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An Estimate of Avian Mortality at Communication Towers in the United States and Canada

Travis Longcore
*The Urban Wildlands Group*, longcore@urbanwildlands.org

Catherine Rich
*The Urban Wildlands Group*, crich@urbanwildlands.org

Pierre Mineau
*National Wildlife Research Centre*, Pierre.Mineau@ec.gc.ca

Beau MacDonald
*The Urban Wildlands Group*, beaumacdonald@sbcglobal.net

Daniel G. Bert
*Carleton University*, dan.bert@glel.carleton.ca

*See next page for additional authors*

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Authors
Travis Longcore, Catherine Rich, Pierre Mineau, Beau MacDonald, Daniel G. Bert, Lauren M. Sullivan, Erin Mutrie, Sidney A. Gauthreaux Jr., Robert L. Crawford, Michael L. Avery, Albert M. Manville II, Emilie R. Travis, and David Drake
An Estimate of Avian Mortality at Communication Towers in the United States and Canada

Travis Longcore1,2,†, Catherine Rich1, Pierre Mineau3, Beau MacDonald1, Daniel G. Bert3, Lauren M. Sullivan4, Erin Mutrie3, Sidney A. Gauthreaux Jr.5, Michael L. Avery6, Robert L. Crawford7, Albert M. Manville II8, Emilie R. Travis9, David Drake9

Abstract

Avian mortality at communication towers in the continental United States and Canada is an issue of pressing conservation concern. Previous estimates of this mortality 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 a regression relating avian mortality to tower height. This equation was derived from 38 tower studies for which mortality data were available and corrected for sampling effort, search efficiency, and scavenging where 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 mortality at towers is 6.8 million birds per year in the United States and Canada. Bootstrapped subsampling indicated that the regression was robust to the choice of studies included and a comparison of multiple regression models indicated that incorporating sampling, scavenging, and search efficiency adjustments improved model fit. Estimating total avian mortality is only a first step in developing an assessment of the biological significance of mortality at communication towers for individual species or groups of species. Nevertheless, our estimate can be used to evaluate this source of mortality, develop subsequent per-species mortality estimates, and motivate policy action.

Introduction

On the morning of September 11, 1948, “a good number of dead, dying, and exhausted birds” were found at the base of the WBAL radio tower in Baltimore, Maryland [1]. Reports of such avian mortality at communication towers in North America became common in the 1950s [2-7]. These observations were consistent with the long documented mortality of birds at lights, including lighthouses [8], light towers [9], buildings [1,10], and ceilometers [1,11]. Although initially dismissed as being of minor consequence [12], the ongoing and chronic mortality of nocturnally migrating birds at lighted structures has become a recognized conservation issue [7,13-15]. Bats are also killed in collisions with tall towers in unknown numbers [16-18]. An estimate of the total number of birds killed at communication towers in the United States and Canada is particularly relevant because the current transition from analog to exclusively digital broadcasting in the United States is expected to lead to the construction of more tall towers and a similar trend will likely follow in Canada.

In 1979, Banks [13] developed a widely circulated estimate of avian mortality at television towers, which revised upward a previous estimate by Mayfield [12]. In Banks’s assessment of various sources of human-caused avian mortality, he extrapolated the results of three studies at tall towers – two in Florida [19,20] and one in North Dakota (for which he did not provide a citation but which was almost certainly [21]) – 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 estimate of annual mortality was 1,250,000 [13]. Also in 1979, Avery [22] applied bird mortality results from seven 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 the U.S. Fish and Wildlife Service (USFWS) in 2001 [14,23] adjusted the Banks estimate by accounting for the increased number of towers since 1979. Application of Banks’s...
method today results in an estimate of 4–5 million birds killed annually by tall towers, with Manville [15,24] indicating a possibility of mortality an order of magnitude higher.

No estimate of avian mortality at communication towers has been made for the United States and Canada as a whole, and the only estimate for Canada was presented in a preliminary unpublished report preceding this paper. The bulk of species killed at towers in the United States and Canada are Neotropical migrants, i.e., birds that breed in Canada and the United States and spend the non-breeding period south of the U.S. border [13,25]. Because the ranges of these species extend into Canada, mortality in both the United States and Canada contribute to their population dynamics.

In this paper we develop a new estimate of avian mortality at communication towers in the United States and Canada. This estimate derives from a review and re-analysis of tower mortality studies (following [26]). We improve on Longcore et al. [26] by adjusting mortality records at towers for sampling effort, search efficiency, and scavenging, and by incorporating additional studies. We produced a regression for avian mortality by tower height and then applied this regression to a geographic database of communication towers for the United States and Canada. This approach recognizes that taller towers kill more birds on average than do shorter towers [26–28], but also incorporates mortality estimates for lighted towers that are less than 600 ft (≈180 m) above ground level (AGL), which have previously been left out of estimates of total avian mortality. These “shorter” (60–180 m) lighted towers, which constitute >95% of lighted towers, do regularly kill birds [28–30] and their sheer number argues against ignoring them. We do not, however, estimate mortality from collisions with other lighted structures. Attraction to light at night leads to avian mortality at buildings, monuments, cooling towers, bridges, offshore platforms, ships, lighthouses, and wind turbines [24,31,32], and the same group of species (Neotropical migrants) are especially susceptible.

Our goal is to improve upon past estimates, which relied on a very limited set of data and did not reflect current understanding of the tower height–mortality relationship. Because of the nature of the existing data on avian mortality at towers and the lack of a systematic continent-wide survey effort, additional field studies will be required to refine further our approach. Our results do, however, increase both the transparency and accuracy associated with the estimate of this source of avian mortality.

