An estimate of avian mortality at communication towers in the United States and Canada

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Travis Longcore,[1] The Urban Wildlands Group, P.O. Box 24020, Los Angeles, CA 90024, USA

Catherine Rich, The Urban Wildlands Group, P.O. Box 24020, Los Angeles, CA 90024, USA

Pierre Mineau, National Wildlife Research Centre, Science and Technology Branch, Environment Canada, Ottawa, CANADA

Beau MacDonald, Department of Geography, California State University, Northridge, CA 91330, USA

Daniel G. Bert, National Wildlife Research Centre, Science and Technology Branch, Environment Canada, Ottawa, CANADA

Lauren M. Sullivan, Department of Geography, University of California, Los Angeles, CA 90024, USA

Erin Mutrie, National Wildlife Research Centre, Science and Technology Branch, Environment Canada, Ottawa, CANADA

Sidney A. Gauthreaux Jr., Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA

Michael L. Avery, United States Department of Agriculture/Wildlife Services, National Wildlife Research Center, Florida Field Station, 2820 East University Avenue, Gainesville, FL 32641, USA

Robert L. Crawford, 208 Junius Street, Thomasville, GA 31792, USA

Albert M. Manville II, U.S. Fish and Wildlife Service, Division of Migratory Bird Management, 4401 N. Fairfax Dr. – MBSP-4107, Arlington, VA 22203, USA

Emilie R. Travis, Archbold Biological Station, Lake Placid, FL 33862, USA

David Drake, University of Wisconsin, Department of Forest & Wildlife Ecology, Madison, WI 53706, USA

[1] E-mail: longcore@urbanwildlands.org

ABSTRACT

Avian mortality at communication towers in the continental United States and Canada is an issue of pressing conservation concern because most birds killed are Neotropical migrants, which are, as a group, under threat. Previous estimates of avian mortality at communication towers have been based on limited data and have not included Canada. We compiled a database of communication towers in the continental United States and Canada and estimated avian mortality by tower with an equation relating avian mortality to tower height. This equation was derived from 40 towers for which mortality data are available, which we corrected for sampling, search efficiency and scavenging as appropriate. Although most studies document mortality at guyed towers with steady-burning lights, we accounted for lower mortality at towers without guy wires or steady-burning lights by adjusting estimates based on published studies. The resulting estimate of annual avian mortality was 3.9 million birds if all studies in the meta-analysis were weighted equally and 5.9 million birds per year if studies were weighted by their duration. Bootstrapped subsampling indicated that the regression was robust to the choice of studies included and comparison of multiple regression models showed that incorporating sampling and scavenging/search efficiency adjustments improved model fit. Although total avian mortality is only a first step to developing an assessment of the biological significance of this phenomenon for individual species or groups of species, our estimate represents an independent derivation of

this cumulative number and is consistent with estimates that have been used recently in motivating policy action on this conservation issue.

INTRODUCTION

In the late 1950s, American birders and ornithologists began reporting mortality of migratory birds at towers erected for the broadcast media (Johnston 1955; Laskey 1956; Brewer and Ellis 1958; Cochran and Graber 1958). These observations were consistent with the long-documented mortality of birds at lights, including at lighthouses (Harvie-Brown and Cordeaux 1880), light towers (Gastman 1886), tall buildings (Overing 1936; Aronoff 1949), and ceilometers (Spofford 1949). Although initially dismissed as a minor concern (Mayfield 1967), the ongoing and chronic mortality of nocturnally migrating species at tall, lighted structures has become a significant conservation concern (Banks 1979; Avery et al. 1980; Manville 2001b, 2005). An estimate of the total number of birds killed at communication towers is of particular current interest because the development of new broadcast media (e.g., High Definition television) are leading to the construction of more tall towers.

In 1979, a widely circulated estimate of avian mortality at television towers was developed by Banks (1979), which revised upward a previous estimate by Mayfield (1967). In Banks' (1979) assessment of various sources of human-caused mortality, he extrapolated the results of three long-term studies at tall towers — two studies in Florida (Stoddard and Norris 1967; Taylor and Anderson 1973) and one in North Dakota (for which he did not provide a citation but which was almost certainly Avery et al. 1978) — to all television towers. He calculated the average mortality at these three sites to be roughly 2,500 birds per year, and multiplied it by the number of television towers (1,010 in 1979). He then assumed that half of all television towers would cause a hazard to migrating birds. The resulting annual estimate of annual mortality was

1,250,000 (Banks 1979). Avery (1979) applied bird mortality results from 7 towers that had been monitored for at least 10 years and derived an overall mortality estimate of 940,000/year for the United States. More recent estimates of total avian mortality at towers in the United States by Evans (1998) and the USFWS (Manville 2001a, b) adjusted the Banks estimate by accounting for the increased number of towers since 1979. Application of Banks' method today results in an estimate of 4–5 million birds killed annually by tall towers, with Manville (2005, 2009) indicating a possibility of mortality an order of magnitude higher.

No estimate of avian mortality at communication towers has been made for North America as a whole, and the only estimate for Canada was presented in a preliminary unpublished report leading to this paper. Considering mortality in Canada would be desirable, because the bulk of species killed at towers are Neotropical migrants (Banks 1979; Shire et al. 2000) with populations that extend into Canada and mortality in both the United States and Canada contribute to cumulative impacts on these populations.

In this paper we develop a new estimate avian mortality at communication towers in the United States and Canada. This estimate derives from a meta-analysis of tower mortality studies (following Longcore et al. 2008). We adjust mortality records at towers for search efficiency, scavenging, and sampling scheme and produce a regression for mortality by tower height and then apply this regression to a geographic database of communication towers for all of North America. This approach recognizes that taller towers kill more birds on average than do shorter towers (Karlsson 1977; Longcore et al. 2008; Gehring et al. 2009), but also incorporates towers that are less than 600 ft (183 m) above ground level (AGL), which have previously been left out of estimates of total avian mortality. These "shorter" towers, which constitute the majority of towers, do regularly kill birds (Seets and Bohlen 1977; Manville 2007; Gehring et al. 2009) and their sheer number argues against ignoring them, even with potentially low per-tower mortality rates. We do not, however, estimate mortality from collisions with other lighted structures. Attraction to light at night leads to avian mortality at tall buildings, monuments, cooling towers, offshore platforms, ships, and lighthouses (Gauthreaux and Belser 2006; Manville 2009), and the same species (Neotropical migrants) are susceptible.

METHODS

We assigned average mortality values to tower height classes (every 30 m) using a regression of tower height by annual mortality in a manner analogous to that used by Longcore et al. (2008). They identified reports of birds killed at 26 communication towers over at least 2 migratory seasons (e.g., spring and fall, two falls), consisting of a minimum of 10 total carcass-searching visits per site. Following the application of an adjustment for migratory bird abundance differences in the spring and fall, Longcore et al. (2008) considered the relationship between the mean annual bird mortality and tower height using linear regression analysis. We added towers from additional studies (Nielsen and Wilson 2006; Gehring et al. 2009; Travis 2009), tested the sensitivity of the regression to inclusion of studies, developed adjustments for search efficiency and scavenging and for sampling scheme, investigated the effect of weighting by study duration, and introduced a few modifications.

Sensitivity of tower height regression

We tested the extent to which the regression model was robust to sampling variation among the towers available for analysis. We used a randomization and resampling procedure to select random subsets of the 40 towers included in the analysis. Although a sample size of 40 is relatively small, we started with the assumption that a minimum of half those towers (20) would be necessary to build a defensible regression model. We then applied the sampling procedure to subsets of the 40 towers from 20–39 and re-iterated the sampling procedure 10,000 times. We used the natural log of both the dependent and independent variables.

