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Direct Mortality of Birds from Anthropogenic Causes

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Abstract

Understanding and reversing the widespread population declines of birds require estimating the magnitude of all mortality sources. Numerous anthropogenic mortality sources directly kill birds. Cause-specific annual mortality in the United States varies from billions (cat predation) to hundreds of millions (building and automobile collisions), tens of millions (power line collisions), millions (power line electrocutions, communication tower collisions), and hundreds of thousands (wind turbine collisions). However, great uncertainty exists about the independent and cumulative impacts of this mortality on avian populations. To facilitate this understanding, additional research is needed to estimate mortality for individual bird species and affected populations, to sample mortality throughout the annual cycle to inform full life-cycle population models, and to develop models that clarify the degree to which multiple mortality sources are additive or compensatory. We review sources of direct anthropogenic mortality in relation to the fundamental ecological objective of disentangling how mortality sources affect animal populations.

INTRODUCTION

The novel human-driven changes that characterize the Anthropocene have increased the number of mortality sources that affect wildlife populations. Birds in particular are experiencing precipitous population declines across the globe as a result of multiple anthropogenic stressors (Sekercioglu et al. 2004, IUCN 2014). In the United States, 100 bird species and subspecies are listed as federally threatened or endangered (USFWS 2014). Without further conservation action, nearly 200 additional species will likely become candidates for listing (USFWS 2008). Species population declines and extinctions can lead to a breakdown of ecosystem processes and services (Wardle et al. 2011, Valiente-Banuet & Verdu 2013), can cost millions of dollars in recovery efforts (USFWS 2013a), and can have implications for human societies (Cardinale et al. 2012). It is therefore essential to disentangle how mortality threats, individually and cumulatively, affect bird populations.

Habitat loss, climate change, and other stressors indirectly cause animal mortality through one or more intermediate mechanisms. However, there exist several anthropogenic stressors that directly kill billions of birds each year (**Figure 1**). Most of these direct mortality sources—including collisions with vehicles and manmade structures, poisoning with toxins, and predation by free-ranging pets—affect hundreds of bird species (Calvert et al. 2013; Loss et al. 2013a,b, 2014a). These mortality sources can cause large die-offs (e.g., poisoning events in agricultural areas and collision events at tall, lighted structures; Longcore et al. 2012, Mineau & Whiteside 2013) or they can kill birds in millions to billions of individual events each year (e.g., free-ranging cats



Figure 1

Major sources of direct anthropogenic mortality include (clockwise from upper left): collisions with automobiles (Northern Cardinal, *Cardinalis cardinalis*, Washington, DC), collisions with building windows (Clay-colored Sparrow, *Spizella pallida*, Oklahoma), predation by domestic cats (Ovenbird, *Seiurus aurocapilla*, North America), collisions with communication towers (Hawfinch, *Coccothraustes coccothraustes*, Slovenia), collisions with wind turbines (White-tailed Eagle, *Haliaeetus albicilla*, Norway), and electrocution at power lines (Crow, *Corvus* spp., UK). Photos used with permission from: upper left and upper middle, Scott R. Loss; upper right, Creative Commons, A. Currie; lower left, Wikimedia Commons, T. Jančar; lower middle, Wikimedia Commons, J. Ferenc; and lower right, Creative Commons, N. Mykura.

and collisions at residential buildings; see Blancher 2013; Loss et al. 2013b, 2014a), resulting in mortality that far exceeds more visible die-offs.

When compared with indirect stressors, direct mortality sources are characterized by relative clarity of cause and effect. The study of direct anthropogenic mortality therefore has the potential to lead to mitigation measures that target the cause and substantially reduce bird mortality. Recent syntheses of the growing number of quantitative mortality studies have led to improved estimates of national bird mortality for the United States and Canada (Calvert et al. 2013; Loss et al. 2013a,b, 2014a–c) (all estimates appear in **Table 1**, and the top mortality sources are summarized in **Figure 2**). Research has also identified correlates of mortality rates (Longcore et al. 2012, Loss et al. 2013a) and disproportionately vulnerable bird species (Arnold & Zink 2011, Longcore et al. 2013, Loss et al. 2014a). However, relatively little is known about spatiotemporal variation in mortality and the abiotic, ecological, and anthropogenic (e.g., socioeconomic and behavioral) drivers of this variation. This information is critical for understanding avian population responses to mortality (Boyce et al. 1999, Jonzén et al. 2002). Another challenge to clarifying population responses to direct anthropogenic mortality is determining the degree to which mortality is compensatory or additive. With regard to compensatory mortality, at least some of the individuals killed would have died in the absence of the mortality source; more formally, density-dependent population processes compensate for the additional mortality. With regard to additive mortality, the individuals killed would not have otherwise died; more formally, mortality exceeds the compensation ability of density-dependent processes (Sinclair & Pech 1996, Peron 2013). We review the scientific literature on the direct anthropogenic mortality of birds, compare the best available estimates for different mortality sources, identify overarching research needs that must be addressed to understand population responses to mortality, and outline management approaches to reduce bird mortality.

APPROACHES TO STUDYING DIRECT ANTHROPOGENIC MORTALITY

Research on the direct anthropogenic mortality of birds generally falls into the following non-mutually exclusive categories: (a) studies that estimate local mortality rates and, in some cases, correlates of mortality; (b) population impact assessments, including both local and large-scale studies and both correlative and intensive demographic analyses; (c) national estimates of mortality based on extrapolation; and (d) systematic syntheses of data across numerous studies.

Studies that use periodic fatality monitoring to quantify variation in mortality rates at local scales comprise most of the research on direct anthropogenic mortality. Most local studies are in the peer-reviewed literature. However, a large proportion of studies on bird collisions with large buildings or wind turbines remain unpublished, are not peer-reviewed, and are not readily available to researchers and the public (Piorkowski et al. 2012, Machtans et al. 2013). Several studies have accounted for factors that contribute negative bias to mortality estimates, including scavenger removal of carcasses and imperfect surveyor detection of carcasses (e.g., for buildings, Hager et al. 2013; for vehicles, Santos et al. 2011; for power lines, Ponce et al. 2010). These biasing factors have been assessed in a relatively large proportion of studies of bird–wind turbine collisions (Smallwood 2013, Zimmerling et al. 2013). Although local mortality estimates form the basis for upscaling analyses, a relatively small proportion of local studies are conducted with the rigor needed for data to be used in regional and national data syntheses (reviewed by Loss et al. 2012, 2014b,c).

