piedmont comprising 530 wind turbines, that 30 wind farms have at least minimal bird mortality data (ie number and species of mortalities), and that datasets vary in sampling duration (2 months to 2 years) and in whether counts are corrected for detectability and scavenger removal.

**Inclusion criteria:** the following criteria can be defined to minimize estimate bias. Include:

- wind farms at which counts are corrected for rates of detection and scavenger removal;
- wind farms with data from  $\geq 5$  turbines;
- wind turbines at which sampling covered at least two entire migratory periods (eg spring and fall or two falls) with each period consisting of  $\geq 10$  sampling occasions (Longcore *et al.* 2012);
- from the remaining wind farms, a random sample of 10 farms that are spatially scattered throughout the Piedmont and random selection of five turbines from each farm

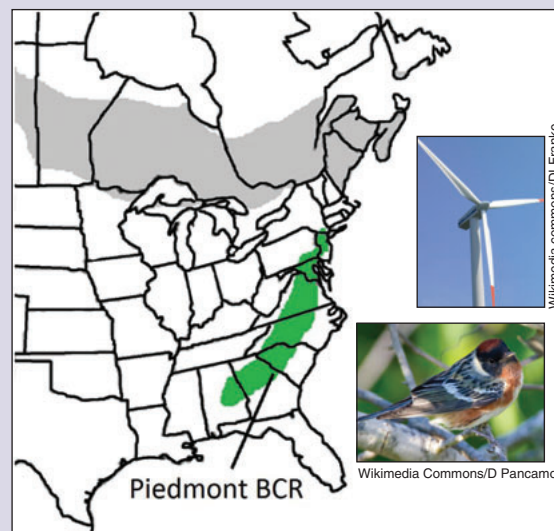
For the resultant set of 50 turbines, sampling protocols are identical within each wind farm, but different farms have varying levels of sampling effort within the above criteria.

**Statistical model:** suppose the resultant simulated dataset contains 1803 bay-breasted warbler mortalities (mean per tower = 36; range = 0–84) and the 50 turbines range in height from 54–125 m (mean = 86 m). Previous research indicates that height of communication towers influences avian mortality (Longcore *et al.* 2008; Gehring *et al.* 2011); therefore, turbine height might also be expected to influence mortality. To assess whether turbine height affects hypothetical bay-breasted warbler mortality, we defined a hierarchical model with simulated mortality from each turbine as the dependent variable and simulated turbine height as a fixed effect. To account for varying sampling effort among wind farms and non-independence of turbines within farms, we treated wind farm as a random effect. A full description of data simulation/analysis is described in WebPanel 1.

**Mortality estimate:** the modeled relationship between simulated tower height and mortality was strong ( $\beta \pm$  standard error =  $0.56 \pm 0.08$ ) and variable among wind farms. Using parameter estimates from the fitted mixed effects model, the hypothetical bay-breasted warbler mortality estimate across all 530 wind turbines in the Piedmont region was 15 584, with a 95% confidence interval of 14 993 and 16 174 mortalities.

### Considerations, limitations, and applications:

- This example is for one species but methods are adaptable for calculating total mortality of multiple species.
- Inclusion criteria will differ depending on species' life history. For a species that migrates through and breeds in the Piedmont, data should cover migration periods and a substantial part of the breeding season because mortality can occur during both periods. For year-round residents, data should cover all seasons.
- The same model structure could also be specified under a Bayesian framework; this approach requires additional specification of prior estimates (ie prior distributions) for all calculated parameters.
- The height–mortality relationship was pre-defined for illustrative purposes; such a strong and clear relationship may not exist in analyses of real data.
- Mortality estimates, including point estimates and the 95% confidence intervals, can be used to assess sustainability of hypothetical mortality among bay-breasted warbler populations using methods described in the text. Use of different mortality values can reflect different precaution levels.



**Figure 4.** Piedmont Bird Conservation Region (BCR, green shading) and eastern portion of bay-breasted warbler (*Setophaga castanea*) breeding range (gray shading).

study locations can be treated as random effects to account for differences between studies. For complex models that include many uncertainty sources, hierarchical Bayesian (HB) models may be useful (Link and Barker 2009). HB models allow uncertainty to be accounted for by modeling parameters as probability distributions and incorporating prior information. All uncertainty in the

data and prior information are propagated to a posterior (ie final) distribution that includes probabilities for all values of the parameter of interest. Credibility intervals from these distributions are useful for the decision process when decision makers wish to state a desired level of confidence about the magnitude of mortality (eg there is an X% chance that mortality is between Y and Z). A draw-



back of HB methods is that the complex models used to generate credibility intervals may not be easily understandable (Royle and Dorazio 2008). We recommend carefully balancing the pros and cons of using HB and traditional likelihood-based hierarchical models, and that HB models be presented in a transparent manner. We present a hypothetical example of a likelihood-based hierarchical model for mortality quantification in Panel 2.