Adjustment for scavenging and search efficiency

Loss of birds to scavengers and failure to detect all dead birds (search efficiency) are sources of error and variation in tower studies. It is customary for searching and scavenging factors to be applied to final kill estimates (e.g., Longcore et al. 2005; Gehring et al. 2009), but we opted to correct for search efficiencies and scavenging losses before regressing estimated losses against tower height.

We assumed that scavenging will be lower at a small tower that generates only a few mortalities in sporadic fashion compared with a well-established tall tower that kills birds reliably and therefore maintains scavenger interest (Stoddard 1962; Crawford 1971). This is supported by high scavenging rates documented at tall towers such as WCTV in Florida (Stoddard 1962; Stoddard and Norris 1967; Crawford 2004) and rapid increases in scavenging when carcasses are provided by researchers (Nielsen and Wilson 2006). Even with extensive scavenger control efforts, Stoddard estimated he was losing at least 10% of bird carcasses to scavengers daily (Crawford and Engstrom 2001). Therefore, we applied a differential scavenging rate to towers of different heights.

We assume that it is easier to find carcasses under a short tower because carcasses are likely to be less dispersed because of shorter guy wire support bases or absence of guy wires. Finally, whether the area around the tower is bare or heavily vegetated will affect both scavenging and search rates. Support for our assumptions on the effect of cover on these rates if found in the literature on the impacts of pesticides, power lines, and wind turbines on birds (Mineau and Collins 1988; Johnson and Erickson 2001; Kostecke et al. 2001; Mineau 2002; Ponce et al. 2010). Open habitats with little concealing vegetation are, predictably, more conducive to efficient searching for carcasses. Scavengers can find the carcasses more easily as well. Habitat type partially cancels itself out as far as one's overall ability to detect mortality as a result of these opposing tendencies.

We avoided attempts to calculate probability of detection by searchers that involved the "life expectancy" of carcasses and average search rates because these methods are biased (Smallwood 2007). If a carcass was not found on the first search day, it is likely well hidden and the probability that it will be found on subsequent days is considerably less than the average search rate would suggest. Therefore, for the purpose of this analysis, the likelihood that a carcass was found more than one day after it was generated is considered negligible.

We divided towers into height classes to which we could assign differential search and scavenging rates. Based on natural breaks in the raw tower mortality data, we chose to divide the towers into three height classes: 0–200 m, 201–400 m, and ≥ 401 m. We used tower height as well as any information about cover as a way to assign search and scavenging corrections to individual towers, unless these had been measured and reported by the authors (Table 1).

Adjustment of study and sampling design

Studies included in the tower height–mortality regression varied in sampling design and duration. Following Longcore et al. (2008), we required a minimum of 10 searches for a study to be included in the regression. Authors of most of the studies used in the regression assumed that most birds would be found by sampling during peak migration, on bad weather days preceding or following the passing of a cold front (e.g., J. Herron, pers. comm.), or both. The logic behind this approach is that many large kill days are correlated with these factors. Nevertheless, “trickle kills” on fair weather days even outside the typical migration period are common at tall towers (Crawford and Engstrom 2001) and can contribute substantially to overall mortality. Large kill days during clear and calm weather during the migration season have also been documented (Avery et al. 1977; Manville 2007). For these reasons we used two studies that carried out daily carcass searches — WCTV Florida tower data from 1956–1967 initiated by Herbert L. Stoddard and Tall Timbers Research Station (Crawford and Engstrom 2001) and North Dakota ‘Omega’ tower (Avery and Clement 1972; Avery et al. 1974; Avery et al. 1978) — to estimate the proportion of birds that might have been missed in the course of other sampling designs.

Most study designs involve sampling during peak migration or on bad weather days preceding or following the passage of a cold front (Avery et al. 1977; Crawford 1981). Removal of dead birds by scavengers also seems to follow an exponential decay model such that the probability of detecting a dead bird is much higher during the time period immediately following the mortality event. For these reasons we considered daily sampling designs to be superior and we used the two daily datasets as a baseline. Daily sampling at a predetermined early hour is consistent with recent communication tower studies (e.g., Gehring et al. 2009; Travis 2009).

We used data from the two daily search studies to develop estimates of the effectiveness of the various sampling designs in the 40 towers included in our dataset. This information was then used to adjust the annual mortality for each of these towers to account for the sampling scheme. The Florida estimates were averaged over 10 years of sampling; the North Dakota estimates for two years of sampling. When the estimate was (partially) based on sampling outside the migratory period (as defined) we only used the Florida dataset. To control for differences between spring and fall migration we developed estimates for both spring and fall separately.

We developed estimates specific to the sampling design for each study based on a) the pattern of sampling (e.g. bad weather days, big kill days), b) the number of days of sampling, and c) timing (spring migration, fall migration, both spring and fall migration, or outside of migration). Many studies do not provide details on some of the above and in these cases we made simplifying assumptions. If more than one sampling strategy was used, we developed estimates for each and used the sum as our overall estimate. For example, sampling may have been done weekly (regular sampling) outside of the migration period *and* also on 'bad weather days' during the migration period.

We defined the spring and fall migration periods as a 60-day window before and after the migration peak for both spring and fall for each dataset, recognizing that for some recent studies (e.g., Gehring et al. 2009) monitoring only occurred during the 3-week peak of migration. We determined the peak for the Florida and North Dakota datasets by plotting the number of birds killed against Julian date for all years of data combined and using negative exponential smoothing.

For some studies, the only information provided was the number of total days sampled and the timing of sampling (during migration or all year). For these studies we assumed that researchers sampled on bad weather days during migration when large bird kills at communication towers are expected.

Several studies reported the total number of days sampled during one or both migration periods and sometimes outside the migration periods. When the sampling interval (e.g., weekly) was identified in the study design, we constrained the re-sampling procedure to randomly select a day within that sampling interval. If no sampling interval was defined, selection was random. In this instance we used a re-sampling approach to develop an estimate based on the two datasets of daily search activity. Based on the number of sampling days in each study, we re-sampled (with replacement) data within each of the spring and fall migration periods by randomly selecting a subset of days and summing avian mortality for the selected days. We calculated the average bird mortality for 5000 iterations and the estimate is the proportion of average bird mortality from the 5000 iterations to the total number of birds killed during either spring or fall migration or outside of the migration period. This applied to studies that sampled on bad weather days (see below) and also on a weekly basis outside the migration period.

Several studies sampled on so called 'bad weather days' or following bad weather nights, i.e., overcast, often associated with advancing cold fronts and sometimes including precipitation. Usually no other information was provided with respect to a clear definition of 'bad weather' or the number of days when bad weather occurred. High bird mortality at communication towers is correlated with bad weather days (Avery et al. 1977; Crawford 1981; Crawford and Engstrom 2001). Figure 1 shows the relationship between bird mortality and mean free airspace (distance between the tip of the tower and the cloud cover base) for the Florida tower dataset for the 1956–1967 fall migrations. Above approximately 335 m (1100 ft) the relationship is no longer functional (as seen by the polygonal pattern in Figure 1) and other factors may be more important. We used days with mean free airspace equal to or below 335 m (1100 ft) as an index of 'bad weather days.'

Several studies sampled only on days where so called "big kills" were reported by the researchers. The definition of 'big kill' was not reported. The typical daily trickle kill for the

Florida dataset over the 1956–1967 period was 5 birds. We therefore made the assumption that large kills would exceed 5 birds killed.

To develop our estimate(s) of sampling effectiveness across various sampling designs, we made several simplifying assumptions. In particular we defined distinct migratory periods (120 days surrounding peak), assumed big kill days were any day with bird mortality greater than 5, and assumed that bad weather days could be indexed by the distance between the top of the tower and the base of the cloud cover.