Several local-, regional-, and national-scale studies have assessed population-level impacts of direct mortality sources. At local scales, intensive population modeling—based on field collection of mortality data and locally collected or literature-derived demographic data—has indicated that

Table 1 Systematic, data-driven estimates of national bird mortality from direct anthropogenic stressors

Mortality source	Country	Estimate ^a			Estimate type	Source
		Central	Lower	Upper		
Cats (all)	Canada	204,000,000	105,000,000	348,000,000	Median, 95% CI	Blancher 2013
	United States	2,407,000,000	1,306,000,000	3,992,000,000	Median, 95% CI	Loss et al. 2013b
Cats (unowned, feral)	Canada	116,000,000	49,000,000	232,000,000	Median, 95% CI	Blancher 2013
	United States	1,652,000,000	803,000,000	2,955,000,000	Median, 95% CI	Loss et al. 2013b
Cats (owned, free-ranging)	Canada	80,000,000	27,000,000	186,000,000	Median, 95% CI	Blancher 2013
	United States	684,000,000	221,000,000	1,682,000,000	Median, 95% CI	Loss et al. 2013b
Buildings (all)	Canada	24,900,000	16,100,000	42,200,000	Mean, range	Machtans et al. 2013
	United States	599,000,000	365,000,000	988,000,000	Median, 95% CI	Loss et al. 2014a
Buildings (low-rises)	Canada	2,400,000	300,000	11,400,000	Mean, range	Machtans et al. 2013
	United States	339,000,000	136,000,000	715,000,000	Median, 95% CI	Loss et al. 2014a
Buildings (residences)	Canada	22,400,000	15,800,000	30,500,000	Mean, range	Machtans et al. 2013
	United States	253,000,000	159,000,000	378,000,000	Median, 95% CI	Loss et al. 2014a
Buildings (high-rises)	Canada	64,000	13,000	149,000	Mean, range	Machtans et al. 2013
	United States	508,000	104,000	1,600,000	Median, 95% CI	Loss et al. 2014a
Automobiles	Canada	13,810,906	8,914,341	18,707,470	Mean, 95% CI	Bishop & Brogan 2013
	United States	199,600,000	88,700,000	339,800,000	Median, 95% CI	Loss et al. 2014b
Power line collisions	Canada	25,600,000	10,100,000	41,200,000	Mean, 95% CI	Rioux et al. 2013
	United States	22,800,000	7,700,000	57,300,000	Median, 95% CI	Loss et al. 2014c
Communication towers	Canada	220,650	NA ^b	NA ^b	Mean	Longcore et al. 2012
	United States	6,581,945	NA ^b	NA ^b	Mean	Longcore et al. 2012
Power line electrocutions	Canada	481,399	160,836	801,962	Mean, range	Calvert et al. 2013
	United States	5,630,000	920,000	11,550,000	Median, 95% CI	Loss et al. 2014c
Wind turbines (all)	Canada	16,700	13,330	21,600	Mean, 95% CI	Zimmerling et al. 2013
	United States	573,093	467,097	679,089	Mean, 90% CI	Smallwood 2013
Wind turbines (monopole)	United States	234,000	140,000	328,000	Mean, 95% CI	Loss et al. 2013a
Agricultural pesticides	Canada	2,695,415	960,011	4,430,819	Mean, range	Calvert et al. 2013
Fisheries: marine gill nets	Canada	20,612	2,185	41,528	Mean, range	Ellis et al. 2013
Marine oil and gas activities	Canada	2,244	188	4,494	Median, range	Van Wilgenburg et al. 2013
Fisheries: marine longlines/trawls	Canada	1,999	494	4,058	Mean, range	Ellis et al. 2013

^aEstimates are for independent birds only (i.e., estimates of destroyed nests, eggs, and nestlings are excluded; see Calvert et al. 2013), and systematic, data-driven estimates that apply to only one or a few species are excluded.

^bNo range of uncertainty produced in original study.

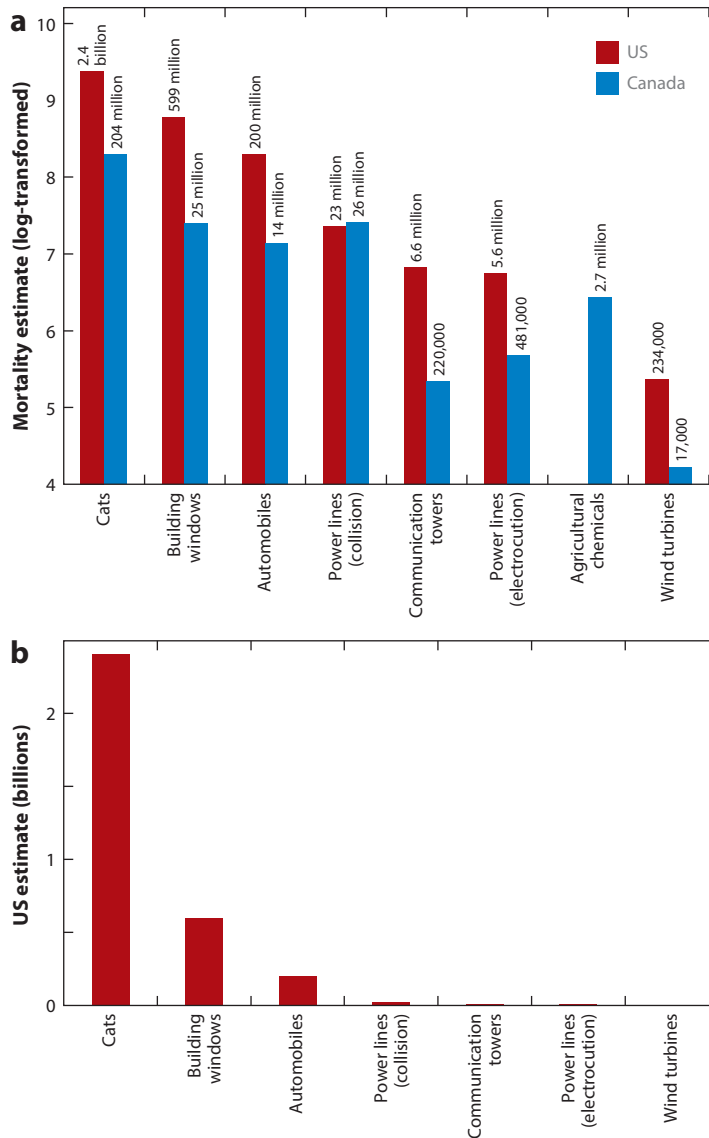


Figure 2

Comparison of major sources of direct anthropogenic bird mortality for the United States and Canada. Note the logarithmic scale for panel *a* and the absolute scale for panel *b* (estimate sources: Longcore et al. 2012, Calvert et al. 2013, Loss et al. 2013a,b, 2014a–c).