### Methods

We assigned average mortality values to tower height classes (every 30 m) using a regression of tower height by annual mortality (following [26]). Longcore et al. [26] identified reports of birds killed at 26 communication towers over at least two migratory

#### Table 1. Average search and scavenging rates taken from pesticide impact studies [42].

| Habitat            | Body size    | Search rate (# study plots) | Percentage lost to scavenging | Detection rates (studies combining search and scavenging rates) |
|--------------------|--------------|----------------------------|-------------------------------|---------------------------------------------------------------|
| Shrub/wood edge    | Small-medium | 41.0% (301)                | 20.9%                         | 22.8% (94)                                                   |
| Shrub/wood edge    | Large        | 67.6% (29)                 | -                             | -                                                             |
| Bare/open          | Small-medium | 64.6% (359)                | 28.4%                         | 18.6% (56)                                                   |
| Bare/open          | Large        | 88.1% (17)                 | -                             | -                                                             |

Search and detection rates are based on daily averages weighted by the number of study plots. Search rates represent the proportion of carcasses found over the total number still present at the time of search. Scavenging rates represent daily measurements averaged over all plots without regard for the number of placed carcasses. Search rates are undoubtedly at the high end of that which is possible because the search procedures were optimized, always including trained lines of searchers spaced optimally for the habitat as well as the use of search dogs in some studies.

#### Table 2. 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%                       |
|                                 | Brush and other visual obstructions | 50%                                                  | 85%                                                       | 42%                       |
| Height class 2 (201–400 m), regular mortality, more dispersed | Open habitat       | 65%                                                  | 55%                                                       | 36%                       |
|                                 | Brush and other visual obstructions | 40%                                                  | 70%                                                       | 28%                       |
| Height class 3 (≥401 m), dependable mortality, carcasses widely dispersed | Open habitat       | 55%                                                  | 30%                                                       | 16%                       |
|                                 | Brush and other visual obstructions | 30%                                                  | 55%                                                       | 16%                       |

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### Table 3. Summary of factors used to develop the search and scavenging correction for bird mortality at communication towers.

| Reference | Cover Description | Cover Daily | Tower Height (m) | Scavenger Control | Scavenging Measured | Search Efficiency Measured | Measured or Assumed Search Rate | Measured or Assumed Scavenging Rate | Overall Detection Rate |
|-----------|-------------------|-------------|------------------|-------------------|---------------------|---------------------------|-------------------------------|----------------------------------|------------------------|
| [69]      | burned spring, hayed fall | No          | 30.5             | no                | no                  | no                        | 0.750                         | 0.200                            | 0.600                  |
| [49]      | cleared periodically | No          | 60               | yes               | yes                 | yes                       | 0.406                         | 0.392                            | 0.247                  |
| [34]      | mowed at least once per season | Yes         | 60               | no                | yes                 | yes                       | 0.294                         | 0.076                            | 0.271                  |
| [34]      | mowed at least once per season | Yes         | 60               | no                | yes                 | yes                       | 0.294                         | 0.076                            | 0.271                  |
| [34]      | mowed regularly     | Yes          | 79               | no                | yes                 | yes                       | 0.294                         | 0.076                            | 0.271                  |
| [40]      | Mowed               | Yes          | 90               | no                | yes                 | no                        | 0.750                         | 0.100                            | 0.675                  |
| [34]      | mowed at least once per season | Yes         | 97.5             | no                | yes                 | yes                       | 0.290                         | 0.113                            | 0.257                  |
| [34]      | mowed regularly     | Yes          | 108.5            | no                | yes                 | yes                       | 0.290                         | 0.113                            | 0.257                  |
| [34]      | mowed regularly     | Yes          | 110.3            | no                | yes                 | yes                       | 0.290                         | 0.113                            | 0.257                  |
| [70]      | bare ground and pavement under tower, weeds/grasses elsewhere | No          | 133              | no                | no                  | no                        | 0.750                         | 0.200                            | 0.600                  |
| [34]      | mowed regularly     | Yes          | 141.7            | no                | yes                 | yes                       | 0.380                         | 0.213                            | 0.299                  |
| [34]      | alfalfa field, mowed infrequently | Yes         | 142              | no                | yes                 | yes                       | 0.380                         | 0.213                            | 0.299                  |
| [33]      | rocky, some shrub   | No           | 152              | no                | yes                 | yes                       | 0.850                         | 0.030                            | 0.825                  |
| [71]      | most birds measured fell on roof of building | No          | 161              | *yes (roof)       | no                  | no                        | 0.750                         | 0.200                            | 0.600                  |
| [34]      | mowed regularly     | Yes          | 163              | no                | yes                 | yes                       | 0.380                         | 0.213                            | 0.299                  |
| [3,72-88] | wooded/rocky and roof of building | No          | 287              | *yes (roof)       | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [89]      | cut grass (cut to different lengths)/paved | Yes but only in the first year 1971 | 293              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [5]       | corn/soybean field  | No           | 299              | no                | no                  | no                        | 0.400                         | 0.300                            | 0.280                  |
| [90]      | unknown (probably open or mowed) | No          | 300              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [91]      | Open                | Yes          | 305              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [40]      | Mowed               | Yes          | 308              | yes               | no                  | no                        | 0.650                         | 0.100                            | 0.585                  |
| [89]      | cut grass (cut to different lengths)/paved | Yes but only in the first year 1971 | 323              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [89]      | cut grass (cut to different lengths)/paved | Yes but only in the first year 1971 | 328              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [89]      | cut grass (cut to different lengths)/paved | Yes but only in the first year 1971 | 330              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [90]      | unknown (probably open or mowed) | No           | 342              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [92]      | dirt, weedy sand, grass/low weed under guy wires, dense vegetation everywhere else | No           | 362              | no                | no                  | no                        | 0.400                         | 0.300                            | 0.280                  |
| [21,50,51] | Dense               | Yes          | 366              | no                | yes                 | no                        | 0.400                         | 0.100                            | 0.360                  |
| [93]      | Unknown             | No           | 366              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
| [90]      | unknown (probably open or mowed) | No           | 390              | no                | no                  | no                        | 0.650                         | 0.450                            | 0.358                  |
seasons (e.g., spring and fall, two falls), consisting of a minimum of 10 total carcass-searching visits per site. We added figures from additional studies [33,34], tested the sensitivity of the regression to inclusion of studies, and developed adjustments for sampling effort, search efficiency, and scavenging to produce estimates of mortality.

