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Review

Estimation of Bird-Vehicle Collision Mortality on U.S. Roads

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ABSTRACT Roads have numerous direct and indirect ecological impacts on wildlife. Vehicle collisions are a top impact of roads on birds, with tens of millions of birds thought to be killed each year in the United States. However, currently available mortality estimates are extrapolated from a single study. We reviewed the literature and used 20 mortality rates extracted from 13 studies to systematically quantify data-driven estimates of annual U.S. mortality from bird-vehicle collisions. We generated 4 separate estimates along with uncertainty using different subsets of data deemed to be rigorous enough to contribute relatively little bias to estimates. All of our estimates of vehicle mortality are higher than previous U.S. figures. When averaging across model iterations, we estimated that between 89 and 340 million birds die annually from vehicle collisions on U.S. roads. Sensitivity analyses indicated that uncertainty about survey-related biases (scavenger removal and searcher detection of carcasses) contributes the greatest amount of uncertainty to our mortality estimates. Future studies should account for these biases to provide more accurate local estimates of mortality rates and to inform more precise national mortality estimates. We found relatively little information available to quantify regional, seasonal, and taxonomic patterns of vehicle collision risk, and substantial uncertainty remains about whether collisions contribute to large-scale impacts on bird populations. Nonetheless, the large magnitude of bird mortality caused by vehicle collisions combined with evidence that collisions can contribute to local population declines for some species highlights the need for implementation of conservation and management actions to reduce this mortality. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS anthropogenic mortality, automobiles, birds, detection probability, roadkill, roads, scavenger removal, systematic review, United States, vehicles.

The global proliferation of road networks has led to a multitude of ecological impacts that affect biological diversity. In the United States, the greater than 6.5 million kilometers of roads (U.S. Department of Transportation 2012) ecologically affect at least 22% of the nation's land area (Forman 2000), causing loss and fragmentation of habitat; pollution with chemicals, light, and noise; alteration of animal movement and behavior; and direct mortality of wildlife from vehicle collisions (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003, Coffin 2007). For birds, vehicle collisions are one of the greatest threats posed by roads (Kociolek et al. 2011), with as many as 80 million birds thought to be killed annually in the United States (Erickson et al. 2005) and roughly 13 million birds estimated to be killed annually in Canada (Bishop and Brogan 2013). Moreover, roadkills have the potential to constitute the vast majority of total mortality for some bird species—most notably, barn owls (*Tyto alba*) (Moore and Mangel 1996, Newton et al. 1997). Roadkill mortality can also result in the creation of population sinks (Mumme et al. 2000, Boves and Belthoff 2012, Grilo et al. 2012) and may be an additive source of mortality that contributes to population declines (Bujoczek et al. 2011).

A large body of literature has identified numerous factors that influence bird-vehicle collision rates. Mortality rates have been found to increase with increasing traffic speed and volume (Case 1978) and rates are generally highest during spring and summer. Mortality rates are also greater for juvenile birds, in areas with favorable bird habitat in close proximity to the road, and where bird populations are abundant (Loos and Kerlinger 1993, reviewed by Erritzoe et al. 2003, Gunson et al. 2010, Boves and Belthoff 2012). In some cases, mortality rates have been found to increase with increasing width of the road corridor (Oxley et al. 1974) or to be greater along road segments that are elevated above the surrounding land (Baudvin 1997, Lodé 2000). Often, 2 or

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more of the above factors are strongly correlated—i.e., wider roads usually have a higher traffic volume than narrow roads—making it difficult to dis-entangle the relative impact of each factor. Furthermore, exceptions to the above relationships occur and are illustrative of how mortality rate correlates are often region-, taxa-, and habitat-specific. For example, several studies have found no link between traffic volume and mortality rates (Massemin et al. 1998, Lodé 2000, Coelho et al. 2008, Kambourova-Ivanova et al. 2012).