Evaluation of model correction factors

The two correction factors (sampling correction and a combined search and scavenging correction) were tested by evaluating a series of regression models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to find the most parsimonious model relating tower height (main predictor) to the unadjusted kill rate (dependent variable).

Description of communication towers and their characteristics

We used a Geographic Information System ("GIS") to extract the locations and characteristics of towers in the FCC's Antenna Structure Registration ("ASR") database and the NAV CANADA obstruction database by Bird Conservation Region. The FCC data are freely available and we licensed the Canadian obstruction data for the limited purpose of this study. We compared and crosschecked these with the FCC's microwave tower database and the commercial TowerMaps database, which provides locations of cellular towers to potential lessees and incorporates both data for shorter towers and information that was not included in the FCC databases. We did considerable quality control on the tower data, confirming from independent sources that all towers greater than 300 m existed. This was necessary because the data were prone to multiple types of errors; for example, the FCC database included a record claiming to be located in the "Land of Oz" in Kansas, but associated with geographic coordinates in Minnesota. Full details of the quality assurance are available from the authors.

The NAV CANADA database did not contain comprehensive information on either the presence of guy wires or the presence and type of lighting (steady burning vs. strobes), which are two factors that have been shown to influence the number of bird fatalities (Longcore et al. 2008; Gehring et al. 2009). We therefore relied on data from the FCC and TowerMaps and assumed that lighting and guy wire use was similar in both countries for towers of the same height class, an assumption supported by the similarity in regulations between the two countries (Federal Aviation Administration 2000).

Calculation of annual mortality

Most recorded tower kill events take place at guyed towers, and steady-burning lights increase the probability of large tower kills (Longcore et al. 2008; Gehring et al. 2009). We assumed that unguyed towers caused 85% less mortality than guyed towers (midpoint of 69–100% estimate in Gehring and Kerlinger 2007) and that towers without steady-burning lights caused 60% less mortality than towers with such lights (midpoint of 50–71% estimate in Gehring et al. 2009). Following Longcore et al. (2008), all estimates assumed that when both seasons were not measured, fall constituted 75% of annual mortality and spring 25% (Crawford and Engstrom 2001).

We overlaid locations of towers with Bird Conservation Regions and calculated the number of guyed towers in each 30 m height class. BCRs are divisions defined by habitat and topography that have been delineated for the purpose of bird conservation by the North American Bird

Conservation Initiative and are endorsed by a range of bird conservation organizations. They are based on the North American ecoregions developed to promote international conservation efforts (Commission for Environmental Cooperation 1997). For each height class within each BCR we calculated the average number of birds killed per year, using the tower height–mortality regression adjusted for scavenging, detection, and sampling scheme described above. For purposes of calculating total mortality we included all towers in the continental portions of the United States and Canada. Although most literature on tower mortality in North America describe studies from east of the Rocky Mountains, we included the west as well for purposes of estimating total mortality, which is supported by records of tower mortality in Colorado (Nielsen and Wilson 2006), New Mexico (Ginter and Desmond 2004), and Alaska (Dickerman et al. 1998), in addition to well-documented kills at lighthouses in California and British Columbia (Squires and Hanson 1918; Munro 1924).

RESULTS

Tower height–mortality regression

Log-transformed annual avian mortality, when adjusted for sampling scheme, scavenging, and search efficiency, was significantly explained by log-transformed tower height in a linear regression ($r^2 = 0.84$, $F_{1,38} = 194.55$, $p < 0.001$). Confidence intervals for the curve were tight through most of the range of heights, widening only at the lower end (Figure 2). The curve steepened slightly when the regression was weighted by study duration ($r^2 = 0.59$, $F_{1,38} = 55.26$, $p < 0.001$). Towers used in this regression were spread throughout the eastern United States (Figure 3).

Tower height–mortality regression sensitivity to study inclusion

The median r^2 values of the re-sampled distributions are essentially the same as the r^2 obtained from using all of the available data (Figure 4, Table 4). The results of the re-sampling procedure for subsets of 20 studies (half of the studies) and for 39 studies (1 less than the total) show the extreme cases (Table 4) and indicate that the height–mortality regression is robust to the choice of studies included in the meta-analysis.

Effect of adjusting for sampling scheme

We inspected the rank order of towers before and after adjusting for the sampling scheme and ran the regression model with and without these adjustments. Aside from a few changes in the relative rank of each tower, the most notable difference was a very slightly steeper regression line for the corrected data, which has the most influence on kills estimated at the taller towers. The fit is essentially the same with an improvement in r^2 as a result of smaller residuals for the taller towers.

Evaluation of model adjustment factors

Models using either sampling correction alone or the combination of sampling correction with the search/scavenging correction were found to be superior to the model using tower height alone at explaining annual kills (Table 5). Although the model using a sampling correction alone was the most parsimonious, we opted for the more complex model to account for search efficiency and scavenging losses as necessary to create a total mortality estimate.

Tower characteristics

Our database of towers included 85,286 towers in the continental United States and Canada after all quality assurance and quality control was done (Figure 5). Most towers in the United States dataset (39,418, 46.2%) were freestanding with steady-burning lights at night, while the fewest towers (5,115, 6.0%) were guyed with strobe lights only. Some towers had strobe lights during the day but red flashing and red solid lights at night so these were included as having solid lights.

Total mortality and estimates by bird conservation region

Combination of the height–mortality regression with estimates of reduced mortality at towers without guy wires or steady-burning lights produced a matrix of mortality by height class and tower characteristics. These estimates, which are adjusted for search efficiency, sampling scheme, and scavenging, ranged from zero for short unguyed towers to over 10,000 birds per year for the tallest guyed towers with steady-burning lights.

The tower height–mortality regression and subsequent application to towers in the continental United States and Canada produces an annual mortality estimate of 3.9 million birds per year (Table 6). Weighting the regression by study duration yields an estimate of 5.4 million birds per year. Two-thirds of the estimated mortality is attributable to towers over 300 m tall, of which only 1,040 were found in our database (1.2% of all towers; Table 6). Shorter towers, even those > 150 m, contribute approximately 20% of all mortality because of their sheer numbers (Table 6).

Mortality varies by region, influenced both by the size of the region and the number and height distribution of towers (Figure 6). The number of towers in each Bird Conservation Region does not directly correlate with estimated annual mortality because of the different numbers and heights of towers in the regions. As a result, Peninsular Florida is associated with more mortality than all of Canada; even though fewer towers are reported in Florida, they are on average much taller. The concentration of migrants from Florida's position would increase mortality even more, but this factor is not considered in our method since mortality rates for any given tower height are assumed to be constant across the study area. The Canadian tower data included far more shorter towers (< 60 m) than did the U.S. data, but this is probably a reporting issue. The Southeastern Coastal Plain accounts for greater mortality than other BCRs, followed by Eastern Tallgrass Prairie, Oaks and Prairies, and Piedmont. The number and characteristics of the towers found in the southeastern United States also cause greater annual mortality per area than regions to the northern United States and in Canada (compare Figure 3 and Figure 6). Canadian mortality accounts for only a fraction of the total (approximately 4%), because Canada simply has fewer and much shorter towers.

Although we extended mortality estimates to all towers in Canada and the continental United States, few studies are available from the west (Figure 3). This may be a function of a higher number of nocturnal migrants in the east, different patterns of migration, or different weather patterns, or it may simply reflect the fewer and shorter towers in the west as a whole. We investigated the effect of location on annual mortality by regressing the residuals of our height regression against longitude. The resulting plot showed slightly higher mortality in the east, but the relationship was not significant and was largely driven by a single data point. More comprehensive surveys of towers in the west are needed to see if this point represents an anomaly or a different pattern of mortality in the west.