cat predation increases the probability of population extinction or decline for some bird species (van Heezik et al. 2010, Balogh et al. 2011). In addition, relatively low mortality rates for some sources can lead to significant population declines [e.g., vehicle collisions for owls in Portugal (Borda-de-Agua et al. 2014), wind turbine collisions for vultures in Spain (Carrete et al. 2009) and eagles in Norway (Dahl et al. 2012)].

At regional and national scales, population impacts have been indirectly assessed by dividing estimated mortality by estimated population abundance (Calvert et al. 2013, Longcore et al. 2013)

or by correlating population abundance or trends with exposure or vulnerability indices (Arnold & Zink 2011, Mineau & Whiteside 2013). Significant population declines in birds have been associated with agricultural pesticide use in the United States and the Netherlands (Mineau & Whiteside 2013, Hallmann et al. 2014). Such correlative analyses may be useful for highlighting the broad conservation importance of a mortality source, but they do not identify particular species and locations experiencing population-level impacts. Two quantitative approaches hold promise for clarifying how populations respond to direct sources of mortality: integrated population models (IPMs; Hoyle & Maunders 2004, Schaub et al. 2007) and potential biological removal (PBR) models (Wade 1998). Both approaches allow for uncertainty in model inputs to be propagated into estimates of population responses. IPMs allow the combination of multiple data types (e.g., census and mark-recapture data) to jointly estimate population responses (Rhodes et al. 2011). PBR models allow shortcuts for difficult-to-estimate parameters (e.g., substituting intrinsic population growth rate with generation time or adult survival and age of first reproduction; Niel & Lebreton 2005, Dillingham & Fletcher 2011). These shortcuts allow population analyses to be conducted for far more bird species than would be possible using more complex demographic models.

Data-driven estimates of mortality at regional, national, and continental scales are needed to understand impacts of mortality sources on bird populations and to provide an evidence base for policy and management decisions (Longcore & Smith 2013, Machtans & Thogmartin 2014). Large-scale estimates of direct anthropogenic bird mortality have traditionally been based on nonsystematic analyses and extrapolation of mortality rates from one or a few studies to entire regions or countries. Authors of these studies have been careful to qualify limitations of the estimates (Banks 1979, Klem 1990, Erickson et al. 2005); however, the figures are often cited in the scientific literature and popular media without the original qualifications. Recently, several quantitative, data-driven reviews have been conducted for the United States and Canada with the objectives of updating nonsystematic estimates, systematically identifying sources of estimate uncertainty, and assessing spatiotemporal and taxonomic patterns of mortality. We highlight major findings of these studies throughout this article. Although numerous studies of direct, anthropogenic bird mortality have been conducted throughout the world, we are not aware of systematic reviews of direct anthropogenic mortality outside of North America.

MAJOR SOURCES OF DIRECT ANTHROPOGENIC BIRD MORTALITY

Predation by Free-Ranging Domestic Cats

Predation by domestic cats (*Felis catus*) has caused the decline and extinction of numerous bird populations on small islands (Nogales et al. 2013). Impacts of free-ranging pet cats and unowned feral cats in mainland areas are less clear, despite evidence that predation impacts local population processes (van Heezik et al. 2010, Balogh et al. 2011). A recent quantitative review incorporating data from 17 studies generated the first data-driven national estimate of cat predation mortality (Loss et al. 2013b). The estimate of between 1.4 and 4.0 billion birds killed annually by cats in the United States was higher than previous speculative estimates and higher than estimates for any other source of direct anthropogenic mortality. A similar analysis for Canada, where the total population of free-ranging cats is estimated to be far lower than in the United States, estimated that between 100 and 350 million birds are killed annually (Blancher 2013). In both studies, the greatest sources of estimate uncertainty—which can be interpreted to indicate major research needs—included estimates of population size and predation rate for unowned feral cats. Both studies also highlighted the scarcity of information about which bird species are most frequently killed, indicating a pressing need for research into species-specific mortality. This information

will facilitate increased precision of mortality estimates and modeling of population impacts of cat predation. Recent research has begun to fill these information gaps, including studies that have (a) assessed fine-scale habitat selection of cats with satellite tracking technology (Recio et al. 2014); (b) documented cat predation events, including the species killed, using cat-mounted cameras (Loyd et al. 2013); and (c) identified bird species that face a high risk of extinction from predation (Bonnaud et al. 2012).

The primary management approach to reduce predation by cats is to prevent or limit their outdoor access. In theory, this approach should be easy to implement for pet cats, given that it is widely accepted and advocated for by conservation and wildlife management groups (e.g., the American Bird Conservancy, National Audubon Society) and most pet owner and animal welfare organizations (e.g., People for the Ethical Treatment of Animals, The Humane Society of the United States). Nonetheless, tens of millions of pet cats remain outdoors in the United States alone (Lepczyk et al. 2010, Loss et al. 2013b), largely as a result of pet ownership behaviors and, in many municipalities, ineffective programs to license pet cats.