Current estimates of annual U.S. bird mortality from vehicle collisions—ranging from 60 to 80 million—are highly speculative, based on extrapolation of mortality rates from a single British study (Hodson and Snow 1965) to the entire U.S. road network (Banks 1979, Erickson et al. 2005). Comprehensive meta-analyses of studies that quantify bird populations have concluded that roads are consistently associated with reductions in bird abundance (Fahrig and Rytwinski 2009, Benitez-Lopez et al. 2010), but no clear evidence exists that vehicle collision mortality is a significant driver of these road-related declines. In addition, no such comprehensive analyses have been completed to assess bird-vehicle collision mortality in the United States. When compared to speculative or extrapolative estimates based on small samples of data, such systematic and quantitative reviews provide a more rigorous approach to estimating mortality, an improved understanding of the sources of uncertainty associated with estimates (Loss et al. 2012, 2013*a*, 2014; Machtans et al. 2013), and a more valid evidence base on which to prioritize policy and management strategies and to identify major research needs (Calvert et al. 2013, Machtans and Thogmartin 2014).

We reviewed the North American and European bird-vehicle collision literature and defined inclusion criteria to screen and remove studies likely to bias our estimates substantially. Based on data extracted from the remaining studies, we 1) systematically quantified the magnitude of bird mortality (along with uncertainty) caused by collisions with vehicles on U.S. roads by combining probability distributions of mortality rates, the length of U.S. roads, and biases associated with surveys for dead birds; 2) used sensitivity analyses to quantitatively investigate factors contributing to estimate uncertainty and to identify major research needs; and 3) summarized the available species-specific data on bird-vehicle collisions in the United States.

METHODS

Literature Search and Inclusion Criteria

We used Google Scholar and the Web of Science database to search for publications about bird-vehicle collisions on roads. The search terms we used were "bird-vehicle collision," "bird-vehicle roadkill," the previous terms with "bird" replaced by "avian" and "vehicle" replaced by "automobile," "car," and "truck." We checked reference lists to locate additional sources, and we also referenced an annotated bibliography that included approximately 670 sources covering the impacts of roads on wildlife (Nietvelt 2002). For 5 North American studies (Nero and Copland 1981, Decker 1987, Smith et al. 1994, Sutton 1996, Potvin and Bishop 2010), we were unable to access full-text articles and instead extracted the data as summarized in a review of bird-vehicle collisions in Canada (Bishop and Brogan 2013). Because of the large quantity of international studies—many that are published in languages other than English or inaccessible online or through North American libraries—we could not exhaustively review this literature. However, our review of the North American literature was comprehensive, and we likely located all studies that included a systematic sampling component. We may have overlooked some North American publications containing descriptions of incidentally found roadkill victims; however, these studies would have been excluded from analyses based on our inclusion criteria described below.

We defined several criteria for studies to be included in our estimation models. We designed inclusion criteria to remove studies that were not useful for generating mortality rate estimates or that were likely to substantially bias estimates. We excluded studies prior to in-depth review if they included no original data; were conducted in a region other than the United States, Canada, or Europe; or were published in a language other than English. In addition, because we sought to generate mortality estimates that were relevant to relatively modern road types and traffic patterns, we arbitrarily selected 1970 as the earliest date for which publications could be included in analyses (see also Bishop and Brogan 2013). Following in-depth review of the remaining 53 studies, we also excluded studies that 1) were retrospective, based on assessment of opportunistically collected data sets or recoveries of banded or radio-tagged birds, 2) focused on particular bird species or groups without sampling or presenting data for all species and groups, 3) included an experimental component without presenting control and treatment data separately, 4) were prospective but also included incidentally collected data without presenting it separately, 5) did not provide information about the proportion of the year covered by sampling, 6) did not present the length of road corridor sampled or a per kilometer mortality rate, 7) were based on a single survey or a series of surveys that covered less than 1 month, and 8) did not separately report fatalities from vehicle collisions and other collision sources (e.g., roadside fences). After implementing the above inclusion criteria, 16 of the 53 reviewed studies remained (9 U.S. and 7 European studies; Table 1; see Table S1 for excluded studies).

For the summary of species representation of mortality, we included data from U.S. studies meeting criteria 1–4 and 7–8 above. We considered criteria 5 and 6 unnecessary for producing unbiased species summaries. We used 7 of the 9 U.S. studies meeting inclusion criteria for the mortality estimate for the species analysis. The 2 excluded studies did not provide data at the species level (Oxley et al. 1974, Gerow et al. 2010).

