

Research



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Author for correspondence:

Chris B. Thaxter
e-mail: chris.thaxter@bto.org

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Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment

Chris B. Thaxter^{1,2}, Graeme M. Buchanan³, Jamie Carr⁴,
Stuart H. M. Butchart^{5,7}, Tim Newbold⁶, Rhys E. Green^{7,8}, Joseph A. Tobias⁹,
Wendy B. Foden¹⁰, Sue O'Brien¹¹ and James W. Pearce-Higgins^{1,2,7}

¹British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

²British Trust for Ornithology, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

³RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, 2 Lochside View, Edinburgh Park, Edinburgh EH12 9DH, UK

⁴International Union for Conservation of Nature, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

⁵BirdLife International, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

⁶Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK

⁷Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

⁸RSPB Centre for Conservation Science, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

⁹Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot SL5 7PY, UK

¹⁰Department of Botany and Zoology, University of Stellenbosch, P/Bag X1, Matieland 7602 Stellenbosch, South Africa

¹¹Joint Nature Conservation Committee, Inverdee House, Baxter Street, Aberdeen AB11 9QA, UK

id CBT, 0000-0003-0341-4199; GMB, 0000-0001-9497-8584; TN, 0000-0001-7361-0051; REG, 0000-0001-8690-8914; JAT, 0000-0003-2429-6179; WBF, 0000-0002-8839-8740; JWP-H, 0000-0003-1341-5080

Mitigation of anthropogenic climate change involves deployments of renewable energy worldwide, including wind farms, which can pose a significant collision risk to volant animals. Most studies into the collision risk between species and wind turbines, however, have taken place in industrialized countries. Potential effects for many locations and species therefore remain unclear. To redress this gap, we conducted a systematic literature review of recorded collisions between birds and bats and wind turbines within developed countries. We related collision rate to species-level traits and turbine characteristics to quantify the potential vulnerability of 9538 bird and 888 bat species globally. Avian collision rate was affected by migratory strategy, dispersal distance and habitat associations, and bat collision rates were influenced by dispersal distance. For birds and bats, larger turbine capacity (megawatts) increased collision rates; however, deploying a smaller number of large turbines with greater energy output reduced total collision risk per unit energy output, although bat mortality increased again with the largest turbines. Areas with high concentrations of vulnerable species were also identified, including migration corridors. Our results can therefore guide wind farm design and location to reduce the risk of large-scale animal mortality. This is the first quantitative global assessment of the relative collision vulnerability of species groups with wind turbines, providing valuable guidance for minimizing potentially serious negative impacts on biodiversity.

1. Introduction

In response to projected impacts of climate change on the environment, human society and health [1], political consensus at the 21st Conference of Parties of the United Nations Framework Convention on Climate Change (UNFCCC) led to agreement to hold the increase in global temperatures to below 2°C,

above pre-industrial levels, and pursue efforts to limit the increase to 1.5°C [2]. Achieving this ambition depends on global emissions peaking around 2020, with negative emissions in the second half of this century [3], requiring large-scale and rapid deployment of renewable energy technologies. Wind farms are the most well-developed, cheapest, widely available and feasible renewable energy technologies for electricity generation [4], and are likely to form an important component of renewable electricity generation strategies.

Wind farms can have negative impacts upon biodiversity [5], including direct collision mortality, displacement from feeding or nesting areas, barrier effects to movement and habitat degradation or loss [6]. For volant species such as birds and bats, the risk of collision is a serious concern [5], and large numbers of birds and bats have been shown to be killed by turbines [5,7,8], particularly at aggregation sites, such as migratory bottlenecks or near breeding colonies [9]. It has been suggested anecdotally that some species groups, such as migratory bats, raptors and seabirds, may be particularly impacted [9,10], which may at least be partly linked to visual acuity [11].