Sensitivity of Tower Height–mortality Regression

We collected as many studies of bird mortality at communication towers as possible from the literature and, when necessary, obtained raw data from study authors. Some studies had to be dropped from our analysis (e.g., [28]) because we were unable to obtain data from study authors and published reports did not allow us to assign mortality to specific towers. Because the number of tower studies available to us was finite, and because the choice of studies may have influenced our results, we tested the extent to which the regression was robust to sampling variation among the towers available for analysis. We used a randomization and resampling procedure to select random subsets of the 38 towers included in the analysis. To explore a range of plausible tower subsets that could produce a regression, we resampled subsets that included just under half of the available towers (18) up to those with one fewer than the complete dataset (37 towers) and reiterated the sampling procedure 5,000 times. We used the natural logarithm of both the dependent and independent variables to normalize their distributions.

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. Some authors have opted to apply searching and scavenging factors to final kill estimates (e.g., [28,35]). Recognizing that search efficiency and scavenging losses are likely tower-specific, we opted to correct the number of kills at each tower before regressing these estimated losses against tower height.

We assumed that scavenging would be lower at a small tower that sporadically generates only a few mortalities compared with a well-established tall tower that kills birds reliably and therefore maintains scavenger interest [36–39]. This assumption is supported by high scavenging rates documented at tall towers such as WCTV in Florida [20,36,38] and rapid increases in scavenging when researchers provide carcasses [33]. Even with extensive scavenger control efforts, Stoddard estimated that he was losing at least 10% of bird carcasses to scavengers daily [40]. Therefore, we adjusted our scavenging rate by tower height.

We assumed that it is easier to find carcasses under a short tower because carcasses are likely to be less dispersed under shorter guy wires or in the absence of guy wires. Whether the area around the tower is bare or heavily vegetated will affect both scavenging and search rates [41]. Open habitats with little concealing vegetation are, predictably, more conducive to efficient searching for carcasses [41]. Scavengers detecting prey by sight can find the carcasses more easily as well. Notwithstanding the use of smell by some carnivores to find prey, dense cover makes it more difficult in general for both scavengers and searchers to find carcasses [42]. Support for our assumptions about the effect of cover on these rates is found in research on avian mortality caused by pesticides, power lines, and wind turbines [41–45]. We avoided attempts to calculate probability of detection by searchers that involved the “life expectancy” of carcasses because these methods are biased [46]. If a carcass was not found on the first search day, 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
Table 4. Summary data with sampling efficiency correction for the 38 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 (raw) | Mean annual fatalities (corrected sampling and scavenging) |
|-----------|-----------------|------------|----------|---------------|---------------------|-------------------|--------------|--------------------------------------|----------------------------------|----------------|---------------------------|----------------------------------------------------------------|
| [89]      | 30.5            | 1998       | 1999     | 25/year       | yes                 | bad weather       | 1            | 0.44                                 | 0.36                             | 0              | 0.0                       | 0.0                                                            |
| [49]      | 60              | 2000       | 2004     | average >70/year | yes               | bad weather       | 4            | 0.50                                 | 0.50                             | 15             | 3.8                      | 30.4                                                           |
| [34]      | 60              | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 3              | 1.5                      | 5.5                                                            |
| [34]      | 60              | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 1              | 0.5                      | 1.8                                                            |
| [34]      | 79              | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 8              | 4.0                      | 14.8                                                           |
| [40]      | 90              | 1998.5     | 2000     | >330/year     | no                 | n/a               | 1.5          | 1.00                                 | 1.00                             | 21             | 14.0                     | 20.7                                                           |
| [34]      | 109             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 7              | 3.5                      | 13.6                                                           |
| [34]      | 110             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 6              | 3.0                      | 11.7                                                           |
| [34]      | 110             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 3              | 1.5                      | 5.8                                                            |
| [70]      | 133             | 1958       | 1960     | <60/year      | no                 | n/a               | 2            | 1.00                                 | 1.00                             | 267            | 133.5                    | 222.5                                                          |
| [34]      | 142             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 14             | 7.0                      | 23.4                                                           |
| [34]      | 142             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 5              | 2.5                      | 8.4                                                            |
| [33]      | 152             | 2004       | 2006     | >52/year      | yes                | bad weather + weekly | 2 | 0.90                                 | 0.58                             | 11             | 5.5                      | 10.5                                                           |
| [71]      | 161             | 1980       | 1986     | 15.25/year average | yes               | bad weather       | 6            | 0.44                                 | 0.36                             | 700            | 116.7                    | 515.6                                                          |
| [34]      | 163             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 20             | 10.0                     | 33.4                                                           |
| [3,72–88] | 287             | 1956.5     | 1973     | <60/year      | no                 | n/a               | 18.25       | 1.00                                 | 1.00                             | 6470           | 354.5                    | 991.7                                                          |
| [89]      | 293             | 1969       | 1999     | unknown       | yes                | bad weather       | 30           | 0.44                                 | 0.36                             | 8011           | 267.0                    | 1998.4                                                         |
| [5]       | 299             | 1955       | 1957     | 7 confirmed   | yes                | big kills         | 2            | 0.66                                 | 0.79                             | 486            | 243.0                    | 1149.1                                                         |
| [90]      | 300             | 1959.5     | 1964     | unknown       | yes                | bad weather       | 4.5          | 0.44                                 | 0.36                             | 199            | 44.2                     | 330.9                                                          |
| [91]      | 305             | 1957       | 1995     | >180/year     | no                 | n/a               | 38           | 1.00                                 | 1.00                             | 121560         | 3198.9                    | 8948.1                                                         |
| [40]      | 308             | 1970       | 1983     | >330/year     | no                 | n/a               | 13           | 1.00                                 | 1.00                             | 8035           | 618.1                    | 1056.5                                                         |
| [89]      | 323             | 1969       | 1999     | unknown       | yes                | bad weather       | 30           | 0.44                                 | 0.36                             | 1043           | 34.8                     | 260.2                                                          |
| [89]      | 328             | 1969       | 1999     | unknown       | yes                | bad weather       | 30           | 0.44                                 | 0.36                             | 11092          | 369.7                    | 2766.9                                                         |
| [89]      | 330             | 1973       | 1992     | unknown       | yes                | bad weather       | 19           | 0.44                                 | 0.36                             | 4310           | 226.8                    | 1697.6                                                         |
| [90]      | 342             | 1958.8     | 1964     | unknown       | yes                | big kills         | 5.25        | 0.66                                 | 0.79                             | 1740           | 331.4                    | 1227.5                                                         |
| [92]      | 362             | 1970       | 1972     | unknown       | yes                | bad weather       | 2            | 0.44                                 | 0.36                             | 995            | 497.5                    | 475.36                                                         |
| [211]     | 362             | 1972       | 1974     | >180/year     | no                 | n/a               | 2            | 1.00                                 | 1.00                             | 785            | 392.5                    | 1090.3                                                         |
| [93]      | 366             | 1962.5     | 1964     | 12 spring, 12 fall | yes               | bad weather       | 1.5          | 0.44                                 | 0.36                             | 125            | 83.3                     | 623.6                                                         |
| [90]      | 390             | 1958.8     | 1964     | unknown       | yes                | overcast          | 5.25        | 0.44                                 | 0.36                             | 3972           | 756.6                    | 566.18                                                         |
| [34]      | 396             | 2007       | 2008     | 45 spring, 45 fall | no                | n/a               | 2            | 1.00                                 | 1.00                             | 760            | 380.0                    | 193.17                                                        |
| [94]      | 400             | 1969       | 1974     | <10/year      | yes                | big kills         | 5            | 0.66                                 | 0.79                             | 3507           | 701.4                    | 2597.8                                                         |
| [95,96]   | 411             | 1969.5     | 1971     | unknown       | yes                | bad weather       | 1.5          | 0.66                                 | 0.79                             | 508            | 338.7                    | 2717.7                                                         |
| Tower height (m) | Start year | End year | No. of years | Sampling strategy | EndYear | Sampling days | Average correction sampling (spring) | Average correction sampling (fall) | No. of birds collected | Mean annual fatalities (corrected sampling and scavenging) | Mean annual fatalities (raw) |
|-----------------|------------|----------|--------------|-------------------|---------|---------------|--------------------------------------|----------------------------------|-----------------------|-------------------------------------------------------------|-------------------------------------------------------------|
| 150.5           | 1965       | 1997     | 32           | no                | 20192   | 1.00          | 0.25                                 | 0.25                             | 20192                 | 794.3                                                       | 794.3                                                       |
| 434             | 2007       | 2008     | 2           | no                | 237     | 1.00          | 0.25                                 | 0.25                             | 237                   | 18.5                                                        | 18.5                                                        |
| 499             | 1999       | 2000     | 2           | yes               | 945     | 0.36          | 0.25                                 | 0.25                             | 945                   | 18.5                                                        | 18.5                                                        |
| 1972            | 1997       | 2000     | 3           | yes               | 91.90   | 0.79          | 0.25                                 | 0.25                             | 91.90                 | 18.5                                                        | 18.5                                                        |
| 1992            | 1987       | 1992     | 5           | yes               | 945     | 0.36          | 0.25                                 | 0.25                             | 945                   | 18.5                                                        | 18.5                                                        |
| 1987            | 1987       | 1987     | 1           | yes               | 945     | 0.36          | 0.25                                 | 0.25                             | 945                   | 18.5                                                        | 18.5                                                        |
| 1975            | 1975       | 1975     | 1           | yes               | 945     | 0.36          | 0.25                                 | 0.25                             | 945                   | 18.5                                                        | 18.5                                                        |

