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Avian mortality at communication towers in the United States and Canada: which species, how many, and where?

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ABSTRACT

Birds migrating to and from breeding grounds in the United States and Canada are killed by the millions in collisions with lighted towers and their guy wires. Avian mortality at towers is highly variable across species, and the importance to each population depends on its size and trajectory. Building on our previous estimate of avian mortality at communication towers, we calculated mortality by species and by regions. To do this, we constructed a database of mortality by species at towers from available records and calculated the mean proportion of each species killed at towers within aggregated Bird Conservation Regions. These proportions were combined with mortality estimates that we previously calculated for those regions. We then compared our estimated bird mortality rates to the estimated populations of these species in the United States and Canada. Neotropical migrants suffer the greatest mortality; 97.4% of birds killed are passerines, mostly warblers (Parulidae, 58.4%), vireos (Vireonidae, 13.4%), thrushes (Turdidae, 7.7%), and sparrows (Emberizidae, 5.8%). Thirteen birds of conservation concern in the United States or Canada suffer annual mortality of 1–9% of their estimated total population. Of these, estimated annual mortality is >2% for Yellow Rail (*Coturnicops noveboracensis*), Swainson's Warbler (*Limnothlypis swainsonii*), Pied-billed Grebe (*Podilymbus podiceps*), Bay-breasted Warbler (*Setophaga castanea*), Golden-winged Warbler (*Vermivora chrysoptera*), Worm-eating Warbler (*Helmitheros vermivorum*), Prairie Warbler (*Setophaga discolor*), and Ovenbird (*Seiurus aurocapilla*). Avian mortality from anthropogenic sources is almost always reported in the aggregate ("number of birds killed"), which cannot detect the species-level effects necessary to make conservation assessments. Our approach to per species estimates could be undertaken for other sources of chronic anthropogenic mortality.

1. Introduction

Avian mortality from collisions with human-made structures is an issue of ongoing conservation concern (Drewitt and Langston, 2008; Longcore et al., 2008, 2012; Manville, 2005, 2009). Mortality at communication towers has generated long-term studies at single sites (e.g., Crawford and Engstrom, 2001; Kemper, 1996), many incidental observations (Avery et al., 1980; Kerlinger, 2000; Trapp, 1998; Weir, 1976), and comparative studies across towers in several regions (Gehring et al., 2009; Johnston and Haines, 1957; Morris et al., 2003; Seets and Bohlen, 1977). The U.S. Fish and

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Wildlife Service (USFWS) has estimated avian mortality from communication towers at 4–5 million birds per year and released guidelines designed to minimize such mortality (U.S. Fish and Wildlife Service, 2000). We derived an updated estimate of 6.8 million birds per year with a tower height–mortality regression and the characteristics of >70,000 towers demonstrating that mortality increases predictably with tower height (Longcore et al., 2012). The USFWS has made recommendations to the Federal Communications Commission (FCC) on how to further reduce incidental take (Manville, 2007) and Environment Canada is currently assessing incidental mortality of migratory bird species at towers as part of a comprehensive effort to address all sources of incidental mortality.

Avian mortality at communication towers occurs most frequently when nocturnal migrants are attracted to tower lights. Birds that enter the zone of influence of lights then circle the towers and are at risk of death from exhaustion, collision with the tower and its guy wires, and collisions with each other (Gauthreaux and Belser, 2006). This usually occurs in inclement weather when other navigational cues are obscured and around the time of passage of cold fronts that drive birds down to altitudes where they are more likely to encounter towers and their lights (Avery et al., 1976).

Estimates of mortality for individual species are needed to assess biological significance of avian mortality at communication towers (Longcore et al., 2005, 2012). The term *biological significance* is not formally defined in the context of environmental impact assessment, but a logical definition might be that a biologically significant impact would adversely affect a species or its habitat and could be expected to affect the population growth or stability of the species and influence the population's long-term viability. Others have concluded that what constitutes a biologically significant population change is not easy to define (Reed and Blaustein, 1997). It may be important to understand the degree to which population growth is suppressed by a mortality source (Loss et al., 2012). Any change in a population has some biological consequence to other species, and therefore any population decline could be important and determining whether it is "significant" may be arbitrary. Biological significance in this context should not be confused with a statistically significant trend in a biological variable. Although statistical significance may influence the judgment about whether an impact is biologically significant, it is not a prerequisite.

To evaluate the biological significance of mortality, species or populations should be the unit of analysis in most instances. For example, barbed wire fences kill a relatively small proportion of birds compared with such hazards as windows and free-roaming cats, but barbed wire fences are a biologically significant source of mortality for Whooping Cranes (*Grus americana*), an endangered species (Allen and Ramirez, 1990). Higher taxonomic groups, such as families or even guilds that cut across taxonomic groups, may be the appropriate unit of analysis if something is known about the conservation status of the units as a whole. For example, oil pits (pits where oil producers dispose of waste fluids) kill an estimated 500,000–1,000,000 birds per year (Trail, 2006). This raw number can be interpreted with the knowledge that 162 species have been killed in oil pits, of which 63% were ground-feeding birds, including several species of conservation concern (Trail, 2006). Mortality at communication towers, up to this point, has been a conservation issue because the species predominantly killed at towers are Neotropical migratory songbirds, which are of conservation concern as a group. Beyond this general observation, however, only crude estimates have been made of the species composition of the millions of birds killed annually at communication towers (Arnold and Zink, 2011; Shire et al., 2000).