Collision mortality with wind turbines may reduce populations, particularly of long-lived, slow-reproducing species [12,13] and wide-ranging or migratory species [12,14]. Consequently, there is an urgent need to quantify species' vulnerability across as wide a range of species and geography as possible. Further, a recent review highlighted most studies to date have focused on the developed world [5]. The need to identify species' vulnerability, however, is crucial for countries in the developing world, where wind farms may be rapidly deployed to achieve climate change mitigation targets. This paper describes analyses designed to improve our understanding of the factors influencing the collision vulnerability of species to onshore wind turbines, and to inform future wind farm location and design in areas and for species for which this has been little studied. We model the extent to which ecological, morphological and life-history traits are likely to influence encounter rates with turbines, accounting for variation in parameters that differ between studies. We also consider other factors, such as turbine size, that might affect the likelihood of collision [15,16], to examine the extent which wind farm design may reduce collision rates.

2. Material and methods

(a) Literature review and data structure

We conducted meta-analyses using Web of Science, Google Scholar[®] and Google[®] to search for peer- and non-peer-reviewed literature. Given the known differences in terminology for 'wind farms', we used the following search terms for birds: (bird* OR avian) AND wind AND (farm* OR energy OR windfarm* OR industry* OR wind-farm* OR park* OR development* OR facilit*). For bats, we repeated the search, replacing 'bird' and 'avian' terms with 'bat'. References reporting collision mortality were identified. Population-level impacts such as mortality rates were rarely available; instead most studies presented the numbers of collisions per species per turbine or per megawatt (MW). The following data were extracted: study reference, wind farm name, geographical location, species' identity, number of deaths, study duration, wind farm and turbine quantity, turbine size and study quality information (see below). In total, 133 studies for birds and 101 for bats reported collision rates. Of these, 88 bird and 87 bat studies were suitable for inclusion, and contained information from 93 and 134 onshore wind farm sites (electronic supplementary material,

appendix A1, figure S1), respectively. Dominant land cover within a 5 km buffer of the centre point coordinate of wind farms was identified from GLC2000 [17]. References and further information on traits are given in electronic supplementary material, file S1 and data collection files S2.

(b) Study quality and site-specific information

The detectability of collision victims is affected by many factors, including frequency of mortality surveys, scavenger removal, observer skill and variation in encounter probability (detectability) between species [18–20], ground and habitat types and ecosystems. Studies varied in the extent to which they corrected for these factors, and did not provide sufficient information to produce a standardized collision rate metric [21,22]. Instead, we categorized studies based on quality as follows: (1) 'very low': no corrections; (2) 'low': correction for aspects of scavenger removal and observer skill, but detectability constant across species; (3) 'medium': as (2) but with multiple corrections for detectability for species' groupings, e.g. 'small bird' or 'large bird'; (4) 'high': species-specific corrections for main sources of error (electronic supplementary material, appendix A2). For bats, no distinctions were made for species groups, therefore a three-level variable was used, combining low and medium categories. Corrections for bat scavenger removal were sometimes based on proxy bird species, which might introduce bias.

The search area around turbines (hereafter, 'buffer area') may influence discovery of collision victims and so was included as a covariate (birds: mean $\pm$ 1 s.d., 2.1 ± 1.4 ha, range 0.1–8.6 ha; bats: 1.2 ± 1.1 ha, 0.1–8.1 ha). We included 'year' (birds: 1.8 ± 1.6 years, 1–10 years; bats: 1.4 ± 0.9 years, 1–5 years), and 'number of days' (birds: 281.7 ± 106.4 days, bats: 238.7 ± 110.1 days, range 42–365 days) as covariates to control for study duration. A binary factor separated peer- and non-peer-reviewed literature. As studies varied in the number of wind farms monitored, this was added as an additional covariate. Turbine size was included as a linear predictor, given its potential impact on mortality rate [12], here assessed as turbine MW output [9] (birds: 1.3 ± 0.7 MW, 0.2–2.5 MW; bats: 1.6 ± 0.6 MW, 0.5–3.0 MW).