Adjustment for Sampling Effort and Design

Studies included in the tower height–mortality regression varied in sampling design and duration. Following Longcore et al. [26], we required a minimum of 10 searches for a study to be included. 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 (Table 4). The logic behind this approach is that many high avian mortality days are correlated with these factors [31]. Nevertheless, “trickle kills” on fair weather days even outside the typical migration period can contribute substantially to overall mortality [40]. Substantial mortality during clear and calm weather during the migration season has also been documented [30,50] (Figure 1). For these reasons we used raw data from 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 [40] and North Dakota “Omega” tower [21,51,52] – as a baseline to develop estimates of the effectiveness of the various sampling designs for the 38 tower studies included in our dataset. The Florida estimates were averaged over the 10 years of sampling during which height of tower and predator control were the same; the North Dakota estimates are for two years of sampling. When the estimate was (partially) based on sampling outside the migratory period (as defined), we used the Florida dataset, which had continuous, year-round sampling. We did not, however, correct upward all kill estimates to account for the trickle of kills recorded in the non-migratory seasons. We believe, therefore, that our estimates are conservative. To control for differences between spring and fall migration we developed estimates for both spring and fall separately.

To adjust for the kills between sampling days during the migratory seasons we resampled (with replacement) daily mortality data from the Florida and North Dakota datasets 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 average bird mortality for 5,000 iterations and then used the ratio of the average bird mortality from the 5,000 iterations to the total number of birds killed during either spring or fall migration or outside of the migration period to adjust mortality estimates for studies without daily sampling. We averaged estimates between the Florida and North Dakota datasets. This adjustment was applied to studies where researchers sampled on bad weather days (see below) and to those with weekly sampling outside the migration period.

For studies that did not provide complete details on their sampling design, we made simplifying assumptions (see below). 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., [28]) monitoring only occurred during the three-week peak of migration. We determined the peak for the Florida and North Dakota datasets by plotting the number of birds killed (from the raw data) against Julian date for all years of data combined and using negative exponential smoothing.

Some investigators 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 resampling procedure to randomly select a day within that sampling interval. If no sampling interval was defined, selection was random.

Some investigators sampled on so-called “bad weather days” or following bad weather nights, i.e., overcast, often associated with advancing cold fronts and potentially including precipitation. Usually no other information was provided to define bad weather or the number of days when bad weather occurred. High bird mortality at communication towers is correlated with bad weather days [40,50,53]. This is shown by plotting ln(n+1)-transformed daily mortality data from the Florida tower dataset for the 1956–1967 fall migrations against the mean free airspace (distance between the top of the tower and the bottom of the cloud cover). Days where maximum free airspace was recorded were excluded from analysis because measurements did not vary for total ceiling greater than 610 m (2,000 ft). Mortality for days with mean ceiling at the maximum was 4.0–8.0 birds per day (95% C.I., n = 871), while mortality for all days with less than the maximum ceiling was 16.0–33.5 birds per day (95% C.I., n = 569). Considering these remaining points, a linear regression reveals a highly significant effect of mean free airspace, but also low explanatory power (Figure 1). Based on these data, we used days with mean free airspace equal to or below 335 m (1,100 ft) as an index of bad weather days because mortality was significantly lower on days with airspace greater than 335 m (10.3–17.8 birds per day, 95% C.I., n = 387) compared with days with airspace below this threshold (21.5–73.3 birds per day, 95% C.I., n = 182).