Data Extraction

From most studies meeting the above inclusion criteria, we extracted a single mortality rate. However, for studies that

Table 1. Meta-data and mortality rates for studies meeting inclusion criteria for 1) estimation of annual bird-vehicle collision mortality on U.S. roads and/or 2) species mortality summary.

Location	Sampling coverage	Used? Total[a]	Used? Species[b]	Road type	Mortality per km[c]	Study
United States						
Southern Idaho	Yr-round	Yes	Yes	4-lane paved	2.01	Boves and Belthoff (2012)
Bow River Valley, AB	Apr–Nov	Yes	Yes	2-lane paved	0.38	Clevenger et al. (2003)—Bow Valley Parkway
Bow River Valley, AB	Apr–Nov	Yes	Yes	4-lane paved	0.37	Clevenger et al. (2003)—Trans-Canada Highway
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	6.54	Glista et al. (2008)—South River Road
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	5.69	Glista et al. (2008)—State Road 26
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	4.85	Glista et al. (2008)—U.S. Highway 231
Central California	25 May–26 Nov	Yes	Yes	4-lane paved	1.20	Moore and Mangel (1996)
Athens County, Ohio	Yr-round	Yes	Yes	4-lane paved	6.56	Seibert and Conover (1991)
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	0.23	Oxley et al. (1974)—Gravel unpaved road 1
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	2.11	Oxley et al. (1974)—Gravel unpaved road 2
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	2-lane paved	2.96	Oxley et al. (1974)—2-lane paved highway
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	4-lane paved	3.22	Oxley et al. (1974)—4-lane paved highway
Long Point, ON	Apr–Oct	No[d]	Yes	2-lane paved	91.43	Ashley and Robinson (1996)
Tippecanoe County, IN	Yr-round	No[d]	Yes	2-lane paved	24.44	Glista et al. (2008)—Lindberg Road
Alachua County, FL	Yr-round	No[d]	Yes	4-lane paved	43.44	Smith and Dodd (2003)
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Rincon Mountain
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Tucson Mountain
Europe						
Northeast France	Yr-round	Yes	No	2-lane paved	1.54	Baudvin (1996)
Northeast Poland	Yr-round	Yes	No	2-lane paved	11.55	Gryz and Krauze (2008)
Galanta, Slovakia	Yr-round	Yes	No	?	17.09	Hell et al. (2005)
Belovo, Bulgaria	Mar–Oct	Yes	No	?	3.00	Kambourova-Ivanova et al. (2012)—1st-class road
Belovo, Bulgaria	Mar–Oct	Yes	No	?	8.09	Kambourova-Ivanova et al. (2012)—Trakia highway
Western France	Apr–Nov	Yes	No	?	8.80	Lodé (2000)
Wroclaw, Poland	Mid-Mar–Oct	Yes	No	?	5.89	Orlowski (2005)
Spain and France	Yr-round	Yes	No	?	0.65	Pons (2000)

[a] Whether we used the mortality rate to estimate bird-vehicle collision mortality on U.S. roads.
[b] Whether we used the source to calculate average proportional representation for individual species (excluded U.S. studies focused on particular bird group(s) without including all species; we excluded all international studies).
[c] We calculated mortality rates using raw data (i.e., we did not directly extract reported rates from studies because calculation approaches varied among studies and were not always calculated transparently). We first divided the total number of fatalities reported for a road segment by the length of road corridor covered by that segment. For rates representing >1 year of sampling, we then divided by the number of years sampled; we applied a partial-year sampling correction in the mortality estimation model (see Methods section in main text for details).
[d] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is a statistical outlier among studies meeting criteria.
[e] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is adjusted for biases associated with carcass surveys (detection probability and scavenger removal); these biases were separately accounted for in our mortality estimation model.

sampled along more than 1 road type (e.g., paved and unpaved roads and/or roads with different numbers of lanes) or used different sampling methods (e.g., different sampling intervals or survey types) for different portions of the study area, we extracted separate mortality rates. This resulted in extraction of 25 mortality rates (17 U.S. and 8 European rates; Table 1) from the 16 included studies. We calculated all rates as the number of dead birds found per kilometer of road corridor sampled. This approach is different than that of some studies that calculate mortality rates using the total length of lanes sampled (e.g., for a 2-lane road, lane-length is twice the length of the road corridor). Some studies did not provide enough information to clarify how they calculated mortality rates. Therefore, rather than directly extracting the reported rates, we recalculated rates based on the number of fatalities reported for a road segment divided by the length of road corridor covered by that segment. Because we recalculated rates using this raw data, the mortality rate we calculated was sometimes different than that presented in the original study.