Arnold and Zink (2011) performed an analysis of the proportion of birds killed at towers and regressed the relative risk of collision against 30-year population trends calculated from Breeding Bird Survey data. They concluded from this regression that tower mortality had no discernible effect on population trajectories and claimed that their methods had statistical power to detect as little as a 4.1% contribution to the observed trends. Arnold and Zink (2011) have been criticized for their methods (Schaub et al., 2011) and for the scope of their inferences (Klem et al., 2012), and we have several additional concerns about their analysis. First, they used a flawed secondary data source (Shire et al., 2000) as their raw data for tower mortality. Shire et al. (2000) included a single list of the number of each species killed at towers, which they obtained by summing the results from 47 towers for which they found data. This unpublished report, however, did not exhaustively cover the literature available at the time, contained tabulation errors, and is now dated. It also presents raw sums, which are heavily influenced by the length of the various studies and do not account for regional variation in mortality. Arnold and Zink (2011) identified species that were killed more or less frequently than expected based on population sizes, but because they failed to obtain the primary sources, their mortality proportions contain the errors inherent in the Shire et al. (2000) report and do not account for regional variation or provide a mechanism to combine studies of different lengths in a way that keeps large datasets from overwhelming smaller ones. Failing to account for geographic variability leads to the unrealistic assumption that each tower in North America kills exactly the same proportion of each species of bird. Furthermore, we are unconvinced that impacts of collision mortality would be seen across hundreds of species in the manner assumed by Arnold and Zink (2011). Rather, it is much more likely that tower mortality represents one of an array of stressors affecting the population trajectories of a more limited number of species. In short, we doubt the ability of their method to definitively identify the cumulative impacts of avian mortality at towers and buildings, and make no such sweeping claim for the approach we develop here.

To better understand the effects of avian mortality at communication towers, we combine our previous geographically stratified estimate of total avian mortality at communication towers (Longcore et al., 2012) with estimates of the proportion of each bird species killed within different regions to develop geographically explicit tallies of avian mortality at communication towers by species. We chose geographically specific estimates because avian mortality and tower height vary regionally, and this additional information should be incorporated into any estimates. We then compare these per species mortality estimates with population estimates for these species to gauge the magnitude of this mortality source on a species-by-species basis.

2. Methods

An estimate of the number of each avian species killed at towers annually can be obtained by multiplying an estimate of total avian mortality for a region by the average proportion of each species found in kills at towers in that region. We previously developed an estimate of avian mortality at communication towers in the United States and Canada by Bird Conservation Region (BCR) (Longcore et al., 2012). This estimate was built from a regression relating tower height to annual mortality first developed by Longcore et al. (2005, 2008). The more recent estimate adjusted the raw annual mortality data obtained from existing studies for search efficiency, scavenging, and the sampling scheme (Longcore et al., 2012). The finding of lower avian mortality rates at towers without guy wires and without steady-burning lights (Gehring et al., 2009) was incorporated in these estimates. The corrected relationship between tower height and mortality was then applied to the towers

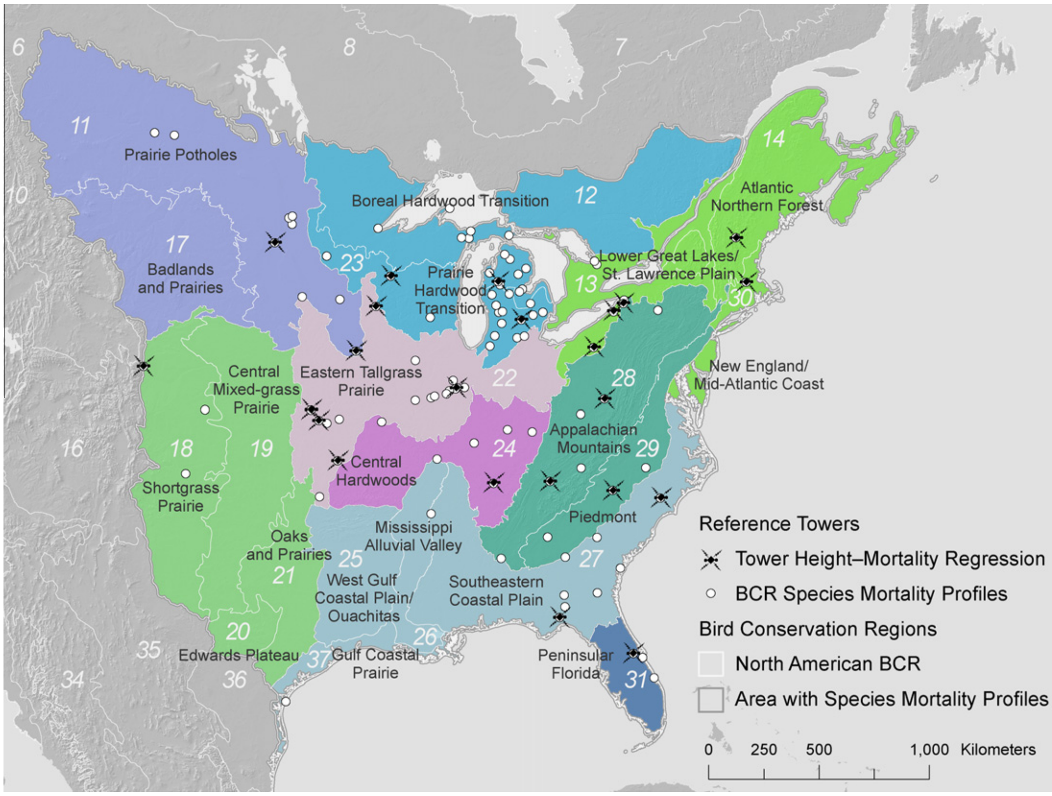

Fig. 1. Bird Conservation Regions in North America with locations of studies used to develop mortality profiles for aggregated regions indicated. Locations of towers used for height–mortality regression are also shown (see Longcore et al., 2012).