Reducing predation by unowned feral cats necessitates reducing feral cat populations. Approaches for achieving this objective are highly controversial (Longcore et al. 2009, Lepczyk et al. 2010) and range from lethal control (by poisoning, lethal injection, and/or legalized hunting) to trap, neuter, and release (TNR) programs (McCarthy et al. 2012, Lohr & Lepczyk 2014). Reducing feral cat populations is further complicated by outdoor feral cat feeding stations, which subsidize abandoned, stray, or semiferal cat populations. These feeding stations range from informal and small scale (e.g., plates of cat food placed in parks or private yards) to large scale (e.g., the extensive feeding and sheltering operations in many US public parks). Central to identifying effective and acceptable solutions for reducing feral cat populations are scientifically sound and consistent regulation and the monitoring of TNR and cat feeding programs. Although TNR programs are widely implemented, little formalized monitoring of the success and impact of these programs exists. Claims that TNR programs consistently reduce cat population sizes are not based on carefully collected scientific evidence (Longcore et al. 2009). Furthermore, the numerous informal cat feeding operations that do not undertake sterilization and adoption programs are likely to escape scrutiny and potentially counteract any positive effects of more official management efforts. Although lethal control options are often portrayed as unacceptable to the public, a survey in Hawaii indicated that most residents favor lethal control over TNR programs (Lohr & Lepczyk 2014). Studies that assess the acceptability of alternative management strategies will lead to more effective and acceptable solutions for managing feral cat populations.

Collisions with Buildings

Klem (1990) called attention to the issue of bird collisions with buildings and with windows in particular. However, relatively few peer-reviewed studies of this topic have been conducted. Three recent quantitative reviews have generated national estimates of bird-building collision mortality and/or species vulnerability. Arnold & Zink (2011) used bird mortality data from three cities in eastern North America to identify supercolliders (i.e., species found dead disproportionate to their abundance). They found that most supercolliders are migratory species and that most urban-adapted species are not vulnerable to collisions. For Canada, Machtans et al. (2013) estimate that between 16 and 42 million birds are killed annually by building collisions. Based on 10 different data sources, they demonstrate that skyscrapers and other large buildings kill the most birds on a per building basis, but individual residences cumulatively kill the most birds. The most extensive review to date—based on 26 studies, including citizen science programs in 13 cities and more than 90,000 fatality records—estimates US building collision mortality at between 365 and 988 million

birds (Loss et al. 2014a). This study corroborates the finding of the Canadian study regarding the large amount of mortality at residences, supports the conclusion that the most vulnerable species are long-distance migrants, and identifies additional supercolliders, including several US Birds of Conservation Concern (USFWS 2008) [e.g., the Painted Bunting (*Passerina ciris*) and the Golden-winged Warbler (*Vermivora chrysoptera*)].

Loss et al. (2014a) summarize the need for further research to better understand the population impacts of bird-building collisions, including studies that (a) quantify collision rates for different building types throughout the year and in diverse geographic and ecological settings, (b) assess survey-related biases that cause underestimation of mortality (e.g., scavenger removal, imperfect carcass detection), and (c) determine best approaches for reducing mortality. Researchers have begun to account for the above biases, to identify correlates of collision rates (e.g., window area, vegetation cover; Klem et al. 2009, Hager et al. 2013), and to take a large-scale approach (Bayne et al. 2012, Hager & Cosentino 2014). Systematic testing of window collision mitigation measures remains limited. Nonetheless, approaches that are likely to reduce collision rates include turning off lights in large buildings during migration, using bird-friendly design elements (e.g., reducing the amount of reflective surface, limiting trapping mechanisms such as deep alcoves, and minimizing features that allow birds to see through to the interior or opposite side of a building), and developing and implementing deterrence techniques (e.g., reflective adhesives keyed to avian visual perception) (Sheppard 2011, Klem & Saenger 2013, Fernandez-Juricic 2015). Tests of window treatments have been based on two approaches: (a) tunnel tests, whereby birds are released at one end of a tunnel and choose between two lighted openings, each covered by a different glass treatment, and (b) field tests, whereby window frames are placed in the field to mimic building windows (Klem & Saenger 2013). Such tests have illustrated that collisions can be reduced by covering glass with UV-reflecting surfaces (with reflectance of 20–40% of the 300–400 nm wavelength), hanging objects in front of windows, or placing objects or patterns on the glass exterior (with 10-cm and 5-cm separation between vertical and horizontal objects, respectively) (Klem 1990, Klem & Saenger 2013).

Collisions with Communication Towers

Collisions with communication towers are a major source of mortality for birds, with several reports of single-night, single-tower casualty events of hundreds to thousands of individuals. Birds are attracted to lights on towers during nighttime migration periods, especially during foggy and otherwise inclement weather. Most fatalities occur when birds collide with towers or their guy wires (Shire et al. 2000). A continental-scale quantitative review estimated that towers kill 6.6 million birds annually in the United States and 220,000 birds in Canada (Longcore et al. 2012). As with buildings, the species most vulnerable to tower collisions are migratory songbirds (e.g., warblers, vireos, thrushes, and sparrows). By combining estimates of species-specific mortality with estimates of total North American population abundance, Longcore et al. (2013) conclude that 29 bird species could experience annual mortality from communication towers greater than 1% of their entire population. Such species include the Yellow Rail (*Coturnicops noveboracensis*), the Pied-billed Grebe (*Podilymbus podiceps*), and 19 warbler species.

Management recommendations for reducing bird collisions with communication towers are based on studies that compare bird mortality rates among towers with varying structural and lighting characteristics. Research on more than 20 towers in Michigan showed that replacing steady-burning lights with either red or white flashing lights can reduce mortality by 51–70% (Gehring et al. 2009) and that towers 116–146 m tall without guy wires cause 16 times less mortality than comparably sized guyed towers (Gehring et al. 2011). Furthermore, taller towers kill more

birds, likely as a combined result of their taller central tower structure and their longer total guy wire length. Gehring et al. (2011) found that guyed tall towers (those >305 m in height) cause roughly five times more mortality than medium-sized guyed towers and 70 times more mortality than medium-sized unguyed towers. A meta-analysis of 26 towers in the United States documented a strong positive relationship between tower height and mortality, even when controlling for the effect of lighting (Longcore et al. 2008). Additional approaches that could reduce bird mortality at communication towers include visually marking guy wires and placing new towers near existing ones rather than in undisturbed locations (USFWS 2013c).