We then used one of several approaches to convert multi-year mortality rates to annual rates. For multi-year studies that sampled across the entire calendar year in every year of the study, we divided mortality rates by the number of years to generate the annual rate (Table 1). We also took this approach for multi-year studies that only sampled a portion of each year; we accounted for partial-year sampling coverage separately (see following subsection). For 4 studies that sampled at least 1 entire calendar year as well as an additional partial year (Seibert and Conover 1991, Baudvin 1997, Hell et al. 2005, Glista et al. 2008), we treated the partial year as a full year when calculating the annual rate. This approach led to conservative rate estimates because mortality was spread across a longer time period than it actually occurred in.

We excluded 3 mortality rates from the above data set for being statistical outliers and 2 for being adjusted for various sampling biases that we accounted for separately in the mortality estimation model (see Supplementary Methods, available online at www.onlinelibrary.wiley.com). The final data set used for estimation of mortality therefore included 20 mortality rates (12 U.S. and 8 international rates) extracted from 13 studies (6 U.S. and 7 European studies; Table 1).

Quantification of Annual Bird Mortality

To increase the comparability of mortality estimates from different studies, mortality rates should ideally be standardized to account for varying proportions of the year being covered by sampling (Loss et al. 2012). Potential standardization approaches include 1) using mortality rates from year-round studies to proportionally correct partial-year studies (Longcore et al. 2012, Loss et al. 2013*a*), 2) including a correction factor in the mortality estimation model that accounts for partial-year sampling (Loss et al. 2014), or 3) using only full-year mortality rates to generate mortality estimates. We were unable to implement the first approach because year-round vehicle collision studies either do not present data separately for different portions of the year or only provide seasonal data for single bird species or taxa other than birds. Because the second and third approaches were both possible, we repeated mortality estimation using each approach. We expected the estimate generated using approach 2 would represent a maximum value because this approach assumed that mortality rates observed during the sampled portion of the year—typically the peak periods of vehicle collision mortality in spring, summer, and/or autumn—also applied to the un-sampled portion of the year (see Supplementary Methods).

Our approach for estimating mortality was to combine a mortality rate probability distribution with a probability distribution for the length of U.S. roads susceptible to that range of mortality rates. We defined the maximum susceptible road length to be the entire U.S. road network and the minimum susceptible length to be only the length of roads in rural areas (see Supplementary Methods). This approach assumes that mortality rates in urban areas are likely lower than in rural areas, but does not entirely discount mortality in urban areas. We also incorporated correction factors to account for sampling coverage of less than the entire calendar year (for estimates that included partial-year morality rates) and for biases associated with carcass surveys (all estimates), including removal of carcasses by scavengers and imperfect detection of carcasses by surveyors (Loss et al. 2013*a*, 2014). Because a preliminary analysis found little support for differences in mortality rates between 2-lane, 4-lane, and gravel roads, and because the sample of mortality rates was too small to generate separate probability distributions for different road types, we applied the same range of mortality rates across all U.S. road types. This simplified approach contributes uncertainty to our mortality estimate; however, we did not have enough available data to allow separate mortality estimates for different road types. In addition to repeating mortality estimation with and without inclusion of partial-year studies, we also estimated mortality with and without inclusion of European mortality rates. Thus, we generated 4 separate estimates of annual mortality using different subsets of data: U.S. year-round mortality rates, U.S. year-round and partial-year rates, U.S. and Europe year-round rates, and U.S. and Europe year-round and partial-year rates.