**Figure 1. Relationship of bird fatalities to free airspace at WCTV Tower, 1956–1967.** Raw data from Crawford and Engstrom (2001) were used to plot daily bird fatalities against the mean free airspace between the top of the tower and the cloud ceiling each day. Days with maximum ceiling were excluded. Daily avian mortality increases significantly as free airspace decreases (Ln(Bird Fatalities +1) = 1.443928 – 0.0016667 · Mean Free Airspace (m), R² = 0.17, p<0.001).

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For some studies, the only information provided was the number of 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 were expected, given that this was the response obtained when we were able to contact researchers to ask about papers where this detail was not provided (e.g., J. Herron, pers. comm.).

Several researchers sampled only on days when so called “big kills” were reported. The definitions of “big kill” were not included. The typical daily trickle of dead birds for the Florida dataset over the 1956–1967 period was five. We therefore defined big kills as six or more birds located after any given night.

We investigated the sensitivity of our results to our assumptions about sampling effort by varying these assumptions for the 13 studies in our dataset that either did not indicate the number of days sampled or did not provide a definition of sampling design, or did neither. Some researchers had indicated that they had sampled on overcast or bad weather days or following bad weather days. For all of these studies and for those that did not mention anything specific, we made the conservative assumption that towers were sampled on bad weather days. We then recalculated the sampling adjustment and total mortality using three different scenarios: 1) researchers sampled on bad weather days and weekly during migration (e.g., [49]); 2) researchers sampled on bad weather days and weekly all year (e.g., [33]; Table 5. Regression results for mean annual fatalities by tower height, when unadjusted, corrected for sampling only, corrected for search efficiency and scavenging only, and corrected for both sampling and search efficiency/scavenging, with estimated annual fatalities after back transformation, adjustment for bias, and application to all towers in the United States and Canada.

| Slope Correction | Slope Intercept | R2 adj | RMSE | F       | P       | Estimated annual fatalities (million) |
|------------------|-----------------|--------|------|---------|---------|---------------------------------------|
| No corrections   | 2.8257          | –10.8626 | 0.78 | 1.110   | 133.5046 | 0.0001  | 1.38                                  |
| Sampling correction | 3.0962       | –11.9490 | 0.80 | 1.151   | 148.8302 | <0.0001 | 2.06                                  |
| Searcher/scavenging correction | 3.2024   | –11.8012 | 0.82 | 1.110   | 171.2329 | <0.0001 | 4.31                                  |
| Both corrections | 3.4684          | –12.8600 | 0.84 | 1.137   | 191.6163 | <0.0001 | 6.80                                  |

Figure 2. Bird Conservation Regions and locations of towers used for tower height–mortality regression.
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Avian Mortality at Communication Towers

Figure 3. Regression and 95% confidence intervals of annual avian fatalities by tower height. Annual avian fatalities were adjusted for sampling effort, search efficiency, and scavenging and regressed by log-transformed tower height ($\ln(\text{Mean Annual Fatalities} + 1) = 3.4684 \cdot \ln(\text{Tower Height}) - 12.86, R^2 = 0.84, p < 0.0001$).

We overlaid locations of towers within each Bird Conservation Region (BCR) in the study area and calculated the number of towers in each 30 m height class for all towers $\geq 60$ m. Bird Conservation Regions 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 and government agencies. BCRs are based on the North American ecoregions developed to promote international conservation efforts [57]. 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 sampling effort, search efficiency, and scavenging as 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 describes studies from east of the Rocky Mountains, we included the West as well for purposes of estimating total mortality, a decision supported by records of tower mortality in Colorado [33], New Mexico [58], and Alaska [39], in addition to documented kills at lighthouses in California and British Columbia [60,61]. We did not attempt to assign differential mortality for so-called flyways because radar studies and other observations strongly support the existence of “broad front” migration [62,63]. To investigate this assumption, we plotted the residuals of the tower height–mortality regression by their geographic coordinates and calculated Moran’s I as a measure of spatial autocorrelation. We acknowledge that local habitat factors may influence mortality at particular towers, but because only 18.4% of towers were originally selected for monitoring on the basis of knowledge of prior mortality (see below), it is unlikely that these variations would result in a systematic bias in the resulting mortality estimates.

To illustrate the contribution of each part of our adjustment to the final estimate of mortality, we calculated the extrapolated mortality estimates for the unadjusted mortality data, with the sampling correction only, with the search efficiency and scavenging corrections only, and corrected for all factors.
We do not report estimates of bird mortality at short (<60 m) towers in this paper because they contribute negligibly to overall annual bird mortality and are not usually illuminated unless located near an airport. We note, however, that single-night mortality events with several hundred identified dead birds at unlit, <60 m towers have been reported, often related to lighting at adjacent infrastructure [30], which is consistent with reports from turbines and towers monitored at industrial wind facilities [64]. Our analysis therefore applies to towers ≥60 m.

Results

Tower Height–mortality Regression

Towers used in the height–mortality regression were located throughout the eastern United States (Figure 2). We were able to confirm from original sources and personal communications that 68.4% of the towers were chosen for study with no prior knowledge of avian mortality; status is unknown for 13.2% of towers; and only 18.4% of towers were chosen with any knowledge of prior avian mortality. Log-transformed annual avian mortality, when adjusted for sampling effort, search efficiency, and scavenging, was significantly explained by log-transformed tower height in a linear regression ($R^2 = 0.84$, $F_{1,36} = 191.62$, $p<0.0001$) (Table 5; Figure 3).

Tower Height–mortality Regression Sensitivity to Study Inclusion

The median $R^2$ values of the resampled distributions are similar to those obtained from using all of the available studies (Figure 4, Table 6) and are not sensitive to the addition or elimination of a few or a set of studies. The results of the resampling procedure for subsets of 18 studies (a little under half of the studies) and for 37 studies (1 fewer than the total) show the range of influence that study inclusion could have on the regression line (Table 6).