Discussion

Our total mortality estimate of 3.9–5.4 million birds per year is consistent with the current USFWS estimate of 4–5 million birds per year (Manville 2001a, b, 2005, 2009), even though these estimates were derived using substantially different methods. Our approach to estimating total avian mortality at towers uses far more data than previous efforts. For example, Banks's (1979) estimate was based on mortality rates from three tower studies and assumed that all towers caused the same rate of mortality, regardless of tower height or location. In contrast, our method incorporates evidence from 40 locations to establish the relationship between tower height and avian mortality. We accounted for the height distribution and physical characteristics of approximately 85,000 towers across North America. Notwithstanding the sources of uncertainty in our estimate, the methodology improves on previous efforts, is transparent, and can be refined in conjunction with additional field studies.

Our mortality estimates must be interpreted with an understanding of the biases and uncertainties inherent in the methods. We have attempted wherever possible to quantify such uncertainty, but this understanding is not sufficient to express a statistical range of confidence the estimate. The tower height–mortality regression is not sensitive to the choice of towers studied, but the range of total mortality estimates that would encompass a 95% confidence interval of the regression line includes annual mortality well outside a range that is biologically possible. Many of the towers included in these studies were not selected randomly, but some studies did include randomly selected towers. We therefore reported only our estimate without confidence estimates surrounding it.

Although the number of birds found at some towers has apparently declined over time (Gauthreaux and Belser 2006), the influence of any such trend, if a true decline in mortality and not the result of increased scavenging, is offset by half of the towers included in the regression having survey end dates after 1990. Furthermore, the residuals of the tower height–mortality regression are not significantly explained by the year the study ended.

Tower mortality estimates are very sensitive to height because of the observed logarithmic relation between height and mortality (Longcore et al. 2008). For example, if the mortality estimates were made by using the top of each height class rather than the middle, then the total mortality estimate would increase 25% to 4.8 million birds per year. The use of the height classifications was necessary because some attributes had to be assigned probabilistically to towers and it would not be possible to know each necessary attribute for each tower from the tower data obtained.

In 1989, the Exxon Valdez oil spill killed approximately 250,000 birds in what has become the epitome of an environmental disaster (Piatt and Ford 1996), now only surpassed by the Deepwater Horizon oil well blowout in 2010. Our estimates show that communication towers are responsible for more than the equivalent of 15 Exxon Valdez spills each year. Our estimate of annual mortality is 1.5–2 times greater than that estimated for lead poisoning of waterfowl before lead shot was phased out for hunting waterfowl (Bellrose 1959). Previous efforts have determined that most of the birds killed at communication towers are neotropical migrants (Shire et al. 2000), which have suffered population declines and are of pressing conservation concern (Robbins et al. 1989). Data on per species mortality would provide even more clarity on the biological significance of avian mortality at communication towers. We have developed a method to produce such estimates (Longcore et al. 2005), and in a companion manuscript have implemented it using the mortality estimate developed here.

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Table 1. Assumed rates for search efficiency and scavenger removal by tower height and habitat type when not provided by investigator.

Tower type and mortality profile	*Habitat*	*Assumed proportion of small birds located by searcher*	*Assumed proportion of small birds remaining after scavenging*	*Combined rate of detection*
Height class 1 (0–200 m), sporadic mortality, more localized	Open habitat	75%	80%	60%
Height class 1 (0–200 m), sporadic mortality, more localized	Brush and other visual obstructions	50%	85%	42%
Height class 2 (201–400 m), regular mortality, more disperse	Open habitat	65%	55%	36%
Height class 2 (201–400 m), regular mortality, more dispersed	Brush and other visual obstructions	40%	70%	28%
Height class 3 (≥ 401 m), dependable mortality, carcasses widely dispersed	Open habitat	55%	30%	16%
Height class 3 (≥ 401 m), dependable mortality, carcasses widely dispersed	Brush and other visual obstructions	30%	55%	16%

Table 2. Summary of factors used to develop the search and scavenging correction for bird mortality at communication towers.

Reference	*Cover*	*Daily*	*Tower Height (m)*	*Scavenger control*	*Scavenger measured*	*Search rate*	*Scavenging rate*	*Overall detection rate*
(Avery and Clement 1972; Avery et al. 1977; Avery et al. 1978)	dense	yes	366	no	yes	0.400	0.100	0.360
(Baird 1970, 1971)	mowed at least once	no	411	no	no	0.550	0.700	0.165
(Boso 1965)	unknown	no	366	no	no	0.650	0.450	0.358
(Brewer and Ellis 1958)	corn/soybean field	no	299	no	no	0.400	0.300	0.280
(Caldwell and Wallace 1966)	unknown (probably open or mowed)	no	300	no	no	0.650	0.450	0.358
(Caldwell and Wallace 1966)	unknown (probably open or mowed)	no	342	no	no	0.650	0.450	0.358
(Caldwell and Wallace 1966)	unknown (probably open or mowed)	no	390	no	no	0.650	0.450	0.358
(Carter and Parnell 1976)	dirt, weedy sand, grass/low weed under guy lines, dense vegetation everywhere else	no	362	no	no	0.400	0.300	0.280
(Carter and Parnell 1976)	dirt, weedy sand, grass/low weed under guy lines, dense vegetation everywhere else	no	608	no	no	0.300	0.450	0.165
(Crawford and Engstrom 2001)	mowed	yes	90	yes	no	0.750	0.100	0.675
(Crawford and Engstrom 2001)	mowed	yes	308	yes	no	0.650	0.100	0.585
(Nielsen and Wilson 2006)	rocky, some shrub	no	152	no	yes	0.850	0.030	0.825
(Gehring et al. 2009)	20 consecutive days (spring + fall 2005)	20	130	no	yes	0.275	0.730	0.477
(Gehring et al. 2009)	summary of 03/04	20	130	no	yes	0.275	0.730	0.477
(Herron 1997)	most birds measured fell on roof of building	no	161	***yes (roof)	no	0.750	0.200	0.600
(Kemper 1996)	open	yes	305	no	no	0.650	0.450	0.358
(Laskey 1960) and others	wooded/rocky and roof of building	no	287	***yes (roof)	no	0.650	0.450	0.358
(Morris et al. 2003)	cut grass (cut to different lengths)/paved	yes but only in the first year 1971	293	no	no	0.650	0.450	0.358
(Morris et al. 2003)	cut grass (cut to different lengths)/paved	yes but only in the first year 1971	323	no	no	0.650	0.450	0.358
(Morris et al. 2003)	cut grass (cut to different lengths)/paved	yes but only in the first year 1971	328	no	no	0.650	0.450	0.358
(Morris et al. 2003)	cut grass (cut to different lengths)/paved	yes but only in the first year 1971	330	no	no	0.650	0.450	0.358
(Mosman 1975)	'heavy' ground cover	no	610	no	no	0.300	0.450	0.165
(Nehring and Bivens 1999)	unknown but open	yes fall only	417	no	no	0.550	0.700	0.165
(Nicholson et al. 2005)	cleared periodically	no	60	yes	yes	0.406	0.392	0.247
(Sawyer 1961)	bare ground and pavement under tower, weeds/grasses elsewhere	no	133	no	no	0.750	0.200	0.600
(Strnad 1975)	mostly pasture but also pavement and bare	no	400	no	no	0.650	0.450	0.358