(c) Species' traits

Traits for bird species were taken from the Birdlife International World Biodiversity Database [23] except wing morphology, which was measured directly from museum skins [24] (electronic supplementary material, appendix A3). Flightless species were excluded. Habitat, foraging strata and diet were specified using binary factors for each factor level. Migratory status and breeding dispersal distance, body size, clutch size, generation length and Kipp's distance (a measure of wing morphology related to manoeuvrability [25]) were also obtained.

To account for species potentially present, but not recorded in collision, we used spatial distribution polygons based on entire breeding ranges for birds [23] and bats [26] to generate species lists of 'pseudo-absences'. Although this approach may produce omission errors due to coarse data resolution [27], it allowed potential species' presences to be modelled. The frequency of collision may depend on local abundance, but such information was inconsistently reported. Therefore, we included global population size as a proxy, which is implicitly related to gross variation in density.

Bat trait data were extracted from the PanTHERIA database [28] but consideration of all traits simultaneously was not possible as data were available for subsets of species per trait. We therefore tested (i) population group size [28]; (ii) forearm length; (iii) body mass; (iv) litter size; (v) age of sexual maturity and (vi) gestation length. Body mass and forearm length were correlated ($R = 0.92$), so forearm length was excluded. As 96% of species were insectivorous [29], diet was not included. Dispersal distance (vii), use of tree roost sites (viii) and hibernation

behaviour (ix) were obtained through field guides (e.g. [30]) and data portals [26,31,32]. For bats, current knowledge gaps and terminology differences between studies prevented migration from being separated from dispersal [32]. Maximum dispersal distance was defined as 'sedentary' less than 10 km, 'regional' 10–100 km and 'long-distance' 100+ km, the last probably equating to long-distance migration [32]. Binary variables were specified for tree roost site and hibernation. Traits 1, 5 and 6 were only available for a smaller proportion of species ($n = 36$), and were not significant ($p > 0.05$) when considered alongside the remaining traits. Therefore, we present models for traits 3, 4 and 7–9 for 67 species (see electronic supplementary material, appendices A3–A5).

(d) Phylogeny

To account for potential phylogenetic non-independence of data, we used bootstrapped estimates of phylogenetic relationships from the BirdTree database [33]. We generated 1000 random trees, reduced further into a single minimum consensus tree using a Python algorithm, taking a minimum of 50% support for branching events [34]. Seven different methods for generating trees were available for birds [33], providing seven alternative models. For bats, we used a phylogenetic tree within the R package 'ape' [35]. This tree had no bootstrapped estimates available, but species with available trait data were well represented (greater than 95%).

(e) Statistical analysis

Bayesian Markov chain Monte Carlo (MCMC) generalized linear mixed models were used to model the variation in collision rates, using the R package MCMCglmm [36,37]. Models were specified using a zero-adjusted Poisson error structure and a response of collisions per turbine, including the logarithm of the number of turbines surveyed as an offset; an R script for birds is provided in electronic supplementary data collection, files S2. Fixed effects were specified for species' traits, study quality and site-specific information (electronic supplementary material, table S1). To assess the effect of inserting pseudo-absences, we repeated our analysis based on recorded collisions, which produced similar results (electronic supplementary material, appendix A5). We therefore present results for models including pseudo-absences. Phylogenetic signals were included by specifying the 'tip label' of species names from the minimum consensus tree as a random effect [38], alongside a matrix inversely proportional to the covariance structure of 'tip label' [37]. Phylogenetic models were better fitting than those excluding phylogeny in all cases ($dDIC < -2.0$). Study ID was included as a random effect to account for repeated measurements of collisions per species and study. Uninformative priors were specified except for $\log(\text{turbine})$ included as an informative prior to represent an offset. We specified 105 000 Monte Carlo iterations with a burn-in of 5000 and thinning of 100, to leave 1000 samples from the posterior distributions. The proportion of variance explained by fixed and random effects was examined [39] to generate conditional (fixed plus random effects) and marginal (fixed effects only) R^2 values. Significance of fixed effects was determined by whether 95% lower and upper credible intervals (LCL, UCL) drawn from the posterior distribution overlapped zero. For birds, model-averaged coefficients were computed across all seven phylogenetic models with equal weighting.