Table 1
Bird Conservation Regions and combinations thereof for which per species estimates of mortality were calculated with number of species and specimens in collections used to describe the regional mortality profile.

Bird Conservation Regions (References)	# Species	# Specimens	# Locations	Estimated Mortality[a]
Southeastern Coastal Plain, Mississippi Alluvial Valley, West Gulf Coastal Plain/Ouachitas, Gulf Coastal Prairie	192	64,554	5	1,988,456
Carter and Parnell (1976, 1978), Crawford (1976), Crawford and Engstrom (2001), James (1956), Johnston (1955, 1957), Johnston and Haines (1957), and Teulings (1972)				
Eastern Tallgrass Prairie	132	20,991	21	754,928
Boso (1965), Brewer and Ellis (1958), Cochran and Graber (1958), Gregory (1975), Kleen and Bush (1973), Mosman (1975), Norman (1987), Parmalee and Parmalee (1959), Parmalee and Thompson (1963), Petersen (1959), Robbins et al. (2000), Seets and Bohlen (1977), and Young and Robbins (2001)				
Appalachian Mountains, Piedmont	91	7123	8	711,900
Alsop and Wallace (1969), Bierly (1968, 1969), Ellis (1997), Herndon (1973), Herron (1997) Nicholson (1984), Norwood (1960), Remy (1974, 1975), Rosche (1971), Trott (1957), Turner and Davis (1980), and Welles (1978)				
Shortgrass Prairie, Central Mixed-grass Prairie, Edwards Plateau, Oaks and Prairies	65	611	3	1,128,718
Barkley et al. (1977), Nielsen and Wilson (2006), and Young (1993)				
Prairie Hardwood Transition, Boreal Hardwood Transition	137	128,796	48	452,887
Caldwell and Cuthbert (1963), Caldwell and Wallace (1966), Feehan (1963), Gehring et al. (2009), Green (1963), Kemper (1996), Kemper et al. (1966), Manuwal (1963), Sharp (1971), Strnad (1962, 1975), and Travis (2009)				
Central Hardwoods	113	16,162	7	346,796
Able (1966), Anonymous (1961), Barbour (1961), Bierly (1973), Elder and Hansen (1967), Ganier (1962), George (1963), Goodpasture (1974a,b, 1975, 1976, 1984, 1986, 1987), Laskey (1962, 1963, 1964, 1967, 1968, 1969a,b, 1971), Nehring and Bivens (1999), and Palmer-Ball and Rauth (1990)				
Peninsular Florida	98	15,261	4	341,774
Case et al. (1965), Kale (1971), and Taylor and Anderson (1973, 1974)				
Prairie Potholes, Badlands and Prairies	125	2520	8	382,315
Avery and Clement (1972), Avery et al. (1978), Ball et al. (1995), Houston and Houston (1975), Janssen (1963), Kemper (1964), Lahrman (1959, 1962, 1965), Nero (1961, 1962), Pierce (1969), and Young and Robbins (2001)				
New England/Mid-Atlantic Coast, Atlantic Northern Forest, Lower Great Lakes/St. Lawrence Plain	71	3375	3	285,405
Baird (1970, 1971), Sawyer (1961), and Westman (1967)				

[a] From Longcore et al. (2012).

in each BCR, extracted from digital geographic records for the United States and Canada. The resulting estimate, calculated by BCR, totaled 6.8 million birds per year (Longcore et al., 2012).

2.1. Development of per species mortality estimates

We used the approach described by Longcore et al. (2005) to assign the estimated total mortality to individual species. We conducted an extensive literature search to identify published reports of avian mortality at towers that included complete lists of birds killed. We located these studies from previous reviews (Avery et al., 1980; Kerlinger, 2000; Shire et al., 2000; Trapp, 1998; Weir, 1976) and directly from other researchers. We obtained copies of each report and transferred the number of each species recorded dead at each tower to a spreadsheet. For multiple studies of the same or adjacent towers we summed all observations of each species. We used raw numbers to develop the mortality proportions at each location and did not adjust for scavenging or search efficiency because >97% of the birds were passerines and such differences in detectability and scavenging would be unlikely to have a substantial effect. We also included all species lists without consideration of date of study to avail ourselves of the maximum number of specimens to develop regional profiles.

To develop profiles of birds killed within each BCR we calculated the proportion (P) of each bird species killed at each tower site within the region and took the mean of these proportions weighted by the number of species (S) documented at that location as follows

$$P_{\text{BCR}} = \frac{\sum_1^n P_i \times S_i}{\sum_1^n S_i} \tag{1}$$

where n is the number of studies in the BCR. We weighted by species number because species number increases rapidly with study length (measured in number of nights sampled) but quickly reaches an asymptote (unpublished results). By using species number as a weight, we emphasize those studies with greater sampling but do not overemphasize the exceptionally long studies or completely discard short studies that may have recorded a small but diverse sample of birds. Because we only use this weighting within geographic regions, it is not prone to the bias of geographic variations in species richness suggested by Loss et al. (2012).

We multiplied the proportion of each species killed within each BCR for which there were records by the estimated annual mortality derived from the tower data and associated regressions (Longcore et al., 2012) to produce estimates of the numbers of birds killed of each species within those BCRs.