	ground directly under the tower							
(Taylor and Anderson 1973, 1974)	water and unvegetated ground/dirt	no	452	no	no	0.550	0.700	0.165
(Travis 2009)	mowed at least once per season	yes	60	no	yes	0.294	0.076	0.271
(Travis 2009)	mowed at least once per season	yes	60	no	yes	0.294	0.076	0.271
(Travis 2009)	mowed regularly	yes	79	no	yes	0.294	0.076	0.271
(Travis 2009)	mowed at least once per season	yes	97.5	no	yes	0.290	0.113	0.257
(Travis 2009)	mowed regularly	yes	108.5	no	yes	0.290	0.113	0.257
(Travis 2009)	mowed regularly	yes	110.3	no	yes	0.290	0.113	0.257
(Travis 2009)	mowed regularly	yes	141.7	no	yes	0.380	0.213	0.299
(Travis 2009)	alfalfa field, mowed infrequently	yes	142	no	yes	0.380	0.213	0.299
(Travis 2009)	mowed regularly	yes	163	no	yes	0.380	0.213	0.299
(Travis 2009)	mowed regularly	yes	395.5	no	yes	0.294	0.332	0.197
(Travis 2009)	higher grasses, mowed infrequently	yes	433.7	no	yes	0.294	0.332	0.197
(Young and Robbins 2001)	burned spring, hayed fall	no	439	no	no	0.550	0.700	0.165
(Young et al. 2000)	burned spring, hayed fall	no	30.5	no	no	0.750	0.200	0.600

Table 3. Summary data with sampling efficiency correction for the 40 studies used to develop an estimate of bird mortality at communication towers.

Reference	*Tower Height (m)*	*Start Year*	*End Year*	*Sampling days*	*Sampling correction*	*Sampling strategy*	*No. of Years*	*Average correction sampling (spring)*	*Average correction sampling (fall)*	*Birds Collected*	*Mean Annual Fatalities*	*Mean Annual Fatalities (corrected sampling and scavenging)*
(Avery and Clement 1972; Avery et al. 1977; 1978)	366	1972	1974	>180/year	no	n/a	2	1.00	1.00	785	392.5	1482.8
(Baird 1970, 1971)	411	1969.5	1971	unknown	yes	bad weather	1.5	0.66	0.79	508	338.0	2500.9
(Boso 1965)	366	1962.5	1964	12 spring, 12 fall	yes	bad weather	1.5	0.44	0.36	125	83.0	456.0
(Brewer and Ellis 1958)	299	1955	1957	7 confirmed	yes	big kills	2	0.66	0.79	486	243.0	1189.6
(Caldwell and Wallace 1966)	300	1959.5	1964	unknown	yes	bad weather	4.5	0.44	0.36	199	44.0	242.0
(Caldwell and Wallace 1966)	342	1958.8	1964	unknown	yes	big kills	5.25	0.66	0.79	1740	331.0	1365.9
(Caldwell and Wallace 1966)	390	1958.8	1964	unknown	yes	overcast	5.25	0.44	0.36	3972	757.0	4140.4
(Carter and Parnell 1976)	362	1970	1972	unknown	yes	bad weather	2	0.44	0.36	995	498.0	3107.8
(Carter and Parnell 1976)	608	1970	1972	unknown	yes	overcast	2	0.44	0.36	2223	1111.0	9710.0
(Crawford and Engstrom 2001)	90	1998.5	2000	>330	no	n/a	1.5	1.00	1.00	21	14.0	34.7
(Crawford and Engstrom 2001)	308	1970	1983	>330	no	n/a	13	1.00	1.00	8035	618.0	1674.6
(Nielsen and Wilson 2006)	152	2004	2006	>52 per year	yes	bad weather + weekly	2	0.90	0.58	11	5.5	15.3
(Gehring et al. 2009)	130	2005	2005	20	yes	n/a	1	0.21	0.20	18.3	18.3	126.1
(Gehring et al. 2009)	?	2003	2004	20	yes	n/a	1.75	0.21	0.20	22.55	12.9	91.0
(Herron 1997)	161	1980	1986	15.25/year average	yes	bad weather	6	0.44	0.36	700	116.0	503.8
(Kemper 1996)	305	1957	1995	>180	no	n/a	38	1.00	1.00	121560	3198.0	12147.1
(Laskey 1960) and others	287	1953.3	1973	<60	no	n/a	19.75	1.00	1.00	4994	253.0	960.2
(Morris et al. 2003)	293	1969	1999	unknown	yes	bad weather	30	0.44	0.36	8011	267.0	1461.4
(Morris et al. 2003)	323	1969	1999	unknown	yes	bad weather	30	0.44	0.36	1043	35.0	190.3
(Morris et al. 2003)	328	1969	1999	unknown	yes	bad	30	0.44	0.36	11092	370.0	2023.4

						weather					
(Morris et al. 2003)	330	1973	1992	unknown	yes	bad weather	19	0.44	0.36	4310	227.0	1241.4
(Mosman 1975)	610	1973.3	1975	unknown	yes	overcast day pairs	1.75	0.44	0.36	3521	2012.0	17576.8
(Nehring and Bivens 1999)	417	1954.3	1997	<60	no	n/a	29.75	1.00	1.00	20485	688.6	4861.7
(Nicholson et al. 2005)	60	2000	2004	average >70/year	yes	bad weather	4	0.50	0.50	15	4.0	22.7
(Sawyer 1961)	133	1958	1960	<60	no	n/a	2	1.00	1.00	267	133.5	356.0
(Strnad 1975)	400	1969	1974	<10	yes	big kills	5	0.66	0.79	3507	701.0	2890.7
(Taylor and Anderson 1973, 1974)	452	1969	1972	at least 5	yes	big kills	3	0.66	0.79	9130	3043.0	22474.0
(Travis 2009)	60	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	3	1.5	7.0
(Travis 2009)	60	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	1	0.5	2.3
(Travis 2009)	79	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	8	4.0	18.8
(Travis 2009)	110	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	6	3.0	14.7
(Travis 2009)	109	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	7	3.5	17.1
(Travis 2009)	110	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	3	1.5	7.3
(Travis 2009)	142	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	14	7.0	30.4
(Travis 2009)	142	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	5	2.5	10.9
(Travis 2009)	163	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	20	10.0	43.4
(Travis 2009)	396	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	760	380.0	2311.7
(Travis 2009)	434	2007	2008	45 spring, 45 fall	no	n/a	2	1.00	1.00	237	118.5	720.9
(Young and Robbins 2001)	439	1999	2001	?	yes	bad weather	2	0.44	0.36	946	473.0	4132.1
(Young et al. 2000)	30.5	1998	1999	25/year	yes	bad weather	1	0.44	0.36	0	0.0	0.0

Table 4. Confidence intervals and median values for model parameters using randomized subsets of 20 or 39 studies (5000 iterations).

Subset/parameter	*5%*	*95%*	*Median*
20 studies			
R^2	0.753	0.901	0.841
coefficient	-14.252	-10.132	-11.850
standard error	0.871	1.265	1.082
39 studies			
R^2	0.827	0.848	0.836
coefficient	–12.158	–11.626	–11.895
standard error	1.051	1.098	1.092

Table 5. Performance of models explaining avian mortality at communication towers.

Variable 1	*Variable 2*	*Variable 3*	*DF*	*AIC*	*Likelihood Ratio Chi-Square*	*p*
ln Tower height	Sampling correction		2	78.52593	39.12642	$3.19 \cdot 10^{-9}$
ln Tower height	Search and scavenging correction	Sampling correction	3	80.51228	39.14007	$1.62 \cdot 10^{-8}$
ln Tower height			1	83.24036	32.41199	$1.25 \cdot 10^{-8}$
ln Tower height	Search and scavenging correction		2	85.1901	32.46225	$8.93 \cdot 10^{-8}$
Search and scavenging correction	Sampling correction		2	104.146	13.50633	0.001167
Search and scavenging correction			1	105.0033	10.64907	0.001101
Sampling correction			1	114.7243	0.928003	0.335383

Table 6. Number of towers by type and associated avian mortality estimates for Canada and the continental United States. Tower attributes (guy wires, lighting type) for Canada are extrapolated from proportions in the United States because these attributes are not found in the NAV CANADA database.