### ***Incorporating mortality estimates into population models***

Interpreting mortality estimates in the context of population models can provide a more complete picture of population impacts than is possible by solely quantifying mortality as a percentage of estimated population sizes (Churcher and Lawton 1987; Baker *et al.* 2005). A study of cat predation in New Zealand (van Heezik *et al.* 2010) investigated mortality effects with population models. The authors of that paper quantified mortality using prey return surveys and estimated bird densities using point counts and detectability modeling. Mortality and density estimates were incorporated into models that included density dependence by assuming a population carrying capacity and included parameters for adult survival, female reproductive rate, juvenile survival to reproductive age, and demographic stochasticity. Models indicated unsustainable predation rates by cats, with local densities for most bird species predicted to reach zero after 50 or 100 years.

Runge *et al.* (2009) proposed a sophisticated and flexible approach for evaluating population effects resulting from incidental take of migratory birds; the framework is grounded in harvest theory and may be especially useful for modeling impacts of anthropogenic mortality. The prescribed take level (PTL) model consists of three parameters: population size ( $N$ ), maximum population growth rate ( $r_{max}$ ), and a user-specified parameter ( $F_o$ ), representing the desired level of population sustainability. This model is advantageous because it (1) can capture uncertainty by treating  $N$  and  $r_{max}$  as probability distributions; (2) allows precautions to be taken (eg by using a minimum population estimate); and (3) reflects the management goals of the decision maker in  $F_o$ . To apply the PTL model, Runge *et al.* (2009) used BBS data to estimate black vulture (*Coragyps atratus*) population size in Virginia. The population estimate and a literature-derived estimate of  $r_{max}$  were used to calculate that 3533 ( $F_o = 1$ ) or 7066 vultures per year ( $F_o = 2$ ) could be removed for nuisance control purposes with fair confidence that the population would remain viable. Although it assumes constant  $r_{max}$  and a simple model of logistic growth, conditions that may not always be met, and although more research is needed to incorporate stochasticity sources, the PTL model shows promise for the assessment of avian population dynamics relative to anthropogenic mortality.

Because the above approaches require knowledge of

many demographic parameters, they are likely to be most useful for well-studied species. The PTL model offers a simplified approach, but calculation of  $r_{max}$  still requires knowledge of several parameters. Among bird species for which the data are incomplete, it may be possible to estimate  $r_{max}$  using proxy parameters (generation time or adult survival and age at first breeding; Niel and Lebreton 2005), and these  $r_{max}$  values can be used in PTL models to estimate allowable incidental take levels (Dillingham and Fletcher 2011). However, the validity of these proxy methods has yet to be tested across a wide range of species.

### **■ Conclusions**

We have outlined a path for advancing the study of direct human-caused mortality of birds that includes standards for improving data comparability, hierarchical models for estimating uncertainty, and population models for assessing population impacts. Widespread implementation of these analytical methods will produce mortality estimates that are more accurate and inferences about population impacts that are more reliable. These improved outcomes will allow decision makers to more effectively develop and prioritize among policies that reduce avian mortality. Failure to adopt these analytical techniques will perpetuate mortality estimates that are fraught with limitations and viewed with skepticism by decision makers and the general public. Such skepticism could delay the development of policies that might otherwise slow population declines among affected species.

The large degree to which avian mortality is caused by direct anthropogenic threats means that the stakes are high. We therefore suggest that decision makers should consider taking a precautionary approach when basing policy development on scientific analyses of mortality. Decision makers should also consider what magnitude of mortality is deemed acceptable and at what point action to mitigate mortality is warranted. In theory, a reasonable criterion on which to base this decision is whether mortality results in a biologically important population decline. In practice, determining what constitutes biological importance is not straightforward, and predicting the annual increment of decline that leads to extinction is difficult (Reed and Blaustein 1997). Finally, researchers should consider quantifying the degree to which future population sizes may be suppressed by direct mortality sources. This approach, which assumes that a proportion of birds killed may have survived to produce additional recruits and that populations could therefore be larger in the absence of a mortality source, is analogous to the approach of Runge *et al.* (2006) that considers waterfowl breeding populations from the following spring in adaptive harvest management models. We believe that simultaneous consideration of numbers of birds lost and the suppression of populations represented by these losses can lead to an approach that seeks to reduce mortality whenever possible and results in a reduction of the burden of mortality experienced by avian populations. Together with

the analytical techniques outlined in this article, this conceptual approach will be important for bird conservation in the context of the increasing abundance of direct anthropogenic mortality sources on the North American landscape and the increasing threat of habitat loss and climate change.

## Acknowledgements

SRL was supported by a postdoctoral fellowship funded by the US Fish and Wildlife Service through the Smithsonian Conservation Biology Institute's Postdoctoral Fellowship program. We thank TW Arnold, DH Johnson, AD Rodewald, JA Royle, and MC Runge for comments that greatly improved the manuscript. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

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