Collisions with Wind Turbines

The impact of wind energy development on birds has become a major conservation focus (Kuvlesky et al. 2007). Numerous studies have assessed indirect impacts of wind facilities on bird abundance (Pearce-Higgins et al. 2012), breeding ecology (LeBeau et al. 2014, McNew et al. 2014), and habitat use in relation to the risks of constructing new facilities (Belaire et al. 2014, Loring et al. 2014). However, most studies of bird–wind turbine collisions are unpublished and not peer reviewed (but see, e.g., Johnson et al. 2002, Smallwood & Karas 2009).

Recent quantitative reviews have provided a large-scale perspective on bird–turbine collisions. A review of data from 71 wind facilities estimated annual US mortality—including mortality from old-generation lattice turbines and new-generation monopole turbines (see **Figure 3** for examples



Figure 3

A wind facility in California with several models of monopole wind turbines (those with solid towers) as well as lattice wind turbines (those with hollow, cage-like towers). Photo used with permission from Scott R. Loss.

of each turbine type)—at between 420,000 and 644,000 birds (Smallwood 2013). Another study based on data from 67 facilities estimated US mortality from monopole turbines at between 140,000 and 328,000 birds (Loss et al. 2013a). The latter study showed that, as for communication towers, mortality rates at monopole turbines increase with height. However, Loss et al. (2013a) and others have been unable to disentangle turbine height from other strongly correlated metrics of turbine size (e.g., rotor diameter). Nonetheless, increased mortality likely occurs because large turbines both reach into altitudes through which large numbers of birds fly and have rotors that affect a larger volume of airspace.

Turbine placement appears to be a major determinant of collision risk, with high mortality rates documented for broad regions (e.g., California and eastern mountains in the United States; Loss et al. 2013a) and particular areas within wind facilities (e.g., ridgelines at California wind facilities; Smallwood & Thelander 2008). Although evidence is currently insufficient to infer the population impacts of wind turbine collisions (Stewart et al. 2007), some raptor species may experience population declines from even a small amount of turbine collision mortality (Carrete et al. 2009, Dahl et al. 2012) or as a result of particular turbine arrays (Schaub 2012). Further research is needed to clarify the factors driving collision rates and to inform decisions about where to install wind farms and individual turbines. In many regions, systematic analyses are needed to assess the accuracy with which preconstruction surveys predict mortality. Most preconstruction studies currently assess entire wind facilities and consider birds as an undifferentiated group. However, an analysis of data from 20 wind facilities in Spain illustrated that preconstruction designations of mortality risk (based on visual observations of birds) were unrelated to total bird mortality following facility construction (Ferrer et al. 2012). The authors concluded that increased accuracy of preconstruction assessments requires a shift to focusing on individual proposed wind turbines and individual bird species.

Current estimates of bird mortality at wind facilities are low compared with many other mortality sources. However, rapid expansion of wind energy along with a projected increase in turbine size could lead to substantially greater mortality (Loss et al. 2013a). Current projections estimate as much as a fourfold increase in the amount of US wind energy generation by 2040 (USEIA 2014) and wind energy is expanding worldwide. Given this expected expansion, we argue that the current small estimates of mortality do not necessarily obviate the need for continued research, management, and policy related to wind energy. In many regions (including most of the United States), wind energy companies are not required to conduct postconstruction monitoring for mortality or to release mortality data to the public. Increased monitoring of proposed and existing facilities and increased public access to unpublished industry reports will facilitate future efforts to identify successful mortality reduction approaches as the wind industry expands.

Collisions with Vehicles

Among the numerous ecological impacts of roads (Forman & Alexander 1998), bird collision with vehicles is one of the most significant (Kociolek et al. 2011). Recent quantitative reviews have generated estimates of between 80 and 340 million birds killed annually by vehicle collisions in the United States (Loss et al. 2014b) and of roughly 13.8 million birds killed each breeding season in Canada (Bishop & Brogan 2013). Both of these studies highlight the need for increased research into surveyor detection and scavenger removal rates to increase the precision of future mortality assessments. The studies also concluded that little information is available to quantify spatiotemporal and taxonomic variation in collision rates. Meta-analyses of the indirect effects of roads have shown clear declines in local bird abundance near roads (Fahrig & Rytwinski 2009, Benitez-Lopez et al. 2010), but these responses may be at least partially driven by other road-related stressors, such as habitat loss and noise. Barn Owls (*Tyto alba*) are vulnerable to vehicle collisions,

and this species is likely experiencing collision-related population declines in some regions (Boves & Belthoff 2012, Borda-de-Agua et al. 2014). Strategies to reduce bird-vehicle collision rates are largely untested. Currently recommended measures to reduce mortality are based on documented correlates of collision rates (Bishop & Brogan 2013) and include erecting fences or other flight diverters, reducing speed limits in problem areas, and removing bird habitats near roadsides.

Collisions and Electrocutions at Power Lines

Bird mortality occurs at power lines as a result of collisions with wires and electrocution at both wires and poles. A recent systematic review estimated that between 8 and 57 million birds are killed annually by colliding with US power lines and that between 0.9 and 11.6 million birds are killed by electrocution (Loss et al. 2014c). This study concluded that not enough rigorous studies have been conducted to quantify spatiotemporal and taxonomic variation in mortality or to infer population-level impacts (see also Bevanger 1994, Lehman et al. 2007). Existing estimates of mortality at power lines may be low, because collision studies typically focus only on transmission lines (large, high-voltage lines) and electrocution studies focus only on distribution lines (small, low-voltage lines). Both types of mortality occur at both line types, however (APLIC 2006, Dwyer et al. 2014). For large-bodied species that fly weakly or are unable to rapidly maneuver in flight, power line collisions can represent a major mortality source with potential population-level impacts. A study in Norway estimated annual national mortality for three grouse species—the Capercaillie (*Tetrao urogallus*), Black Grouse (*Tetrao tetrix*), and Willow Ptarmigan (*Lagopus lagopus*)—at 20,000, 26,000, and 50,000, respectively (Bevanger 1995). These figures represent roughly 90%, 47%, and 9%, respectively, of the annual hunting harvest for the three species. A mark-recapture study in Switzerland estimated that one in four juvenile and one in seventeen adult White Storks (*Ciconia ciconia*) die each year from power line collisions (Schaub & Pradel 2004).