Evaluation of Model Adjustment Factors

Models using either sampling correction alone or the combination of sampling correction with the combined search efficiency and scavenging correction were found to be superior to the model using tower height alone at explaining annual kills ($R^2 = 0.84$ vs. $R^2 = 0.79$; Table 5). Correcting for search efficiency and scavenging losses appeared to provide the best improvement to the overall model (Table 5).
Our database of 60 m towers included 70,414 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 (31,486; 50.3%) were freestanding with steady-burning lights at night, while the fewest towers (4,898; 7.8%) were guyed with strobe lights at night. 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 tower 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, already adjusted for sampling effort, search efficiency, and scavenging, ranged from zero for short unguyed towers to over 20,000 birds per year for the tallest guyed towers with steady-burning lights.

The back-transformed tower height–mortality regression, adjusted for bias (smearing estimator) and applied to towers in the continental United States and Canada, produced an annual mortality estimate of 6.8 million birds per year (Table 5). Extrapolation from the unadjusted data yielded an estimate of 1.4 million birds per year, meaning that our cumulative assumption is that searchers find only around 20% of the birds that are killed, because of search efficiency, scavenging, and incomplete sampling (Table 5).

These results are sensitive to the assumptions that were made about these factors. As an illustration, we calculated total mortality while assuming a constant search efficiency equal to the average of the measured search efficiency from those towers where this was measured (36.4%), which resulted in a total mortality estimate of 9.4 million birds per year. Applying the average scavenging rate (15.8%) to all towers resulted in a mortality estimate of 4.7 million birds per year. Using both averages (for scavenging and search efficiency) yielded an estimate of 6.4 million birds per year. For the sampling effort adjustments, recalculated mortality estimates for the three scenarios applied to studies with unknown sampling schemes were: 5.4 million birds per year for sampling only on big kill days, 5.7 million birds per year for sampling on bad weather days and weekly year round, and 6.2 million birds per year for sampling on bad weather days and weekly during migration only. Finally, if we recalculate mortality after omitting all towers selected with prior knowledge of any mortality on site (18.4% of our sample of towers), the estimate of total mortality declines to 5.5 million birds per year.

Over two-thirds of the estimated mortality is attributed to towers ≥300 m, of which only 1,040 were found in our database (1.6% of towers ≥60 m; Table 7). Fully 71% of mortality is attributed to the tallest 1.9% of towers. Shorter towers (60–150 m)

| Subset  | Parameter | 5%  | 95%  | Median |
|--------|-----------|-----|-----|-------|
| 18 studies | $R^2$ | 0.765 | 0.906 | 0.847 |
|         | slope     | 3.087 | 4.061 | 3.474 |
|         | intercept | −16.205 | −10.775 | −12.882 |
|         | standard error | 0.919 | 1.331 | 1.345 |
| 37 studies | $R^2$ | 0.828 | 0.853 | 0.841 |
|         | slope     | 3.414 | 3.591 | 3.465 |
|         | intercept | −13.556 | −12.556 | −12.845 |
|         | standard error | 1.093 | 1.153 | 1.146 |

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Table 7. Number of communication towers ≥60 m by type and associated avian mortality estimates for Canada and the continental United States.

| Country          | Height class (m) | Guyed towers with steady-burning lights | Guyed towers with strobe lights | Unguyed towers with steady-burning lights | Unguyed towers with strobe lights | Annual fatalities | Percent of fatalities |
|------------------|------------------|----------------------------------------|---------------------------------|-------------------------------------------|----------------------------------|-------------------|----------------------|
| United States    |                  |                                        |                                 |                                           |                                  |                   |                      |
| 60–90            | 5,901            | 863                                    | 17,693                          | 2,575                                     | 115,524                          | 1.76%             |                      |
| 90–120           | 10,023           | 1,696                                  | 10,004                          | 1,683                                     | 531,411                          | 8.07%             |                      |
| 120–150          | 2,938            | 505                                    | 2,922                           | 488                                        | 377,542                          | 5.74%             |                      |
| 150–180          | 1,992            | 311                                    | 661                             | 101                                        | 468,600                          | 7.12%             |                      |
| 180–210          | 343              | 46                                     | 107                             | 12                                         | 142,679                          | 2.17%             |                      |
| 210–240          | 174              | 54                                     | 51                              | 11                                         | 126,507                          | 1.92%             |                      |
| 240–270          | 109              | 57                                     | 29                              | 16                                         | 131,379                          | 2.00%             |                      |
| 270–300          | 76               | 61                                     | 18                              | 14                                         | 146,530                          | 2.23%             |                      |
| 300–330          | 271              | 128                                    | 0                               | 0                                          | 642,858                          | 9.77%             |                      |
| 330–360          | 115              | 28                                     | 0                               | 0                                          | 345,255                          | 5.25%             |                      |
| 360–390          | 78               | 22                                     | 0                               | 0                                          | 317,130                          | 4.82%             |                      |
| 390–420          | 47               | 16                                     | 0                               | 0                                          | 254,809                          | 3.87%             |                      |
| 420–450          | 35               | 10                                     | 0                               | 0                                          | 238,450                          | 3.62%             |                      |
| 450–480          | 66               | 23                                     | 0                               | 0                                          | 579,458                          | 8.80%             |                      |
| 480–510          | 25               | 10                                     | 0                               | 0                                          | 277,580                          | 4.22%             |                      |
| 510–540          | 24               | 8                                      | 0                               | 0                                          | 319,300                          | 4.85%             |                      |
| 540–570          | 8                | 9                                      | 0                               | 0                                          | 165,120                          | 2.51%             |                      |
| 570–600          | 18               | 15                                     | 0                               | 0                                          | 410,068                          | 6.23%             |                      |
| 600–630          | 38               | 27                                     | 0                               | 0                                          | 991,745                          | 15.07%            |                      |
| Subtotal         | 22,282           | 3,888                                  | 31,486                          | 4,898                                      | 6,581,945                        | 100.00%            |                      |
| Canada           |                  |                                        |                                 |                                           |                                  |                   |                      |
| 60–90            | 627              | 323                                    | 1,880                           | 968                                        | 13,980                           | 6.34%             |                      |
| 90–120           | 1,295            | 284                                    | 1,295                           | 284                                        | 69,981                           | 31.72%            |                      |
| 120–150          | 251              | 55                                     | 251                             | 55                                         | 32,797                           | 14.86%            |                      |
| 150–180          | 92               | 23                                     | 31                              | 8                                          | 22,363                           | 10.14%            |                      |
| 180–210          | 44               | 11                                     | 15                              | 4                                          | 19,085                           | 8.65%             |                      |
| 210–240          | 19               | 5                                      | 6                               | 2                                          | 13,757                           | 6.24%             |                      |
| 240–270          | 6                | 2                                      | 2                               | 1                                          | 6,640                            | 3.01%             |                      |
| 270–300          | 3                | 1                                      | 1                               | 0                                          | 4,884                            | 2.21%             |                      |
| 300–330          | 9                | 4                                      | 0                               | 0                                          | 21,267                           | 9.64%             |                      |
| 330–360          | 3                | 1                                      | 0                               | 0                                          | 8,973                            | 4.07%             |                      |
| 360–390          | 1                | 0                                      | 0                               | 0                                          | 2,996                            | 1.36%             |                      |
| 390–420          | 1                | 0                                      | 0                               | 0                                          | 3,912                            | 1.77%             |                      |
| Subtotal         | 2,349            | 709                                    | 3,480                           | 1,321                                      | 220,650                          | 100.00%            |                      |
| Total            | 24,631           | 4,597                                  | 34,966                          | 6,219                                      | 6,802,595                        |                    |                      |