For the estimates based only on year-round mortality rates, we used the model:

$$\text{Mortality}_{\text{year-round studies}} = R \times K_{\text{year-round studies}} \times B \qquad (1)$$

where R is the length of U.S. roads susceptible to the range of mortality rates in the mortality rate probability distribution (K), K is the is the range of collision mortality rates per km of road corridor, and B is a bias correction factor to account for removal of carcasses by scavengers prior to surveys and imperfect detection of carcasses remaining at the time of surveys.

For the estimates based on year-round and partial-year rates, we used the model:

$$\begin{aligned}&\text{Mortality}_{\text{year-round and partial-year}}\\&\quad = R \times K_{\text{year-round and partial-year}} \times Y \times B\end{aligned} \qquad (2)$$

where Y is a correction factor that accounts for the average proportion of the calendar year not covered by sampling in the studies used to develop the mortality rate distribution (Loss et al. 2014). The partial-year sampling correction factor was a fixed value; however, we defined all other parameters as uniform probability distributions (specific distributions shown in Table 2; rationale for distributions in Supplementary Methods). For all estimates, we used the runif function in Program R (R Version 3.0.1., <http://www.r-project.org/>. Accessed 14 Apr 2014) to draw random values from each probability distribution, and we calculated mortality using the above formulas. We repeated this calculation 10,000 times for each of the 4 estimation approaches to generate ranges of uncertainty for mortality estimates.

Sensitivity Analyses

We used sensitivity analyses to quantitatively investigate the factors contributing to uncertainty in our mortality estimates.

Table 2. Probability distributions used for estimation of annual bird-vehicle collision mortality on U.S. roads.

Parameter	Distribution type	Distribution parameters	Source
Total length of road corridors in the United States[a]	Uniform	Min. = 3.76 M; max. = 4.33 M	U.S. Department of Transportation (2012)
Morality rates (per km)			
U.S. studies (yr-round)[b]	Uniform	Min. = 3.48; max. = 6.78	95% CI across 5 rates meeting inclusion criteria
U.S. studies (all)[c]	Uniform	Min. = 2.78; max. = 6.73	95% CI across 12 rates meeting inclusion criteria
U.S. + Europe studies (yr-round)[b]	Uniform	Min. = 2.85; max. = 9.70	95% CI across 9 rates meeting inclusion criteria
U.S. + Europe studies (all)[c]	Uniform	Min. = 4.24, max. = 8.58	95% CI across 20 rates meeting inclusion criteria
Partial-yr sampling correction			
U.S. studies (all)[c]	NA[d]	Estimate = 1.49	1/average proportion of yr covered by mortality rates
U.S. + Europe studies (all)[c]	NA[d]	Estimate = 1.37	1/average proportion of yr covered by mortality rates
Bias correction factor	Uniform	Min. = 3.26; max. = 11.46	Bruun-Schmidt (1994), Gerow et al. (2010), Santos et al. (2011), Boves and Belthoff (2012), Texeira et al. (2013)

[a] Includes length in millions (M) of kilometers of all public roads in all states excluding Alaska and Hawaii.
[b] Estimate is based only on mortality rates from studies with year-round sampling coverage.
[c] Estimate is based on mortality rates from all studies meeting inclusion criteria.
[d] Parameter is a point estimate, not a probability distribution.

We defined univariate regression models with the 10,000 replicated mortality estimates as the dependent variable and randomly drawn values of model parameters as the independent variable. We repeated this analysis 4 times, once for each of the 4 mortality estimate models. We used the adjusted R^2 values for each independent variable (averaged across the 4 sensitivity analysis iterations) to interpret the percentage of estimate uncertainty attributable to each model parameter (Blancher 2013, Loss et al. 2013*a*).

Vehicle Collision Mortality by Species

In addition to estimating total annual mortality for all U.S. birds, we also calculated the average proportional representation of each bird species (Longcore et al. 2013, Loss et al. 2013*a*). We used this calculation rather than estimating species-specific mortality because the data from studies meeting inclusion criteria only represented 100 bird species. This value is likely much lower than the actual number of species killed along U.S. roadways each year. Estimates of species-specific mortality would therefore be biased high for observed species and biased low for species killed but not reported in the literature. Therefore, we would be unable to draw unbiased conclusions about species-specific collision risk. Nonetheless, to provide a rough summary of the findings to date, we estimated average proportional representation of species by 1) calculating the proportion of each study's total count represented by each species (i.e., multiple proportions calculated for each species, 1 from each study), and 2) averaging each species' individual-study proportions across all studies. For averaging, we only included zero-values of proportions (i.e., species was not found in study) when a species could have been found, as determined by overlap of breeding, migration, and/or wintering ranges with study sites (Sibley 2000).