When avian mortality had been recorded at towers in a BCR, but fewer than 3 studies were available to produce a species profile, we combined BCRs for analysis. We also included BCRs where avian mortality at towers had not been recorded but would be expected based on geography (e.g., mortality recorded in adjacent BCRs). Specifically, we combined Prairie Potholes ($n = 8$) and Badlands and Prairies ($n = 0$); Lower Great Lakes/St. Lawrence Plain ($n = 2$), New England/Mid-Atlantic Coast ($n = 2$), and Atlantic Northern Forest ($n = 0$); Southeastern Coastal Plain ($n = 4$), Mississippi Alluvial Valley ($n = 0$), West Gulf Coastal Plain/Ouachitas ($n = 0$), and Gulf Coastal Prairie ($n = 1$); Prairie Hardwood Transition ($n = 12$) and Boreal Hardwood Transition ($n = 1$); Appalachian Mountains ($n = 6$) and Piedmont ($n = 2$); and Shortgrass Prairie ($n = 3$), Central Mixed-grass Prairie ($n = 0$), Edwards Plateau ($n = 0$), and Oaks and Prairies ($n = 0$) (Fig. 1). For Gulf Coastal Prairie we included a record of mortality at streetlights (James, 1956) to develop the species profile because no searches of towers had been reported in the literature from this region. The streetlight kill illustrated the ability of lighted structures to kill migratory birds in this region by attracting and drawing birds down to near ground level. We did not assign the bird mortality to species in BCRs in the western United States and Canada where no studies or only single very short studies were found (Dickerman et al., 1998; Ginter and Desmond, 2004).

Ideally, we would have compared mortality to individual populations of species within BCRs. This is not possible because tower mortality occurs mostly during migration and mortality cannot be connected to local populations. We instead compared per species mortality estimates with estimates of total United States and Canada populations that are available for conservation planning purposes (Brown et al., 2001; Kushlan et al., 2002; North American Waterfowl Management Plan Committee, 2004; Rich et al., 2004). To assess the status of species killed at towers, we cross-referenced them with the most recent list of Birds of Conservation Concern issued by the U.S. Fish and Wildlife Service (2008), the United States and International Union for Conservation of Nature (IUCN) endangered species lists, and the Canadian Species at Risk schedules (http://www.sararegistry.gc.ca/). We regressed $\log_{10}$-transformed total estimated mortality for each species by $\log_{10}$-transformed population size to evaluate whether species are killed in proportion to their population size.

Table 2
Annual avian mortality at communication towers in central and eastern North America by Order, with subtotals by Family in Passeriformes. Only includes BCRs or merged BCRs for which mortality profiles could be developed from more than 1000 specimens.

Order	Number of species	Percent of total mortality (%)	Total mortality estimate
Passeriformes	146	97.35	5,125,205
Parulidae	39	58.42	3,075,659
Vireonidae	8	13.38	704,486
Turdidae	7	7.68	404,203
Emberizidae	24	5.78	304,343
Cardinalidae	9	3.19	167,942
Mimidae	4	2.89	151,898
Regulidae	2	2.03	105,847
Icteridae	10	1.64	86,301
Troglodytidae	6	1.30	68,635
Tyrannidae	9	0.55	29,040
Certhiidae	1	0.13	6586
Calcariidae	5	0.11	5939
Fringillidae	6	0.08	4184
Bombycillidae	1	0.05	2841
Sittidae	2	0.03	1583
Sturnidae	1	0.03	1559
Hirundinidae	6	0.02	1201
Passeridae	1	0.02	958
Corvidae	2	0.01	668
Laniidae	1	0.00	246
Motacillidae	1	0.00	65
Polioptilidae	1	0.00	22
Gruiformes	9	0.97	51,102
Cuculiformes	2	0.49	25,835
Piciformes	7	0.35	18,358
Columbiformes	3	0.32	16,685
Anseriformes	15	0.14	7369
Podicipediformes	4	0.11	6005
Ciconiiformes	14	0.10	5200
Charadriiformes	17	0.07	3623
Apodiformes	1	0.04	2027
Galliformes	5	0.03	1498
Caprimulgiformes	3	0.02	1015
Coraciiformes	1	0.00	226
Falconiformes	2	0.00	146
Strigiformes	2	0.00	65
Pelecaniformes	1	0.00	58
Gaviiformes	1	0.00	22
Procellariiformes	1	0.00	22

3. Results

3.1. Estimates of birds killed by species

We assigned mortality to species for the regions east of the Rocky Mountains with sufficient records to describe mortality profiles (Fig. 1). The studies contributing to these regional profiles documented 259,393 deaths of 239 species at 107 locations. After calculating per species estimates for a combined region of shortgrass prairie BCRs (Shortgrass Prairie, Central Mixed-grass Prairie, Edwards Plateau, Oaks and Prairies), we omitted these results from further reports because of the low number of specimens (611). In our previous analysis (Longcore et al., 2012), the remaining BCRs accounted for 5.26 million annual fatalities, or 77% of all mortality at towers in the United States and Canada. Our regional proportions allowed us to allocate these deaths to species, with 97.4% of estimated mortality consisting of passerines, with the greatest proportion being warblers (Parulidae, 58.4% of all mortality), vireos (Vireonidae, 13.4%), thrushes (Turdidae, 7.7%), and sparrows (Emberizidae, 5.8%) (Table 2). For the regions where we report mortality by species, 234 species were recorded from tower sites. Our database of studies included additional species killed at towers in the shortgrass prairie regions and elsewhere, including Swainson's Hawk (*Buteo swainsoni*) and Hammond's Flycatcher (*Empidonax hammondii*) in New Mexico (Ginter and Desmond, 2004), and Short-tailed Shearwater (*Puffinus tenuirostris*), Fork-tailed Storm-Petrel (*Oceanodroma furcata*), Black-legged Kittiwake (*Rissa tridactyla*), Short-eared Owl (*Asio flammeus*) (Dickerman et al., 1998), Spectacled Eider (*Somateria fischeri*), and Steller's Eider (*Polysticta stelleri*) (E. Lance, U.S. Fish and Wildlife Service, pers. comm.) in Alaska.