1. 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.

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Contribute approximately 17% of all mortality because of their sheer numbers (Table 7).

Our estimates of mortality vary by region, influenced both by the size of the region and the number and height distribution of towers (Figure 6; Table 8). The number of towers in each BCR does not directly correlate with estimated annual mortality because of differing numbers and heights of towers. As a result, Peninsular Florida is associated with more mortality than all of Canada; even though fewer towers are reported in Peninsular Florida, they are on average much taller. The concentration of migrants resulting from Florida’s geographic position would increase mortality even more, but this factor is not considered in our method because mortality rates for any given tower height are assumed to be constant across the continent. The Southeastern Coastal Plain BCR accounts for greater mortality than other BCRs, followed by Eastern Tallgrass Prairie, Oaks and Prairies, and Piedmont (Table 8). Canadian mortality accounts for only a fraction of the total (approximately 3.2%), because Canada has far fewer, and generally 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 2). This may be a function of a higher number of nocturnal migrants in the East, different patterns of migration, 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 and also by testing the residuals for spatial autocorrelation. 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 in Colorado. Residuals were not spatially autocorrelated using inverse Euclidean distance weighting (Figure 7; Moran’s I = 0.09, z = 0.23, p = 0.816). More comprehensive surveys of towers in the West are needed to see if the lower mortality at the site in Colorado represents an anomaly or a different pattern of mortality in the West. Pending such further analysis, extrapolation of mortality at towers in the western portions of the United States and Canada should be regarded as provisional.

Discussion

Our total mortality estimate of 6.8 million birds per year is ~50% greater than the current USFWS estimate of 4–5 million birds per year [14,15,23,24]. Our results do not support the suggestion that mortality might be an order of magnitude higher [14,15], which had been made before this type of synthetic analysis had been attempted. Our approach to estimating total avian mortality at towers uses far more data than previous efforts. For example, Banks’s [13] estimate was based on mortality rates from only three tower studies and assumed that all towers caused the same rate of mortality, regardless of tower height. Our method incorporates evidence from 38 towers to establish the relationship between tower height and avian mortality. We accounted for the height distribution and physical characteristics of ~84,000 towers across the United States and Canada (including towers <60 m, which we mapped but did not include in our mortality estimates). Notwithstanding the sources of uncertainty in our estimate, the method improves previous efforts, is transparent, and can be revised in conjunction with additional field studies.

Although mortality at some towers has apparently declined over time [31], the influence of any such trend (if a true decline in mortality and not the result of increased scavenging) is offset by the large portion (>50%) of towers in the regression having survey end dates after 1990. If only these studies ending after 1990 are used in the regression, the total mortality estimate decreases to 4.8 million birds per year. The residuals of the tower height–mortality regression, however, are not significantly explained by the ending year of the survey (results not shown) so we did not exclude the older studies from our final regression. Even if the decline in number of birds killed at towers is a real phenomenon, the effect of these kills on sensitive species could still be substantial if populations have declined by a greater proportion.

Estimated tower mortality increases exponentially with tower height [26], which makes our results sensitive to the use of the height classes. For example, if we used the top of each height class rather than the middle to calculate total mortality, the estimate would increase by 25%. The use of the height classifications was necessary for ease of calculation and because attributes of the Canadian towers that were not known had to be assigned probabilistically. We used log transformations of both variables to normalize the distributions and because the total volume of airspace occupied by guy wires increases far more rapidly than does height. The increasing length of guy wires provides a mechanistic explanation for the exponentially increasing probability of avian collisions as tower height increases. Extremely tall towers also extend into the “normal” flight altitudes of many migrants so that mortality events can occur under clear skies and favorable migration conditions; this provides another plausible mechanism for the exponential increase in mortality rates observed by height. We also considered using separate regressions for towers less than and greater than 200 m, given the break in the data, but found that doing so had little effect on the overall

Figure 6. Estimated annual avian mortality from communication towers by Bird Conservation Region. High mortality estimates in Peninsular Florida and Southeastern Coastal Plain reflect the more numerous and taller communication towers in these regions. doi:10.1371/journal.pone.0034025.g006

Estimated Annual Mortality (birds/km²)
- 3.63 - 5.39
- 1.51 - 2.43
- 1.14 - 1.41
- 0.54 - 0.84
- 0.13 - 0.38
- 0.00 - 0.66
- North America BCR 1-37

1: 57,500,000
estimate and we could not formulate a functional explanation why the tower height–mortality relationship should change in this manner.

Further research is needed on the mortality rates at the tallest towers (i.e., >500 m). These data are needed to confirm that the tower height–mortality relationship is exponential [26]. The nature of this relationship is important because it leads directly to a policy recommendation of focusing on the tallest towers first for mitigation. If more extensive tower datasets show a different relationship (e.g., logistic) then mitigation actions would be much different, requiring treatment of many more towers to address the same proportion of mortality.