Height Class (m)	*Number Guyed Steady Burning Towers*	*Number Guyed Strobe Towers*	*Number Unguyed Steady Burning Towers*	*Number Unguyed Strobe Towers*	*Annual Fatalities*	*Percent of Fatalities*
United States						
0–30	0	0	581	7	0	0.00%
30–60	136	1	2573	50	976	0.03%
60–90	5901	863	17693	2575	90,275	2.43%
90–120	10023	1696	10004	1683	371,006	10.00%
120–150	2938	505	2922	488	248,660	6.70%
150–180	1992	311	661	101	296,299	7.99%
180–210	343	46	107	12	87,377	2.36%
210–240	174	54	51	11	75,436	2.03%
240–270	109	57	29	16	76,562	2.06%
270–300	76	61	18	14	83,680	2.26%
300–330	271	128	0	0	360,528	9.72%
330–360	115	28	0	0	190,472	5.14%
360–390	78	22	0	0	172,349	4.65%
390–420	47	16	0	0	136,576	3.68%
420–450	35	10	0	0	126,177	3.40%
450–480	66	23	0	0	302,976	8.17%
480–510	25	10	0	0	143,517	3.87%
510–540	24	8	0	0	163,355	4.40%
540–570	8	9	0	0	83,638	2.26%
570–600	18	15	0	0	205,762	5.55%
600–630	38	27	0	0	493,192	13.30%
Subtotal	*22,417*	*3,890*	*34,639*	*4,957*	*3,708,815*	
Canada						
0–30	5	71	177	2,771	0	0.00%
30–60	32	324	609	6,154	1,156	0.80%
60–90	627	323	1,880	968	10,926	7.60%
90–120	1,295	284	1,295	284	48,860	33.97%
120–150	251	55	251	55	21,601	15.02%
150–180	92	23	31	8	14,141	9.83%
180–210	44	11	15	4	11,689	8.13%
210–240	19	5	6	2	8,204	5.70%
240–270	6	2	2	1	3,870	2.69%
270–300	3	1	1	0	2,790	1.94%
300–330	9	4	0	0	11,928	8.29%
330–360	3	1	0	0	4,950	3.44%
360–390	1	0	0	0	1,628	1.13%
390–420	1	0	0	0	2,097	1.46%
Subtotal	*2,386*	*1,104*	*4,266*	*10,247*	*143,840*	
Total	***24,803***	***4,994***	***38,905***	***15,204***	***3,852,654***	

Table 7. Total estimated annual avian mortality at towers in the United States and Canada by BCR.

BCR	USA (lower 48 states)	Alaska	Canada	Total
1–Aleutian Bering Sea		0		0
2–Western Alaska		115		115
3–Arctic Plains and Mountains		63	369	432
4–Northwestern Interior Forest		1,464	213	1,677
5–Northern Pacific Rainforest	13,132	215	1,716	15,063
6–Boreal Taiga Plain			16,893	16,893
7–Taiga Shield and Hudson Plains			1,852	1,852
8–Boreal Softwood Shield			13,819	13,819
9–Great Basin	12,843		268	13,111
10–Northern Rockies	5,517		1,373	6,890
11–Prairie Potholes	146,566		39,600	186,166
12–Boreal Hardwood Transition	83,476		22,504	105,980
13–Lower Great Lakes/St. Lawrence Plain	50,825		32,485	83,310
14–Atlantic Northern Forest	20,510		12,749	33,259
15–Sierra Nevada	233			233
16–Southern Rockies/Colorado Plateau	16,719			16,719
17–Badlands and Prairies	31,302			31,302
18–Shortgrass Prairie	136,506			136,506
19–Central Mixed-grass Prairie	188,193			188,193
20–Edwards Plateau	46,010			46,010
21–Oaks and Prairies	257,399			257,399
22–Eastern Tallgrass Prairie	430,334			430,334
23–Prairie Hardwood Transition	162,734			162,734
24–Central Hardwoods	198,996			198,996
25–West Gulf Coastal Plain/Ouachitas	181,395			181,395
26–Mississippi Alluvial Valley	103,312			103,312
27–Southeastern Coastal Plain	620,551			620,551
28–Appalachian Mountains	155,782			155,782
29–Piedmont	251,790			251,790
30–New England/Mid-Atlantic Coast	57,429			57,429
31–Peninsular Florida	187,621			187,621
32–Coastal California	53,381			53,381
33–Sonoran and Mojave Deserts	27,190			27,190
34–Sierra Madre Occidental	606			606
35–Chihuahuan Desert	10,482			10,482
36–Tamaulipan Brushlands	59,008			59,008
37–Gulf Coast Prairie	197,098			197,098
Total	**3,706,940**	**1,857**	**143,841**	**3,852,638**

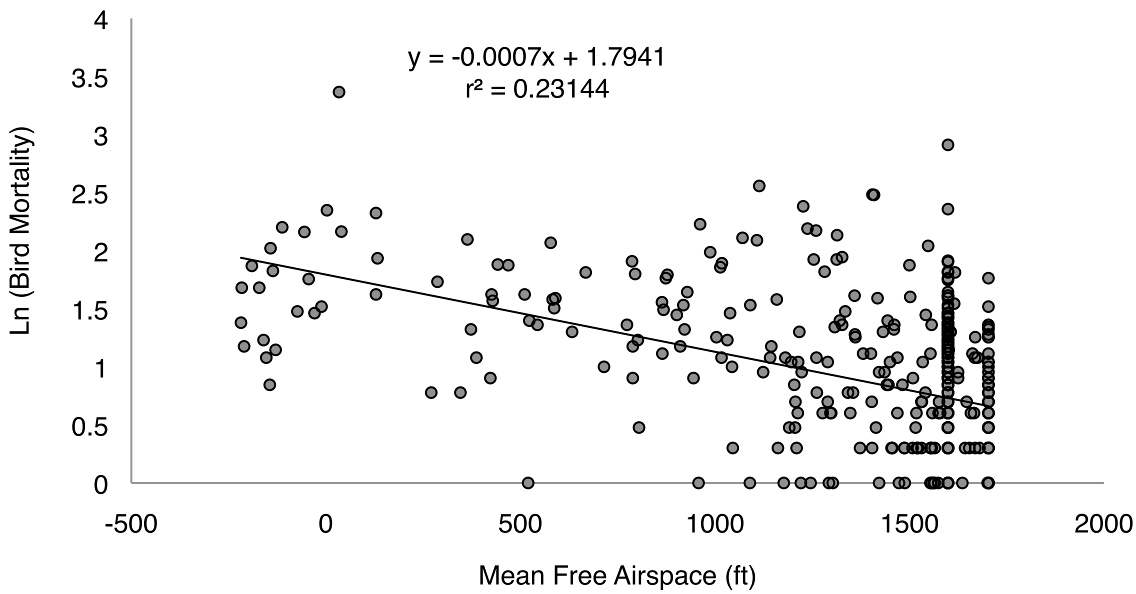

Figure 1. The relationship between bird mortality and mean free airspace at the Florida WCTV tower (data used in Crawford and Engstrom 2001) during fall migration from 1956–1967.