3.2. Comparison of per species tower mortality to population size

Avian mortality at towers was estimated to be ⩾1% of total population per year for 29 species (Table 3). Annual mortality was estimated to exceed 0.5% of population size for an additional 15 species. Fifty-four species identified as Birds of Conservation Concern (U.S. Fish and Wildlife Service, 2008), 1 federally endangered species, and 1 IUCN endangered species have been killed at towers (Tables 3 and 4). Thirteen of the 20 bird species killed most frequently by percentage of population are identified as either Birds of Conservation Concern or endangered.

Warblers (Parulidae) are 15 of the 20 species most frequently killed and 12 of the 20 species with highest proportions killed. Some species from other groups show high mortality as a proportion of population size. For example, 9.0% of the population of Yellow Rails and 5.6% of Pied-billed Grebes are estimated to be killed at towers each year.

Regional mortality profiles do show marked differences, which are evident in the ranking of species killed in each region (Table 5). This provides evidence in support of a regional approach to estimate mortality. The correlation between population size and tower mortality is significant but has low explanatory value (regression of $\log_{10}$ transformed variables; coefficient = 0.56, 95% CI = 0.40–0.72; $r^2 = 0.17$; $F_{1,224} = 44.37$, $p < 0.001$).

4. Discussion

Many bird species are killed at towers disproportionate to their abundance. Tower mortality is, therefore, not a random factor affecting all migrating birds. Mayfield (1967) argued that mortality at towers did not affect bird populations in part because birds are

Table 3
Per species avian annual mortality at communication towers in central and eastern North America, for species with >1% annual mortality from communication towers. Older names or lumped species groups are used to accommodate taxonomic changes. Status: BCC Birds of Conservation Concern in United States. SARA1 Endangered under Canada's Species at Risk Act, SARA2 Threatened, and SARA3 Special Concern.

Species	Family	North Am. population estimate	Est. annual mortality	Percent of population (%)	Status
Yellow Rail *Coturnicops noveboracensis*	Rallidae	25,000[b]	2245	9.0	BCC/SARA3
Swainson's Warbler *Limnothlypis swainsonii*	Parulidae	84,000[a]	7473	8.9	BCC
Pied-billed Grebe *Podilymbus podiceps*	Podicipedidae	100,000[b]	5589	5.6	BCC
Bay-breasted Warbler *Setophaga castanea*	Parulidae	3,000,000[a]	165,257	5.5	BCC
Black-throated Blue Warbler *Setophaga caerulescens*	Parulidae	2,000,000[a]	98,578	4.9	
Golden-winged Warbler *Vermivora chrysoptera*	Parulidae	210,000[a]	5276	2.5	BCC/SARA2
Kentucky Warbler *Geothlypis formosa*	Parulidae	1,100,000[a]	27,441	2.5	
Worm-eating Warbler *Helmitheros vermivorum*	Parulidae	700,000[a]	16,153	2.3	BCC
Prairie Warbler *Setophaga discolor*	Parulidae	1,400,000[a]	30,401	2.2	BCC
Ovenbird *Seiurus aurocapilla*	Parulidae	24,000,000[a]	498,714	2.1	
Scarlet Tanager *Piranga olivacea*	Cardinalidae	2,200,000[a]	35,270	1.6	
Henslow's Sparrow *Ammodramus henslowii*	Emberizidae	80,000[a]	1261	1.6	BCC/SARA1
Canada Warbler *Cardellina canadensis*	Parulidae	1,400,000[a]	20,622	1.5	BCC/SARA2
Gray Catbird *Dumetella carolinensis*	Mimidae	10,000,000[a]	139,050	1.4	
Seaside Sparrow *Ammodramus maritimus*	Emberizidae	110,000[a]	1513	1.4	BCC
Louisiana Waterthrush *Parkesia motacilla*	Parulidae	260,000[a]	3572	1.4	BCC/SARA3
Yellow-throated Vireo *Vireo flavifrons*	Vireonidae	1,400,000[a]	17,402	1.2	
Common Yellowthroat *Geothlypis trichas*	Parulidae	32,000,000[a]	386,484	1.2	
Connecticut Warbler *Oporornis agilis*	Parulidae	1,200,000[a]	14,324	1.2	
Trumpeter Swan *Cygnus buccinator*	Anatidae	23,647[c]	280	1.2	
Chestnut-sided Warbler *Setophaga pensylvanica*	Parulidae	9,400,000[a]	108,634	1.2	
Black-and-white Warbler *Mniotilta varia*	Parulidae	14,000,000[a]	149,485	1.1	
Hooded Warbler *Setophaga citrina*	Parulidae	4,000,000[a]	41,551	1.0	
Blackburnian Warbler Setophaga fusca	Parulidae	5,900,000[a]	60,487	1.0	
Blue-winged Warbler *Vermivora cyanoptera*	Parulidae	390,000[a]	3852	1.0	BCC
Prothonotary Warbler *Protonotaria citrea*	Parulidae	1,800,000[a]	17,645	1.0	BCC/SARA1
Philadelphia Vireo *Vireo philadelphicus*	Vireonidae	4,000,000[a]	38,431	1.0	
Cape May Warbler *Setophaga tigrina*	Parulidae	3,000,000[a]	28,731	1.0	

[a] Rich et al. (2004).
[b] Kushlan et al. (2002).
[c] North American Waterfowl Management Plan Committee (2004).