RESULTS

We found considerable variation (41.8%) among median mortality estimates produced using the 4 models (Table 3). The model using only year-round mortality rates from the United States produced the lowest annual estimate (median = 145.7 million; 95% CI = 61.9–274.6 million), and the model including both year-round and partial-year mortality rates and rates from both the United States and Europe produced the highest estimate and the estimate with the greatest range of uncertainty (median = 250.5 million; 95% CI = 103.8–476.8 million). Averaging across all 4 models (i.e., averaging the 4 estimates produced in each model iteration and then averaging these values across 10,000 iterations) resulted in a median annual mortality estimate of 199.6 million birds (95% CI = 88.7–339.8 million). Regardless of the model used, sensitivity analyses indicated that the bias correction factor for scavenger removal and searcher detection contributed the greatest uncertainty to estimates (average variance explained = 63.2%), followed by the mortality rate (32.5%) and the road corridor length over which the mortality rate applies (1.3%).

Among the species documented in studies meeting inclusion criteria, the barn owl had the highest average proportional representation across studies, averaging 32.4% of total counts (all species proportions in Table S2). Four other species, including 3 in the Corvidae family, had average proportional representation of at least 5%: common raven (*Corvus corax*; 6.3%), gray jay (*Perisoreus canadensis*; 6.0%), black-billed magpie (*Pica hudsonia*; 5.0%), and European starling (*Sturnus vulgarus*; 5.0%). Several species were found in 3 or fewer studies, and these species' proportions were more likely to be biased by abnormally high or low counts documented in single studies. Given the small sample of

Table 3. Estimates of annual bird-vehicle collision mortality on U.S. roads.

Mortality data used	Total mortality (millions)		Mortality per km	
	Median	95% CI	Median	95% CI
United States	145.7[a]	61.9–274.6[a]	36.0[a]	15.3–68.0[a]
	197.1[b]	78.2–397.9[b]	48.8[b]	19.4–98.5[b]
United States + Europe	171.0[a]	59.6–381.5[a]	42.3[a]	14.8–94.4[a]
	250.5[b]	103.8–476.8[b]	62.0[b]	25.7–118.0[b]
Average across models	199.6	88.7–339.8	49.4	22.0–84.1

[a] Estimate based only on mortality data from studies with year-round sampling coverage.
[b] Estimate based on data from all studies meeting inclusion criteria.

studies included in the species summaries (7 studies including 3,246 total fatality records), caution should be used when interpreting these results.

DISCUSSION

Annual Bird-Vehicle Collision Mortality on U.S. Roads

All of our estimates of annual bird-vehicle collision mortality exceed the previous estimates of between 60 and 80 million birds, which were produced by extrapolating the results of 1 British study (Hodson and Snow 1965) across the entire U.S. road network (Banks 1979, Erickson et al. 2005). We improved upon these earlier estimates by systematically incorporating 20 mortality rates from 13 studies that used a prospective sampling design and reported results for all potentially killed bird species. Even when considering the lowest estimate range (between 62 and 275 million birds), our results suggest that bird-vehicle collisions outrank many other sources of direct anthropogenic mortality. Among threats with estimates that are data-driven and systematically derived, only predation by free-ranging domestic cats (Loss et al. 2013*a*) and collisions with buildings and their windows (Loss et al. 2014) are estimated to cause greater annual bird mortality in the United States. Estimates of total numbers of birds killed by anthropogenic threats are useful for prioritizing conservation and management efforts. However, increased attention should also be given to documenting which species and regions are most vulnerable to vehicle collisions and other mortality sources (Longcore et al. 2013; Loss et al. 2013*b*, 2014).