For birds, predicted numbers of collisions/turbine/year were generated from full models for 9568 species worldwide based on trait relationships. Predictions were generated marginal to the random effect of study ID, and were made at highest data quality level for a 365-d duration, equating to rates of collision per annum. Estimates for each species were treated as a final collision vulnerability index. For bats, full trait data were available for the 67 species modelled. To maximize the global generality of our

predictions, we based predictions on phylogenetic correlation only (for 888 species) from a model including only study and site fixed effects (no-traits model). All modelling was conducted in R v. 3.3.1 [40]. Full predictions are given in electronic supplementary material, files S3 and S4.

For an independent check of correspondence, predicted vulnerability values were compared with a previous expert assessment of species' vulnerability to the threat of 'renewable energy' in the IUCN Red List (Threats Classification Scheme v. 3.2 [26]). Modelled predictions were summarized in 5% percentiles, and presented for those threatened species identified in the IUCN Red List. To assess whether threatened species may be more at risk of collisions than other species, we used a generalized linear model to test whether collision rates varied by Red List category (Least Concern, Near Threatened and 'Threatened', i.e. Vulnerable, Endangered or Critically Endangered) in interaction with taxon (bird versus bat), weighted by the reciprocal of collision rate error.

(f) Turbine capacity effects on bird and bat mortality

We generated predictions of mean collisions/turbine/year across all species for increasing turbine capacity, for the range of turbine sizes included in this review (0.1–2.5 MW). The number of turbines required to meet a hypothetical 10 MW energy demand were then multiplied by these estimates to investigate the mean number of predicted deaths per year across species for birds and bats with increasing turbine capacity.

(g) Spatial variation in vulnerability to wind energy

Spatial variation in the potential impact of turbines on collision rates was mapped globally, based on the predicted occurrence of species within a grid (resolution, 5 km $\times$ 5 km), derived from overlaps with species range maps [23]. For birds and bats, the MCMC posterior predictions for each species were extracted. The predicted collision rates for each species that occurred in a 5 km cell (v_i) were summed across all species ($v_1 + v_2 + v_3 \dots v_{ij}$), up to the total number j occurring in that cell. A mean cumulative value, with 95% credible intervals, was then generated and mapped as a 'vulnerability' surface for birds and bats. Spatial data processing was undertaken in SAS v. 9.3 (SAS Institute Inc.) and ArcMap v. 9.3.

3. Results

(a) Data summary

A total of 362 bird and 31 bat species were recorded as collision victims with 407 and 41 further bird and bat species included as pseudo-absences. Data were obtained from 16 countries for birds and 12 countries for bats. The dataset was spatially biased to North America (birds, 64.0%, bats 48.6%) and Europe (birds, 31.0%, bats 50.6%), although South Africa, Japan, Australia and New Zealand were represented (electronic supplementary material, appendix A1, figure S1). In total, 36% of studies were in forests and 29% were in agricultural areas (e.g. artificial landscapes) with fewer in shrub (9%) and grassland (14%) landscapes. Agricultural land cover was over-represented in the review compared with global land cover (17%), whereas shrub (21%) and grassland (26%) were under-represented and forest was sampled approximately in proportion (37%) (electronic supplementary material, appendix A4).