An extensive list of best practices has been developed for reducing mortality at new and existing power lines (APLIC 2006, 2012). Examples of electrocution reduction approaches include: (a) using low-conductivity (i.e., nonmetal) materials whenever possible, (b) capping energized parts, and (c) ensuring that distances between adjacent wires, between wires and other energized components, and between energized components and grounded hardware exceed the wrist-to-wrist and head-to-foot distance of at-risk bird species (APLIC 2006). A meta-analysis of 21 studies illustrated that marking wires with flight diverters can reduce collision mortality by as much as 78% (Barrientos et al. 2011). Additional collision reduction approaches that have been suggested but remain largely untested include: managing surrounding land to reduce the number of birds near power lines, using narrower line corridors, and assessing bird habitat use and migratory patterns before constructing power lines (APLIC 2006). For both collisions and electrocutions, retrofitting existing lines to meet suggested practices can reduce bird mortality (Janss & Ferrer 1999, Harness & Wilson 2001, Dwyer et al. 2014). However, the length of installed power lines that must be retrofitted to significantly reduce total mortality is uncertain and likely to be substantial.

Poisoning from Pesticides

Pesticides, including herbicides, insecticides, fungicides, and rodenticides, can directly cause bird mortality as a result of birds coming into contact with sprayed chemicals or consuming contaminated food material. Pesticides broadcast in high volumes and across large areas of agricultural land pose the greatest risk to bird populations. At least 113 pesticides directly cause bird mortality, and the use of pesticides correlates with declining bird populations in the Canadian prairies (Mineau 2005b) and US agricultural lands (Mineau & Whiteside 2013). The high-concentration use of

neonicotinoids—the fastest-growing class of insecticides used globally—has also recently been associated with population declines in insectivorous bird species in the Netherlands (Hallmann et al. 2014).

The difficulty of linking rates and locations of chemical applications with the presence and amount of bird poisoning mortality has largely prevented estimation of national bird mortality from this source. An exception is a quantitative review that estimated that between 1 and 4.4 million birds are killed annually by pesticides in Canada (Calvert et al. 2013). This estimate was based on a combination of pesticide toxicity data, the estimated proportion of cropland at risk of experiencing a poisoning event, and the number of birds estimated to be killed in a poisoning event. The study showed that exposure risk can be modeled precisely if pesticide use data are available. However, in most cases, little field-collected information exists to predict bird mortality following exposure.

The large amount of mortality estimated for Canada suggests that poisoning from agricultural chemicals is likely a top mortality source in countries with extensive cropland. One analysis suggested that between 17 and 91 million birds were killed by a single chemical—carbofuran, one of the most toxic chemicals to birds—during its peak period of use in the Midwestern US Corn Belt (Mineau 2005a). The use of this chemical has been banned in Canada and Europe, and nearly all uses have been banned in the United States. However, given the large number of pesticides that cause bird mortality, continued reduction and elimination of highly toxic chemicals (e.g., chlorpyrifos and neonicotinoids; Mineau & Whiteside 2006, Hallmann et al. 2014) and of the amount of cropland receiving broadcast pesticide applications are likely necessary to substantially reduce avian mortality from pesticide poisoning.

Other Sources of Direct Anthropogenic Mortality

Several other sources of direct anthropogenic bird mortality have not been studied sufficiently for systematic analyses to be conducted, including collision and burning at solar power plants (Kagan et al. 2014), burning at natural gas flares (CBC News 2013), entrapment and starvation in open-top PVC and metal pipes used for gates and mine markers (Hathcock & Fair 2014), and entrapment in heater treaters and dehydrators at oil and natural gas well sites (USFWS 2013b). Other mortality sources have comparatively speculative and/or very low estimates of mortality (e.g., drowning mortality at oil mining pits and other examples in **Table 1**). A lack of information about a mortality source or a low overall mortality estimate does not preclude the possibility that a mortality source is biologically significant for some species, locations, and/or time periods. We encourage further study of these mortality sources.

COMPARISONS AMONG MORTALITY SOURCES

The range of estimated bird mortality for different direct anthropogenic sources is enormous; however, overlapping uncertainty ranges among some estimates suggest that rankings should only be approximated to orders of magnitude. Data-driven estimates of annual US mortality vary from billions (cat predation) to hundreds of millions (building and automobile collisions), tens of millions (power line collisions), millions (power line electrocutions, communication tower collisions), and hundreds of thousands (wind turbine collisions) (**Table 1**). Strong agreement between analyses conducted for Canada and the United States exists for the ranking of mortality sources (**Figure 2**). Cat predation is overwhelmingly estimated as the top source of direct anthropogenic mortality in both countries, and the next three mortality sources are also similar (building, automobile, and power line collisions). Estimated mortality related to energy development (e.g., collisions with wind turbines and nest loss, poisoning, and collisions related to oil and gas exploration and development) is relatively low. However, avian mortality from these

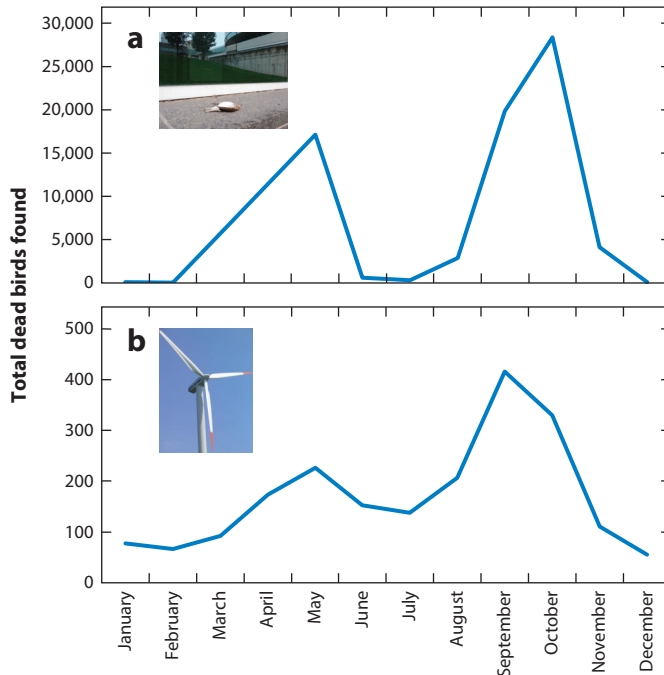


Figure 4

Seasonal mortality patterns for: (a) bird-building collisions (summarized across 90,767 records and 26 North American sites in Loss et al. 2014a) and (b) bird-wind turbine collisions (summarized across 2,045 records and 73 North American sites in Loss et al. 2013a). Numbers are raw counts that are not corrected for surveyor effort or other methodological differences among studies; nonetheless, seasonal patterns are robust across most study locations. Photo of Swainson's Thrush used with permission from Scott R. Loss; photo of wind turbine used with permission from Wikimedia Commons.

industrial sectors will likely increase with the ongoing development of wind, oil, natural gas, and solar resources (Ellis et al. 2013, Van Wilgenburg et al. 2013, USEIA 2014).