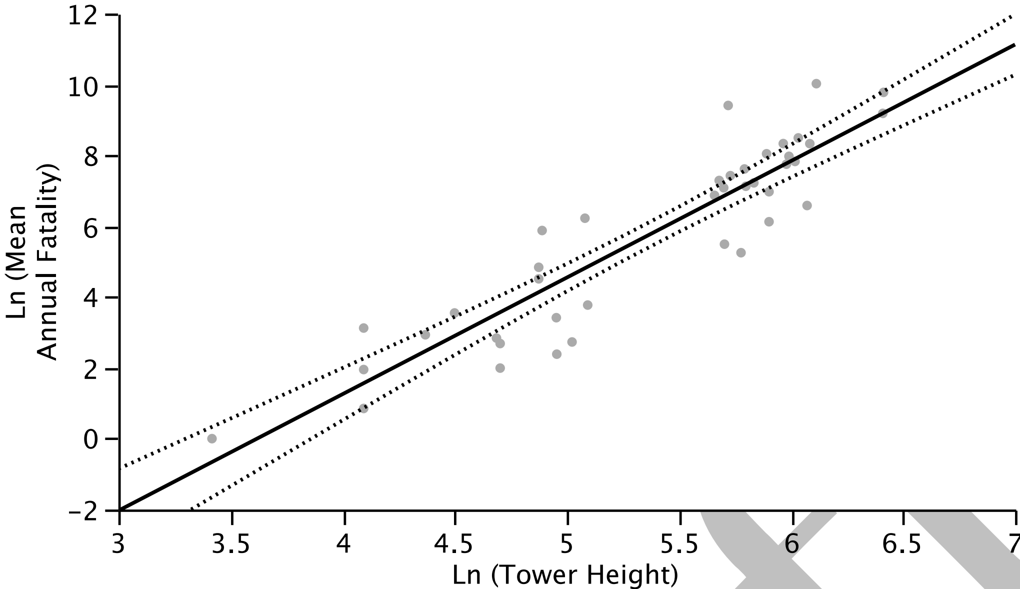

Figure 2. Regression and confidence intervals of annual avian fatalities adjusted for scavenging, search efficiency, and sampling scheme by tower height (Ln (Mean Annual Fatality) = –11.90236 + 3.2894304· Ln (Tower Height), r^2=0.84, p<0.0001).

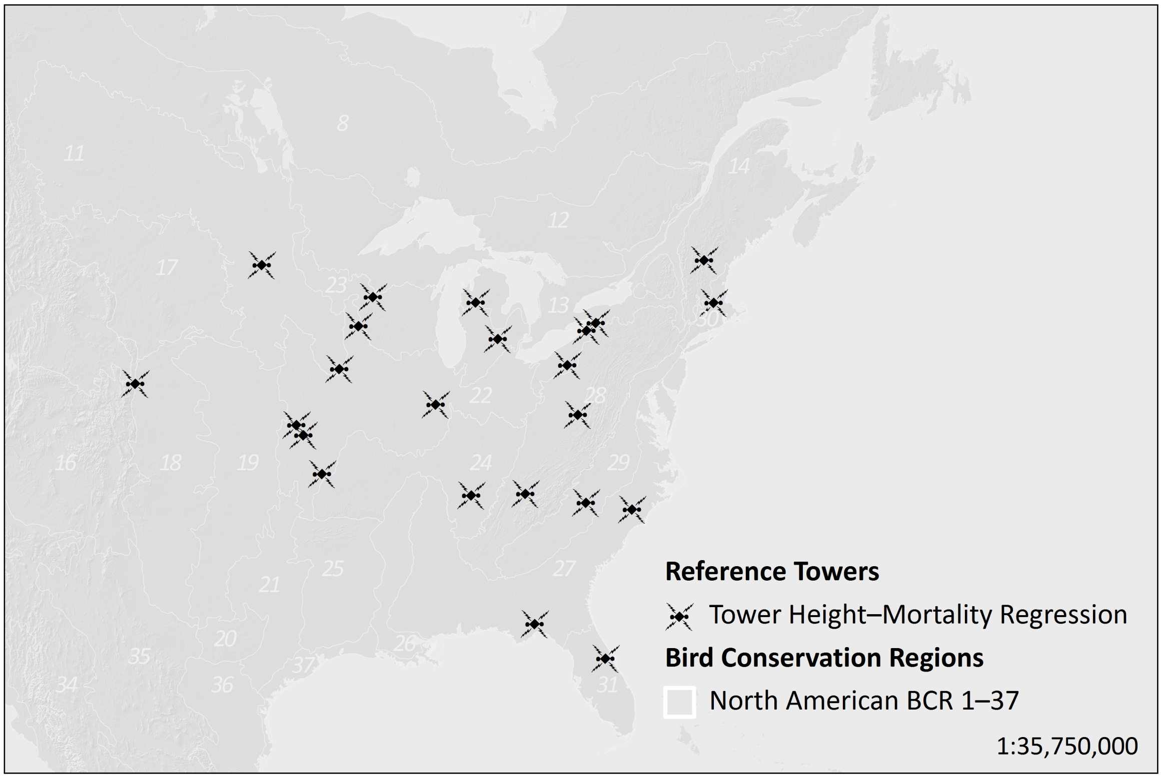

Figure 3. Bird Conservation Regions in North America with locations of towers used for height–mortality regression. Towers that are close to each other are indicated by a single symbol, and the towers studied by Gehring et al. (2009) in Michigan, which we use as aggregated data, are not shown.