(b) Study quality and site-specific variables

Studies that had not corrected for carcass detection probability (birds 'very low'; bats 'low') or the size of birds (low),

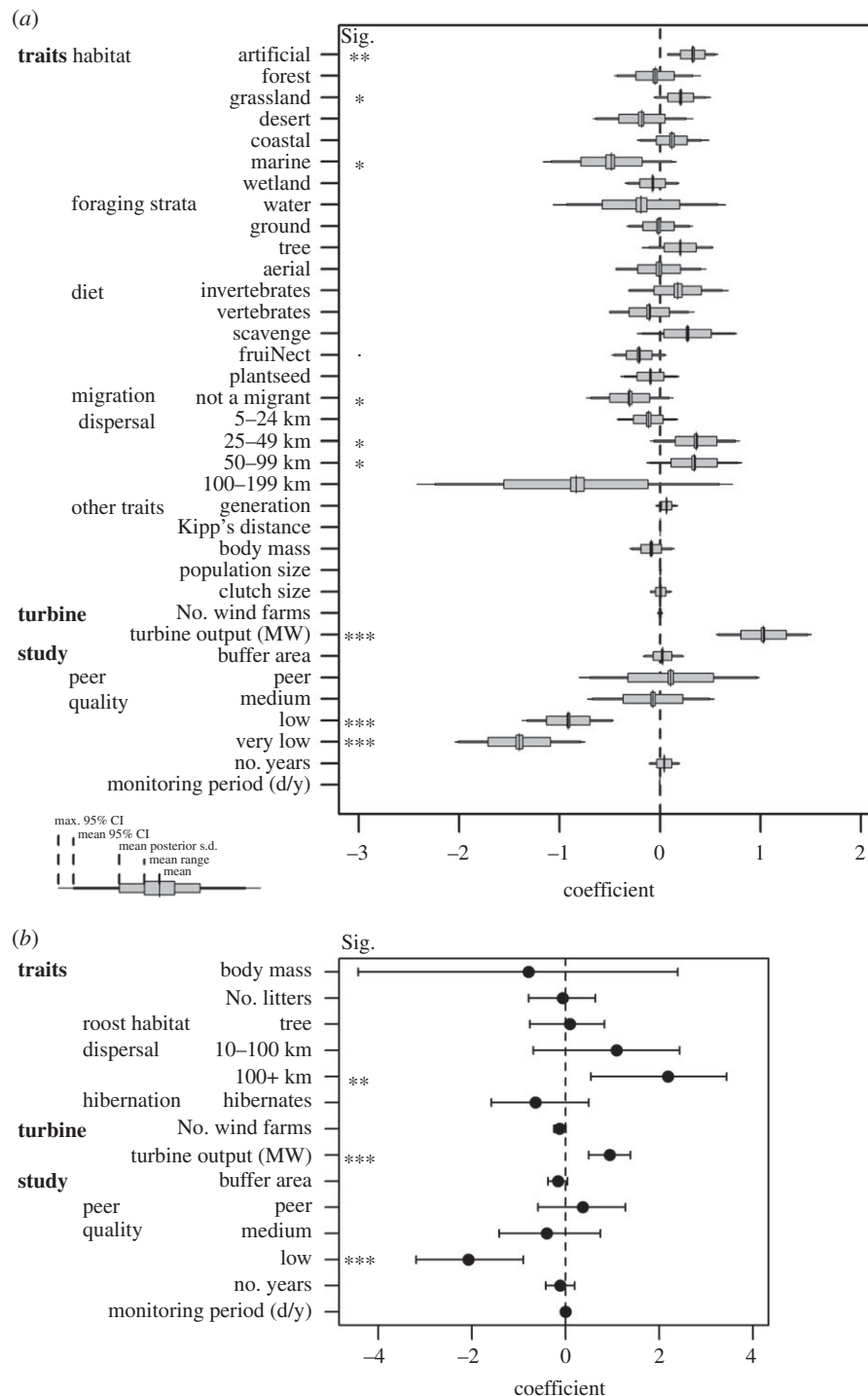


Figure 1. Coefficients from MCMCglmm models for (a) birds, and (b) bats. For birds, model-averaged coefficients are presented from seven models using alternative phylogenetic reconstruction methods, presenting (i) mean posterior predictions averaged, (ii) range of mean estimates, (iii) posterior standard deviations averaged, (iv) mean 95% credible intervals (CIs) and (v) maximum 95% CIs. For bats, the posterior mean estimate, and lower and upper 95% CIs, are given from the single trait-based model; the significance of each term (Sig.) is presented using the maximum level of significance attained ($p < 0.1$; $*p < 0.05$, $**p < 0.01$; $***p < 0.001$).