When collectively assessing multiple mortality sources, researchers face the same data limitations as they do for individual source estimates: Information is insufficient to derive a clear picture of spatiotemporal and taxonomic variation in cumulative mortality. The general patterns that emerge from quantitative and qualitative review of the current literature should be viewed as working hypotheses that require additional testing and confirmation. Perhaps the most evident pattern is that spring and fall migration periods are characterized by peak mortality for many migratory passerine species (e.g., thrushes, vireos, warblers, and sparrows) at tall, lighted structures (communication towers, buildings, and turbines at some wind facilities). Of more than 90,000 bird-building collision fatalities analyzed by Loss et al. (2014a), the vast majority occurred during spring and fall migration periods (**Figure 4a**), a pattern that is robust across most study locations. Patterns of mortality are similar, although less dramatic, for wind turbines (**Figure 4b**). This dampened seasonal pattern emerges because although some wind facilities have the highest mortality during migratory periods (e.g., for songbirds in eastern US mountains), others have relatively high mortality during breeding or wintering seasons [e.g., for Horned Larks (*Eremophila alpestris*) in summer (Young et al. 2007) and Western Meadowlarks (*Sturnus neglecta*) in winter in the western United States (Kerlinger et al. 2007)]. A relatively large cumulative amount of

mortality also occurs in summer, as a result of the increase in breeding season bird activity and abundance creating elevated risk from stressors such as pesticides and cats. Comparatively little mortality appears to occur during winter, with exceptions including the wind turbine examples above, owl-automobile collisions in northern latitudes (Bishop & Brogan 2013), and window collisions of songbirds at residences with bird feeders (Dunn 1993).

Because many sources of direct anthropogenic mortality are related to urban and suburban land development and industrial activities, spatial patterns of cumulative mortality are related to patterns of human activity and population density. A rough spatial extrapolation—based on allocation of mortality to different areas using estimated mortality for each stressor and the proportion of stressor activity occurring in each province—estimated that the vast majority of bird mortality in Canada occurs in urban areas (Calvert et al. 2013). However, when the three largest mortality sources (cats, buildings, and roads) are excluded, mortality was more evenly distributed across the country. These stressor–human population patterns are likely to be generalizable to other countries. Urban and suburban areas—with their large numbers of cats, buildings, and roads—are likely to have the greatest overall mortality. Mortality from wind turbines, communication towers, power lines, and energy extraction activities is likely to be more broadly dispersed across exurban and rural areas.

RESEARCH NEEDS

Several overarching research needs emerge from our previous reviews of direct anthropogenic mortality sources (Loss et al. 2013a,b, 2014a–c). These needs apply to two different categories of research: (a) field studies that assess local mortality rates and population impacts and (b) large-scale data syntheses that quantify overall mortality, spatiotemporal and taxonomic variation in mortality, and impacts of mortality across bird species' entire geographic ranges.

Research Needs for Local Field Studies

To facilitate minimally biased local estimates of mortality that contribute to large-scale estimates and population impact assessments, local field studies must: (a) conduct replicated, controlled, and a priori–designed research in addition to post hoc analysis of opportunistically collected data; (b) randomly select sampling sites in addition to sampling at locations already known to experience high rates of mortality; (c) search for, record, and present data for all bird species in addition to investigating focal species and species groups; (d) sample throughout the calendar year—in addition to focusing on periods thought to have the highest mortality rates—to provide season-specific data that can better inform full life-cycle population models; and (e) follow study design and data collection protocols that are standardized to other studies of the same mortality source and, when appropriate, other mortality sources. Relatively few existing local field studies meet all of these criteria, and standardized protocols for study design and data entry, management, and analysis do not exist for most mortality sources. These limitations significantly hamper efforts to quantify local mortality and its correlates, to identify effective approaches for mitigating mortality, and to synthesize data from local field studies into large-scale analyses.

Research Needs for Large-Scale Data Syntheses

Loss et al. (2012) discussed research needs that apply to large-scale data syntheses, but subsequent quantitative reviews have provided additional insights. To elucidate large-scale spatial variation in mortality rates and species vulnerability—and therefore to inform inferences about population

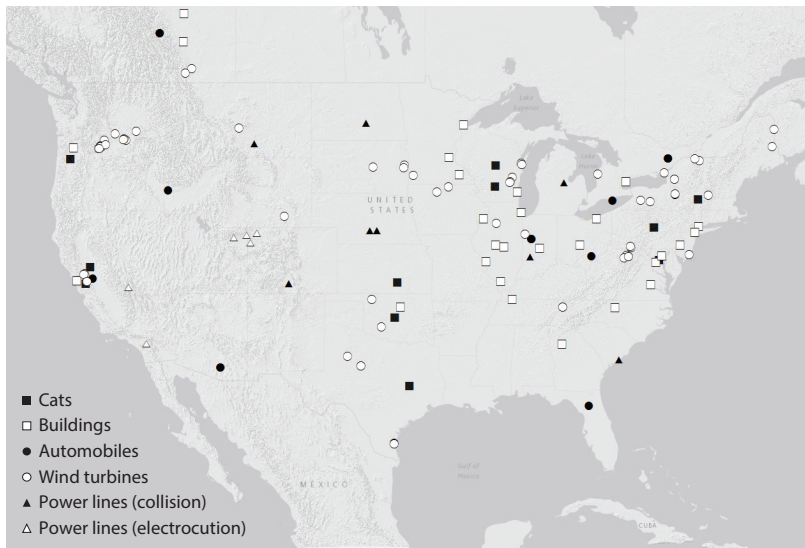


Figure 5

Locations of North American data sources for US estimates of direct anthropogenic bird mortality. All studies met inclusion criteria for a national mortality estimate, a summary of species killed, or both. Some studies met inclusion criteria but were eventually removed for being statistical outliers. For studies that covered large areas (e.g., states or provinces), points are placed in the center of the study area.