Table 4
Sensitive species killed at communication towers with estimated annual mortality <1% of estimated population size in decreasing order (except King Rail, which has no population estimate). Status: E listed Endangered by United States or International Union for Conservation of Nature, BCC Birds of Conservation Concern in United States. SARA1 Endangered under Canada's Species at Risk Act, SARA2 Threatened, and SARA3 Special Concern.

Blue-winged Warbler *Vermivora cyanoptera*	BCC	Field Sparrow *Spizella pusilla*	BCC
Prothonotary Warbler *Protonotaria citrea*	BCC/SARA1	American Bittern *Botaurus lentiginosus*	BCC
Northern Parula *Setophaga americana*	BCC	Rusty Blackbird *Euphagus carolinus*	BCC
Black-capped Petrel *Pterodroma hasitata*	E	Song Sparrow *Melospiza melodia*	BCC
Cerulean Warbler *Setophaga cerulea*	BCC/SARA3	Marsh Hawk (Northern Harrier) *Circus cyaneus*	BCC
Least Bittern *Ixobrychus exilis*	SARA2	Painted Bunting *Passerina ciris*	BCC
Blackpoll Warbler *Setophaga striata*	BCC	Red-headed Woodpecker *Melanerpes erythrocephalus*	SARA2
Bachman's Sparrow *Peucaea aestivalis*	BCC	Solitary Sandpiper *Tringa solitaria*	BCC
Black-throated Green Warbler *Setophaga virens*	BCC	Little Blue Heron *Egretta caerulea*	BCC
Bobolink *Dolichonyx oryzivorus*	BCC	McCown's Longspur *Rhynchophanes mccownii*	BCC/SARA3
Black Rail *Laterallus jamaicensis*	BCC	Chimney Swift *Chaetura pelagica*	SARA2
Sharp-tailed Sparrow (Nelson's & Saltmarsh) *Ammodramus nelsoni, Ammodramus caudacutus*	BCC	White Ibis *Eudocimus albus*	BCC
Yellow-billed Cuckoo *Coccyzus americanus*	BCC	Upland Sandpiper *Bartramia longicauda*	BCC
Marsh Wren *Cistothorus palustris*	BCC	Horned Grebe *Podiceps auritus*	BCC
Yellow-breasted Chat *Icteria virens*	SARA3	Common Tern *Sterna hirundo*	BCC
Le Conte's Sparrow *Ammodramus leconteii*	BCC	Loggerhead Shrike *Lanius ludovicianus*	BCC/SARA1
Sedge Wren *Cistothorus platensis*	BCC	Common Nighthawk *Chordeiles minor*	SARA2
Red-cockaded Woodpecker *Picoides borealis*	E	Chestnut-collared Longspur *Calcarius ornatus*	BCC
Black-whiskered Vireo *Vireo altiloquus*	BCC	Eared Grebe *Podiceps nigricollis*	BCC
Grasshopper Sparrow *Ammodramus savannarum*	BCC	Sage Thrasher *Oreoscoptes montanus*	BCC
Western Grebe *Aechmophorus occidentalis*	BCC	Black-throated Gray Warbler *Setophaga nigrescens*	BCC
Yellow Warbler *Setophaga petechia*	BCC	Lark Bunting *Calamospiza melanocorys*	BCC
Acadian Flycatcher *Empidonax virescens*	BCC/SARA1	Northern Bobwhite *Colinus virginianus*	SARA1
Harris's Sparrow *Zonotrichia querula*	BCC	Semipalmated Sandpiper *Calidris pusilla*	BCC
Bell's Vireo *Vireo bellii*	BCC	American Pipit *Anthus rubescens*	SARA2
Savannah Sparrow *Passerculus sandwichensis*	SARA3	Olive-sided Flycatcher *Contopus cooperi*	SARA2
Dickcissel *Spiza americana*	BCC	King Rail *Rallus elegans*	SARA1

killed at towers in proportion to their abundance. More recently Arnold and Zink (2011) claimed that population size explained almost 43% of variation in tower collision mortality. Our results show that some species experience mortality far out of proportion with their population size (Fig. 2), as was also shown by Graber (1968), and that population size only explains 18% of variation in tower mortality. Our divergence from Arnold and Zink's (2011) results is most likely attributable to methodological differences in developing species proportions. They did not account for regional variation in mortality or differentially weight the contribution of different tower studies, but rather simply pooled all mortalities at all towers at all locations to develop the proportions of birds killed.

Our estimates indicate that some species of birds experience mortality from towers up to several percent of their total population each year. Neotropical migrants are most affected by collisions with communication towers. For these species, the migratory period has been suspected to be "the critical period contributing to long-term declines in some species" (Hutto, 2000). Sillett and Holmes (2002) presented a long-term study of Black-throated Blue Warbler, one of many species killed at communications towers (our estimate is ~55,000 per year). They found that survival of individuals was high during the summer (0.99 ± 0.01) and winter (0.93 ± 0.05), while survival during both spring and fall migration was only 0.67–0.73. Their study was the first quantification of migration mortality for a Neotropical migrant, and the results reinforced concerns that risks encountered during migration can contribute to species declines. Sillett and Holmes (2002) concluded that both habitat quality before migration as well as conditions during migration, including the number of communication towers encountered along the migratory route, affect mortality.