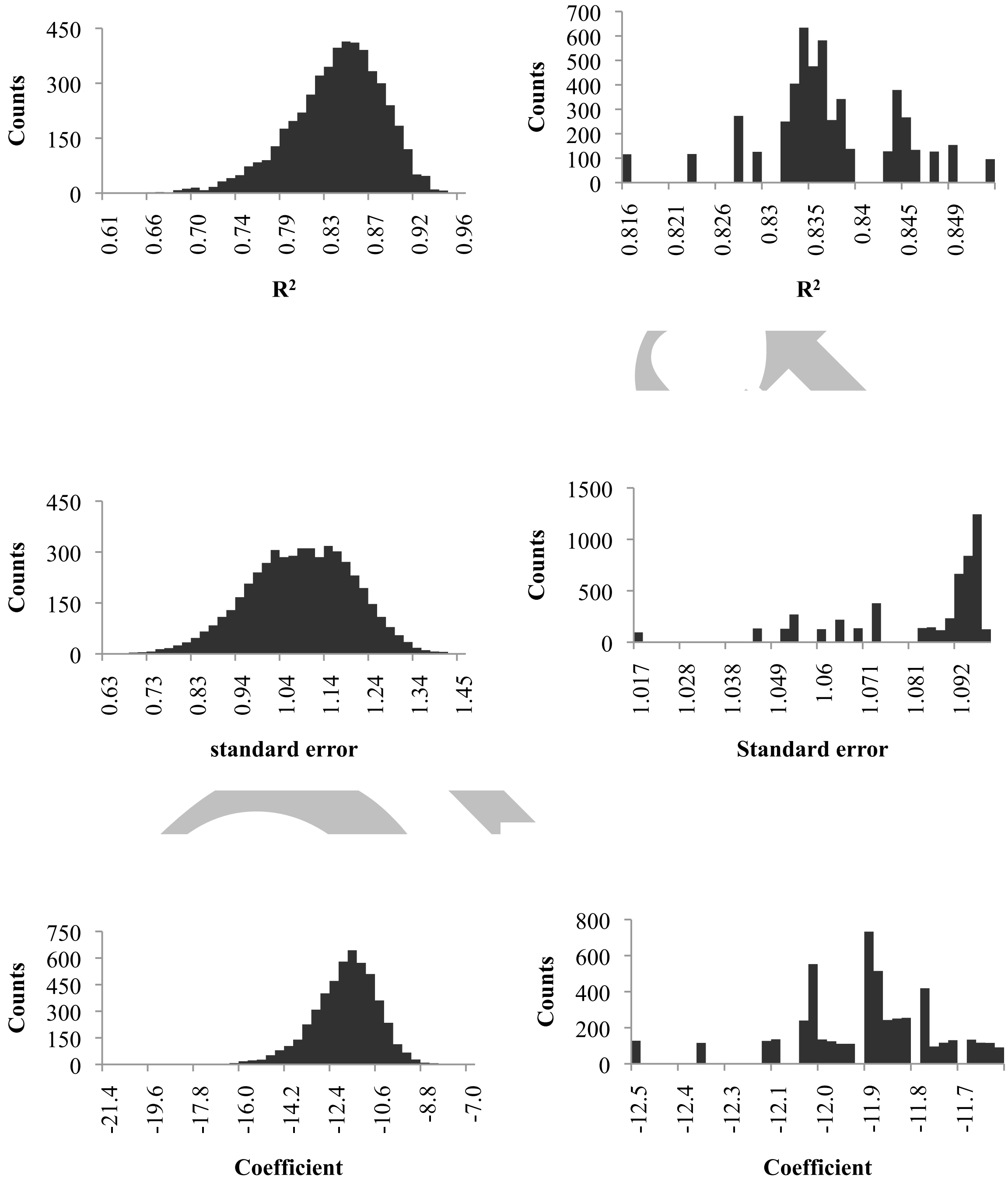

Figure 4. Distribution of counts for R^2 (adjusted), standard error and coefficient or 5000 iterations (subset = 20 studies, left; subset = 39 studies, right) for a linear regression model between the natural logs of tower height (m) and mean annual fatalities.

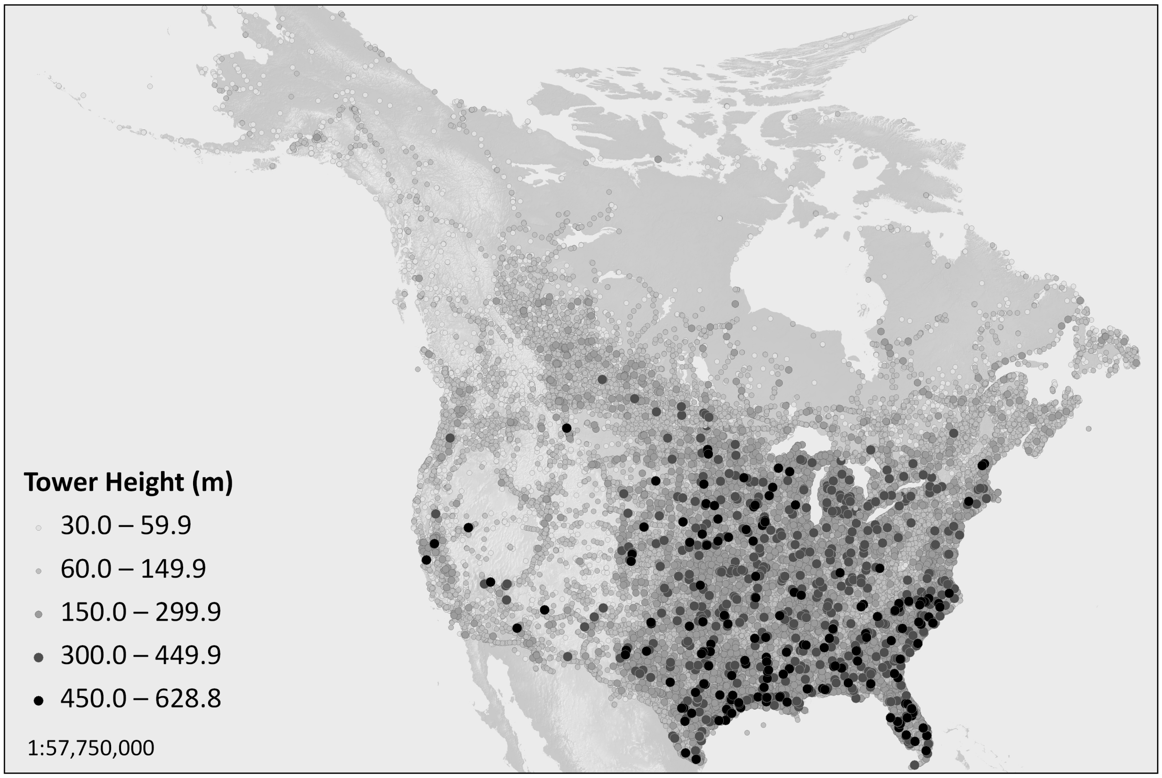

Figure 5. Map of communication towers in the U.S. (FCC database) and Canada (NAV CANADA database) by height class.

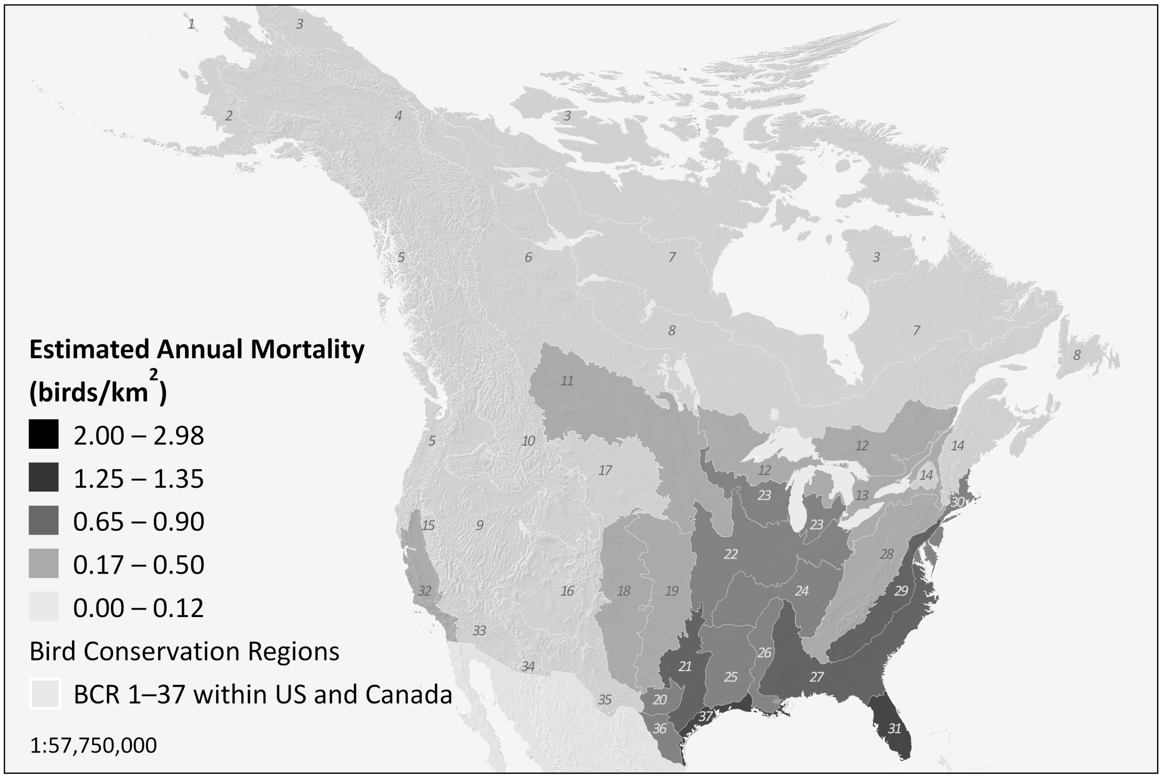

Figure 6. Estimated annual avian mortality by area within Bird Conservation Regions.