As expected, estimates that incorporated both year-round and partial-year mortality rates were higher than those that used only year-round rates. This likely occurred because the partial-year correction factor was calculated under the assumption that mortality rates were constant across all seasons. Among the studies we used, sampling periods typically covered spring, summer, and/or autumn, seasons characterized by relatively high mortality rates for most species (Loos and Kerlinger 1993, Smith and Dodd 2003, Orlowski 2005, Gryz and Krauze 2008). Extrapolating mortality rates from these peak seasons to un-sampled seasons that are generally characterized by lower mortality rates may have inflated our estimates. Estimates from models including partial-year rates should therefore be viewed as maximum values. Additional year-round studies that present results separately by month and/or season are needed to clarify intra-annual variation in vehicle collision mortality rates.

Estimates that included European mortality rates were higher than those that used only U.S. rates. This may have occurred due to the inclusion of 2 European rates that were not statistical outliers but were higher than all U.S. rates meeting inclusion criteria (11.6 and 17.0 birds/km/yr; Hell et al. 2005, Gryz and Krauze 2008). Although exceptionally high annual mortality rates of up to 91 birds/km (Ashley and Robinson 1996) have been documented locally in the United States, such rates likely do not apply across most roads. Roadkill fatalities are often clustered in hotspots (e.g., Gunson et al. 2010), and these areas are often the focus of mortality studies. This tendency to focus on areas already known to experience bird mortality may have contributed positive bias to individual estimates of mortality rates and to our national mortality estimates. Nonetheless, we sought to minimize this source of bias by removing mortality rates that were identified as statistical outliers.

We were unable to assess regional variation in bird-vehicle collision mortality rates and to produce regional mortality estimates. Only 6 U.S. studies met our inclusion criteria; this sample was insufficient to allow for quantification of regional variation. Filling this data gap will require rigorous and prospective studies across a broad cross-section of the United States within numerous ecosystems, states, and regions. Individual studies that randomly sample roadkill mortality across a large spatial scale (e.g., entire states or regions) will also provide increased understanding of regional variation.

Research Needs and Estimate Limitations

The relatively small sample of data meeting inclusion criteria resulted in substantial uncertainty in our mortality estimates. When assessing specific uncertainty contributions of individual model components, sensitivity analyses indicate that the model parameter contributing the greatest uncertainty to our estimates is the bias correction factor, which accounts for both scavenger removal and imperfect detection of carcasses. Further research on these biases may decrease the uncertainty associated with this correction factor and allow for increased precision of future mortality estimates. However, the magnitude of these biases depends on a suite of factors, including the local scavenger community, habitat type, traffic volume, and weather conditions (Santos et al. 2011, Boves and Belthoff 2012, Guinard et al. 2012, Texeira et al. 2013). Development of a narrow distribution of bias correction factors that apply across a national scale may therefore not be possible. An alternative approach is for future studies to estimate scavenger removal and searcher detection rates to calculate adjusted mortality rate estimates. A large sample of locally adjusted mortality rates would obviate the need for post hoc correction factors (Loss et al. 2013*b*). Recent studies outline considerations for scavenger removal and detection trials (Santos et al. 2011, Texeira et al. 2013). Of particular promise are approaches that allow for estimation of both biases using a single experimental trial incorporated into standard fatality monitoring (Smallwood 2013) or using only the dead birds found during fatality monitoring, thus removing the need for separate experimental trials (Etterson 2013).

Mortality rate probability distributions also contributed substantial uncertainty to our estimates. The relatively small sample of studies meeting inclusion criteria along with the inherently variable nature of collision rates likely contributed to this uncertainty. To increase the number of mortality rates that can be used to estimate national mortality, future studies should seek to meet the level of rigor captured by our inclusion criteria. In particular, more studies are needed that sample and present data for all bird species. When summarizing average proportional representation of collision mortality, we found that a few species (particularly barn owls and several corvids) comprise a relatively large percentage of all fatalities that have been identified to species. However, sample sizes of usable studies and available data were small, and results of the species summary were likely biased by high detection probabilities for large species and by geographical biases in sampling. Taking a more species-inclusive approach to studying bird-vehicle collisions will improve understanding of species- and taxa-specific vulnerabilities to vehicle collisions. Because of the above limitations, species proportions should not be used to draw conclusions about national-scale vulnerabilities of bird species to vehicle collisions. Nonetheless, they provide a descriptive summary of the bird species that have been documented as roadkill victims along U.S. roads.