For short-lived species where a large proportion of individuals may only expect to have a single breeding season, spring mortality is biologically far more important and much less likely to be compensatory. Parulids can have annual mortality of 0.5–0.6 (Sillett and Holmes, 2002) and collectively have the second to shortest maximum lifespan (~6 years maximum) of all passerine families (Wasser and Sherman, 2010). Although tower mortality is typically higher in the fall (both because of the presence of juvenile birds and the higher probability of weather patterns conducive to kills), it is estimated that 25% of mortality still occurs in the spring (Crawford and Engstrom, 2001). Whatever the split between spring and fall, a loss of 1–9% of the total population of a species each year to tower mortality may indeed influence population trajectories, especially for species already in decline (Robbins et al., 1989).

4.1. Uncertainty

Estimates of regional species profiles that were documented as part of long-term records from multiple sites are more reliable than those from shorter records encompassing fewer locations, but it is not possible to provide confidence estimates for our quantification of these estimates. Some regions have not reached asymptotes in species accumulation; the addition of new tower mortality locations and further data would result in spreading the calculated mortality for those regions across more species, potentially changing the apparent effect on those species identified here. It is for this reason that we have not reported the results for the shortgrass prairie regions, which had fewer than 1000 specimens available from towers (Table 1).

The accuracy of the total population estimates also influences the per species assessments. The method of calculating these estimates from breeding bird surveys (Rosenberg and Blancher, 2005) was well received, but has acknowledged limitations (Thogmartin et al., 2006). These population estimates have associated measures of accuracy and precision. For the 20 species ranked as highest annual percent mortality in our analysis, nearly all estimates of accuracy for landbirds are described as either "likely to be well within correct order of magnitude, often within 50% of true number" or "in correct order of magnitude" (Rich et al., 2004). Obviously, higher or lower estimates by an order of magnitude could increase or decrease the estimated population impact dramatically. For example, incorporating a 50% range around the population

Table 5
The ten species of birds killed most at communication towers in each region, as calculated by weighted averages of proportions killed at each location (see 2. Methods).

Overall rank and species	Prairie Potholes, Badlands and Prairies	Southeastern Coastal Plain and others	Central Hardwoods	Eastern Tallgrass Prairie	Prairie Hardwood Transition, Boreal Hardwood Transition	Appalachian Mountains, Piedmont	Peninsular Florida	New England/ Mid-Atlantic Coast and others
1 Red-eyed Vireo	1	1	3	2	3	1		4
2 Ovenbird	2	3	1	1	1	4	2	1
3 Common Yellowthroat	6	2	2	7		6	1	5
4 Tennessee Warbler			4	4	5	5		
5 Swainson's Thrush	7		8	10	2	3		7
6 American Redstart		5			9	10	5	9
7 Magnolia Warbler		6	5	6	7	7		10
8 Bay-breasted Warbler			7	8	8	2		6
9 Black-and-white Warbler		8	10		10		6	
10 Yellow-rumped Warbler		4		5				
11 Gray Catbird	8	9	6	9		9		
12 Blackpoll Warbler					4		4	3
13 Chestnut-sided Warbler		10	9					8
14 Palm Warbler		7					8	
15 Black-throated Blue Warbler							3	
16 Nashville Warbler				3				
17 Ruby-crowned Kinglet								2
18 Northern Waterthrush							10	
20 Northern Parula							7	
21 Gray-cheeked Thrush					6			
25 Wood Thrush						8		
33 Yellow Warbler	3							
39 Dark-eyed Junco	5							
40 Cape May Warbler							9	
42 Sora	10							
44 Lincoln's Sparrow	9							
55 American Tree Sparrow	4							

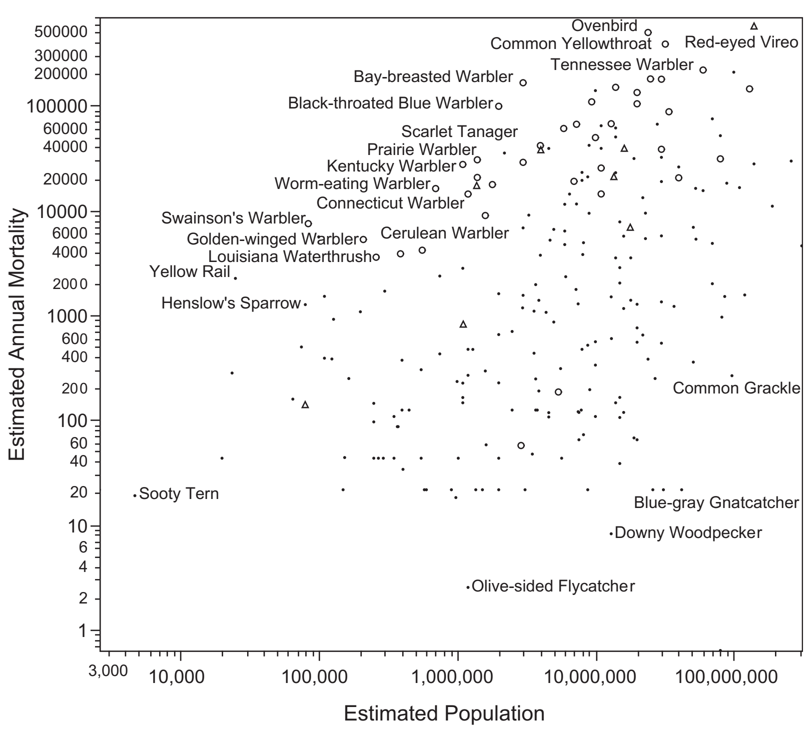

Fig. 2. Relationship of estimated population size of bird species killed at communication towers to estimated annual mortality at communication towers. The species killed at highest and lowest proportions of population size are labeled with standard abbreviations. All warbler species (Parulidae) are marked with circles, and all vireos (Vireonidae) are marked with triangles.