Producing this estimate of avian mortality at towers required many assumptions, the implications of which we have explored to the degree possible with the data available. By undertaking this exercise, we have reaffirmed what elements should be included in tower studies going forward – explicit measurement of search efficiency, scavenging rates, and the effect of sampling schemes for any study, as well as investigation of geographic variation in mortality and inclusion of towers representative of the extremes of

### Table 8. Total estimated annual avian mortality at towers ≥60 m in the United States and Canada by Bird Conservation Region (BCR).

| BCR | USA (lower 48 states) | Canada | Alaska | Total |
|-----|-----------------------|--------|--------|-------|
| 1–Aleutian Bering Sea | 0 | 0 | | |
| 2–Western Alaska | 155 | 155 | | |
| 3–Arctic Plains and Mountains | 542 | 83 | 625 |
| 4–Northwestern Interior Forest | 288 | 2,228 | 2,516 |
| 5–Northern Pacific Rainforest | 21,170 | 2,411 | 333 | 23,914 |
| 6–Boreal Taiga Plains | 24,591 | 24,591 | | |
| 7–Taiga Shield and Hudson Plains | 2,754 | 2,754 | | |
| 8–Boreal Softwood Shield | 20,650 | 20,650 | | |
| 9–Great Basin | 20,744 | 339 | 21,083 |
| 10–Northern Rockies | 8,653 | 1,925 | 10,578 |
| 11–Prairie Potholes | 265,244 | 63,032 | 328,276 |
| 12–Boreal Hardwood Transition | 139,535 | 34,564 | 174,099 |
| 13–Lower Great Lakes/St. Lawrence Plain | 83,185 | 51,175 | 134,360 |
| 14–Atlantic Northern Forest | 36,469 | 18,378 | 54,847 |
| 15–Sierra Nevada | 343 | 343 | | |
| 16–Southern Rockies/Colorado Plateau | 29,175 | 29,175 | | |
| 17–Badlands and Prairies | 54,040 | 54,040 | | |
| 18–Shortgrass Prairie | 243,791 | 243,791 | | |
| 19–Central Mixed-Grass Prairie | 333,211 | 333,211 | | |
| 20–Edwards Plateau | 81,827 | 81,827 | | |
| 21–Oaks and Prairies | 469,889 | 469,889 | | |
| 22–Eastern Tallgrass Prairie | 754,928 | 754,928 | | |
| 23–Prairie Hardwood Transition | 278,788 | 278,788 | | |
| 24–Central Hardwoods | 346,796 | 346,796 | | |
| 25–West Gulf Coastal Plain/Ouachitas | 321,983 | 321,983 | | |
| 26–Mississippi Alluvial Valley | 185,746 | 185,746 | | |
| 27–Southeastern Coastal Plain | 1,107,118 | 1,107,118 | | |
| 28–Appalachian Mountains | 263,368 | 263,368 | | |
| 29–Piedmont | 448,533 | 448,533 | | |
| 30–New England/Mid-Atlantic Coast | 96,197 | 96,197 | | |
| 31–Peninsular Florida | 341,774 | 341,774 | | |
| 32–Coastal California | 99,873 | 99,873 | | |
| 33–Sonoran and Mojave Deserts | 50,179 | 50,179 | | |
| 34–Sierra Madre Occidental | 875 | 875 | | |
| 35–Chihuahuan Desert | 16,559 | 16,559 | | |
| 36–Tamaulipan Brushlands | 105,545 | 105,545 | | |
| 37–Gulf Coastal Prairie | 373,609 | 373,609 | | |
| **Total** | **6,579,147** | **220,649** | **2,799** | **6,802,595** |

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the height distribution. Such research will help refine our regionalized mortality estimates.

In 1989, the Exxon Valdez oil spill killed approximately 250,000 birds in what has become the benchmark for a major environmental disaster [65]. Our estimates show that communication towers are responsible for bird deaths equivalent to more than 27 Exxon Valdez disasters each year. Our estimate of the number of birds killed annually by communication towers is 2–4 times greater than the estimate for annual fatalities from lead poisoning before lead shot was phased out for hunting waterfowl [66]. Previous efforts (e.g., [25]) and our compiled database illustrate that most of the birds killed at communication towers are Neotropical migrants, which have suffered population declines and many of which are formally recognized as “Birds of Conservation Concern” [67,68]. Data on per species mortality would provide even more clarity about the biological significance of avian mortality at communication towers. In a companion manuscript, we estimate species-specific losses based on total losses estimated here and species-specific casualty reports for Bird Conservation Regions following methods we developed previously [35]. But even without such estimates, the aggregate mortality numbers developed here should lead policymakers to pursue mitigation measures to reduce this source of chronic mortality.

Mitigation of avian mortality at communication towers could most practically be achieved by implementing several measures: 1) concomitant with permission from aviation authorities, remove steady-burning red lights from towers, leaving only flashing (not slow pulsing) red, red strobe, or white strobe lights [24,26,28,31]; 2) avoid floodlights and other light sources at the bases of towers, especially those left on all night [64]; 3) avoid guy wires where practicable [26,28]; 4) minimize the number of new towers by encouraging collocation of equipment owned by competing companies; and 5) limit height of new towers when possible. Concentrating on removing steady-burning lights from the roughly 4,500 towers ≥150 m tall in the United States and Canada with such lights should be a top priority because, according to our model, it would reduce overall mortality by approximately 45% through remedial action at only 6% of lighted towers.

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Author Contributions

Conceived and designed the experiments: TL CR PM DGB BM SAG. Performed the experiments: TL PM DGB BM LMS EM. Analyzed the data: TL PM DGB BM LMS EM. Contributed reagents/materials/analysis tools: TL PM DGB BM LMS EM ERT DD. Wrote the paper: TL CR PM DGB BM SAG MLA RLC AMM ERT.

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Figure 7. Distribution of residuals of tower height–mortality regression for 38 towers in the United States as adjusted for sampling effort, search efficiency, and scavenging. Contour lines indicate regions above and below the regression line. Although exhibiting a geographically variable pattern, the residuals are not significantly spatially autocorrelated. doi:10.1371/journal.pone.0034025.g007
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