impacts across species' annual cycles—the collective body of mortality research must provide improved geographical and seasonal coverage. Globally, data on direct anthropogenic mortality are lacking from most regions outside of North America and Europe. Given rapidly increasing human populations in many understudied regions, direct anthropogenic bird mortality is likely to increase substantially. Even within North America, where the greatest amount of research has been conducted, most studies have occurred in the eastern third of the continent, and vast interior and western areas are virtually unstudied for many mortality sources (**Figure 5**). Additional research on mortality rate correlates (e.g., structural design features of buildings, road characteristics, behaviors of cat owners) is also needed to predict spatiotemporal variation in mortality and identify mortality reduction approaches.

Of central importance to both basic ecology and applied conservation is an improved understanding of how direct mortality sources impact population abundance. Studies addressing population responses to anthropogenic mortality have led to crucial theoretical developments and management applications, but most studies focus on a single mortality source—the purposeful harvest of animals for recreation and/or population management (Burnham & Anderson 1984, Pöysä 2004). Rigorous empirical methods have only begun to be developed for assessing effects for more than one stressor and for mortality sources other than harvest. As mentioned above, PBR models (Wade 1998) and IPMs (Hoyle & Mauner 2004) hold particular promise for assessing population abundance responses of multiple species experiencing mortality from multiple sources (Milner-Gulland & Akcakaya 2001, Weinbaum et al. 2013). The relative clarity of cause-and-effect relationships characteristic of direct anthropogenic mortality sources provides a fruitful arena for further developing modeling approaches that clarify links between mortality sources and population responses. Such models can also be used to assess the degree to which populations compensate for mortality. Rather than testing only for complete additivity versus complete

compensation—a common false dichotomy in the population ecology literature and policy and management discourse—analyses should consider the entire continuum of possible responses, including partial compensation, overcompensation, and superadditivity (Sinclair & Pech 1996, Abrams 2009, Peron 2013).

MANAGEMENT RECOMMENDATIONS

Several broad management recommendations apply across all mortality sources. First, we recommend that data-driven scientific evidence form the basis for decisions regarding the distribution of funding, direction of management attention, and development of specific mitigation guidelines. Ideally, this evidence should be weighed using a structured decision-making approach that allows adaptive management (Nichols & Williams 2006, Williams & Brown 2012), transparent identification of desired levels of precaution (Gregory & Long 2009), and evaluation of the potential success of management actions. Examples of criteria by which to judge the potential success of alternative actions include the expected magnitude of mortality reduction, feasibility, regulatory constraints, societal resistance, scale of the action, and estimated cost.

Second, we recommend further research into the magnitude, nature, and impacts of direct human-caused mortality. This research is necessary given the broad uncertainty ranges in national estimates of mortality and the uncertainty about population-level impacts. In particular, we highlight the need for small-scale analyses of population impacts that can inform local management measures. These small-scale studies should be complemented by large-scale studies that examine cumulative effects of multiple mortality sources on species population dynamics across the entire annual cycle (e.g., on breeding grounds and for migratory species during winter and migration).

Third, we recommend adherence to a precautionary approach to management (Foster et al. 2000, Gregory & Long 2009), whereby lack of evidence for a population decline owing to one or more mortality sources does not necessarily preclude implementation of mortality reduction measures. As reviewed by Longcore & Smith (2013), a precautionary approach is desirable because: (a) even substantial population declines can be difficult to observe with current monitoring resources and approaches; (b) impacts of a single stressor are difficult to identify, except in small areas with intensively monitored populations; and (c) direct mortality can also lead to indirect effects on habitats and ecosystem services that affect populations.

Finally, we recommend that ecologists, managers, and policymakers demonstrate leadership in addressing anthropogenic mortality of birds and other wildlife. National-scale estimates and comparisons of different mortality sources can and should provide broad strategic direction on where to invest management, policy, and research effort. Such strategic direction can be paired with focused research that incorporates both social and biological tools to identify and implement viable management solutions for the recovery of declining species.

SUMMARY POINTS

1. Several sources of direct anthropogenic mortality collectively affect a large proportion of Earth's bird species, and many species are affected by multiple direct mortality sources. Currently, large gaps exist in our knowledge about spatiotemporal variation in mortality, ecological and human-related factors driving variation, population-level impacts, and the best management approaches to reduce mortality.

2. The amount of bird mortality is highly variable across direct anthropogenic mortality sources, with annual mortality estimates for different threats ranging from thousands to billions of birds.
3. Much additional information is needed about most direct mortality sources, and a greater proportion of future studies must be randomized, replicated, and transparent to generate local and large-scale insights into the nature, magnitude, and impacts of mortality.
4. The study of direct anthropogenic mortality provides a promising avenue for the development and application of modeling approaches that clarify the individual and cumulative effects of mortality sources on bird populations. Such models will be transferable to other animal taxa and useful for evaluating increasingly important indirect threats, such as habitat loss and global climate change.
5. Given estimate uncertainty and the potential for biologically significant effects on some species at some locations, the information provided by gross mortality estimates alone should not be used to exonerate particular mortality sources from further research and regulation. Likewise, lack of evidence of an impact at the population level should not prevent widely accepted and effective actions to reduce mortality.
6. Decisions about specific mortality reduction measures and broad management directions and regulations should be based on scientifically rigorous data, a precautionary approach, structured and adaptive decision making, and a combination of intensive small-scale studies and broad-scale, data-derived estimates of mortality and population impacts.

DISCLOSURE STATEMENT

The authors are unaware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. The conclusions and opinions expressed in this review are those of the authors and do not necessarily reflect official positions or policy of the US Fish and Wildlife Service or Smithsonian Conservation Biology Institute.

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