estimate for Golden-winged Warbler (*Vermivora chrysoptera*) gives a range of annual mortality from 1.2% to 5.0% for our annual estimated mortality of ~5300 birds. Furthermore, the uncertainty of population estimates for species that are secretive, or whose ranges or habitats are not covered well by the Breeding Bird Survey, would likely be high.

The results of the mortality assessment illustrate the potential complications of extrapolated species mortality from historical records. Yellow Rails (*Coturnicops noveboracensis*) winter along the Gulf Coast and breed in Canada (Bookhout, 1995). They have been recorded dead at towers across a large range and consequently are estimated to experience losses of ~2200 individuals per year. Towers almost certainly no longer kill as many Yellow Rails as they once did because of the dramatic decline of this species (Bookhout, 1995), although more recent mortality events do include 34 recorded in October 1986 (Ball et al., 1995) and 1 in Fall 2000 (Young and Robbins, 2001), both near Topeka, Kansas. We have assumed that the proportion of each species of bird killed has not changed, so estimates of mortality for some species that have declined dramatically may reflect historical rather than current patterns.

Additional uncertainty could arise from differential detectability of carcasses among species of different sizes (Smallwood, 2007). The effect of carcass size on overall mortality estimates is not likely to be substantial, however, because 97% of birds recovered at towers are small passerines (Table 2). We have not provided statistical estimates of uncertainty, but rather present the best possible estimates from the data currently available, with an explicit and transparent methodology that will allow improvement in these estimates as additional data are collected. It is, however, necessary to make such estimates because policies are currently being formulated to address incidental take from towers that could be informed by these efforts.

4.2. Biological significance

Advocates for the tower industry frequently compare avian mortality at towers to other sources of avian mortality and argue, implicitly or explicitly, that those sources that kill more total birds are more important by virtue of sheer numbers alone (e.g., Woodlot Alternatives, 2005). This approach is flawed for conservation assessments because it lumps all birds together without regard for their status as rare or common. Species are affected differentially and although total tower-related mortality is lower than some other sources of human-caused avian mortality, it can still be significant for individual species. This also applies to other sources of direct avian mortality, such as industrial-scale wind farms, where aggregate mortality numbers can appear to be low compared with other sources, but analysis for individual species can indicate significant impacts (Carrete et al., 2009).

An analysis of the biological significance of avian mortality at towers should consider other sources of human-caused mortality when those other sources are additive and can contribute to an assessment of cumulative impacts. For example, Klem (1990) estimated that glass windows kill on the order of 97.6 million to 976 million birds per year. Although no synthetic analyses of window collision mortality similar to this effort have been undertaken, Klem (1989) identified 20 avian species killed most frequently by windows from inquiries to 125 museum curators for information from their collections. Some of these species, such as Ovenbird (*Seiurus aurocapilla*), Swainson's Thrush (*Catharus ustulatus*), Common Yellowthroat (*Geothlypis trichas*), and Tennessee Warbler (*Oreothlypis peregrina*), are also killed in great numbers at towers. Although not comparable to our analysis, this approach helps to identify species for which cumulative impacts are likely to occur. For species at risk in such situations, addressing both tower and window mortality would be advisable and indeed the species killed in window strikes at tall buildings will be similar to those killed at communication towers. Although the 20 avian species killed most frequently at all windows reported by Klem (1989) do not contain any Birds of Conservation Concern, the 20 avian species killed most frequently at towers contain two such species (Bay-breasted Warbler [*Setophaga castanea*], and Blackpoll Warbler [*Setophaga striata*]) and 11 of 20 species killed in greatest proportion to their populations at towers have special conservation status.

The example of mortality at windows illustrates how mortality estimates from several human-caused sources can be used to weigh alternative policy options to protect migratory birds. First, per species estimates (or at least ranks) are needed. Then, for any particular species of concern, conservation action can be focused on a single source of mortality or address the cumulative effects of multiple sources. This decision cannot be made without some quantification of which bird species are killed by which causes or by integrating multiple sources of mortality into lifecycle models for individual species (Loss et al., 2012). For example, Gray Catbirds (*Dumetella carolinensis*) are among the birds killed most frequently at towers (Table 1) and are killed frequently by free-roaming cats (Balogh et al., 2011) and windows (Klem, 1989). Indeed, mortality from domestic cats alone is capable of reducing local catbird populations (Balogh et al., 2011). Cumulatively, these mortality sources may affect local and regional distribution and abundances even if no rangewide population-level effect is detected from any one source.

Finally, we have illustrated that it is feasible to develop per species estimates of avian mortality, even if the data are imperfect and assumptions are many. Notwithstanding these limitations, our method improves on current approaches to describing lethal effects of human activities on birds, where comparisons are made routinely of the number of "birds" killed with little consideration of which species are affected (e.g., Erickson et al., 2005; Gore, 2009). Such comparisons of undifferentiated totals of birds killed are insufficient to assess the biological significance of different mortality sources. We therefore encourage increased consideration and description of the species composition of avian casualties resulting from human actions and policies.

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