In addition to estimate bias caused by scavenger removal and imperfect detection of carcasses, an unknown number of birds that collide with vehicles fly out of detection range (i.e., crippling bias; Slater 2002, Texeira et al. 2013) or are destroyed or carried away by vehicles (Stewart 1973, Mumme et al. 2000). Because these biases have never been formally quantified in the context of vehicle collisions, substantial uncertainty remains about to what degree they contribute to under-estimation of roadkill mortality rates. Future research of these bias sources is necessary for fully understanding the magnitude of bird mortality caused by vehicle collisions.

Numerous biotic and abiotic factors influence bird collision mortality rates along roads. These correlates collectively result in bird fatalities being clustered along particular road segments (Clevenger et al. 2003, Smith and Dodd 2003, Glista et al. 2008, Gunson et al. 2010). Further research is needed to clarify the combination of factors that lead to carcass clustering (e.g., habitat, characteristics of the road and its cleared corridor, and community composition and population abundance of birds) and to assess how these correlates vary seasonally and regionally. When possible, studies should employ sampling designs that allow for separation of often-confounded mortality correlates (e.g., road width, traffic volume, and traffic speed).

The negative bias contributed to mortality rate estimates by scavenger removal is amplified with increasing time intervals between surveys. This occurs because—with all other factors held constant—more collisions occur between surveys, and a greater proportion of carcasses are removed by scavengers. Because carcass removal adjustment factors are less accurate across long search intervals (Smallwood 2013) and because carcass removal rates appear to be especially high along roadways (Bruun-Schmidt 1994, Antworth et al. 2005, Santos et al. 2011, Texeira et al. 2013), optimal search intervals for documenting roadkill mortality are very short (e.g., sampling on alternate days for large birds and daily for small birds; Santos et al. 2011). Because the search intervals in the studies we used were between 2 and 15 days, mortality rates in individual studies could have been substantially under-estimated. This under-estimation could have contributed negative bias to our mortality estimates.

In addition to using long search intervals for carcass surveys, the studies we used conducted surveys using various transportation methods, including foot, bicycle, and automobile. Because of the relatively high speed at which sampling is conducted, automobile surveys usually detect only a small fraction of carcasses (Slater 2002, Gerow et al. 2010, Guinard et al. 2012, Texeira et al. 2013). In the sample of mortality rates extracted from studies meeting our inclusion criteria, the majority of rates (15 of 20) were based on automobile surveys, and estimated mortality rates for automobile surveys averaged 2.3 times lower than for other survey types. Therefore, the use of automobile surveys may have contributed additional under-estimation bias to our mortality estimates. The use of automobile surveys may have also influenced our species summary, with surveys likely over-representing large-bodied species (e.g., raptors and corvids) that are relatively easy to detect from a fast-moving automobile.

MANAGEMENT IMPLICATIONS

The large magnitude of mortality caused by vehicle collisions combined with the potential for impacts at the population level highlights the need for conservation and management attention to mitigate this threat. Mitigation efforts may be most relevant at areas known to experience exceptionally high rates of collision mortality (e.g., clear examples include the studies that were identified as statistical outliers for our mortality estimate). Following identification of mortality hotspots, potential options to reduce bird collision mortality along roads include (see also Boves and Belthoff 2012, Bishop and Brogan 2013) placing flight deflectors along roadsides to force birds to fly above vehicle height (Bard et al. 2001, Ramsden 2003, Gomes et al. 2009), locally reducing speed limits and erecting signage to alert drivers, reducing or removing the amount of favorable bird habitat along roadsides, and using visual or auditory deterrents. All of these approaches have rarely been implemented and remain largely untested. Research is therefore needed to determine which combinations of the above approaches are most effective at reducing mortality and to clarify how responses vary by bird species, region, habitat, season, and road type. Identification and implementation of effective conservation measures is especially crucial given the increasing length of U.S. roadways, increasing traffic volume, and an increasing number of direct and indirect anthropogenic threats to bird populations.

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