significantly underestimated the number of collisions compared with studies that had made such corrections ($p < 0.001$ in all cases, figure 1; see also electronic supplementary material, tables S3 and S4). By contrast, 'high' and 'medium' quality levels were not significantly different from the average (figure 1, $p > 0.05$). There was no residual variation explained by peer- and non-peer-review studies, buffer area, number of wind farms and study duration in days or years, after accounting for overall study-level variation using random effects ($p > 0.05$). There was, however, a strong positive correlation between turbine capacity (MW) and collisions per turbine (figure 1, $p < 0.01$ in all models).

(c) Species' traits

For birds, habitat association was an important predictor of collision rates (figure 1a, electronic supplementary material, tables S3 and S4). Species using artificial (such as farmland and urban areas) and grassland habitats had significantly higher collision rates than species not using these habitats ($p < 0.01$ in all cases). Species using marine habitats had significantly lower collision rates than species not using marine environments, probably influenced by a paucity of data for offshore wind farms. Species feeding on fruit and nectar had lower collision rates than species with other diets. Diet and foraging strata had smaller effects than habitat, with

Table 1. Summary of MCMCglmm model fits, assessed using pseudo- R^2 values, for birds (model-average across seven phylogenetic models, electronic supplementary material, table S2) and bats.

taxa	model type	marginal: fixed effects		conditional: random ID + phylo		conditional: random ID	
		mean	posterior mode (95% CI)	mean	posterior mode (95% CI)	mean	posterior mode (95% CI)
birds	traits model	0.46	0.45 (0.35–0.56)	0.85	0.85 (0.82–0.88)	0.66	0.65 (0.57–0.72)
bats	traits model	0.30	0.30 (0.11–0.50)	0.84	0.83 (0.77–0.92)	0.58	0.64 (0.37–0.75)
bats	no-traits model	0.19	0.08 (0.04–0.42)	0.88	0.87 (0.81–0.95)	0.39	0.39 (0.16–0.62)

coefficients being mostly non-significant (figure 1a). Migrants exhibited higher estimated collision rates than non-migrants (figure 1). One model gave significant support to migratory status (electronic supplementary material, appendix A5), and the direction of the effect was consistent across all models, but the mean effect size across models just overlapped zero. Species with median dispersal rates of 25–49 km or 50–99 km had significantly higher estimated collision rates from some models than those dispersing smallest (less than 25 km) or longest distances (greater than 100 km).

For bats, species dispersing furthest had significantly greater collision rates than sedentary species (figure 1), but roost site and hibernation were not significant predictors (figure 1). When fitted without dispersal, however, tree-roosting species had significantly higher collision rates than other species (electronic supplementary material, appendix A5).

(d) Model fit

The marginal R^2 explained by fixed effects was 0.46 for birds, and for bats it was 0.30 for the trait-based model and 0.19 for the no-traits model (table 1). For birds, the phylogenetic models produced similar β -coefficients (figure 1, electronic supplementary material, appendices A4 and A5, tables S3 and S4). Phylogeny explained a high proportion of variance in all models (table 1). Effective sample sizes greater than 200 and diagnostic plots indicated that autocorrelation within MCMC chains was appropriately accounted for.

(e) Model predictions

For birds, 936 species had collision rates of more than 0.046 collisions/turbine/yr (90% quartile), of which 174 species were Accipitriformes (figure 2), 57% of species in that order. Accipitriformes had the highest predicted collision rates of any taxonomic order (0.073 ± 0.064 s.d. collisions/turbine/year, mean lower credible interval less than 0.001, mean upper credible interval, 0.288). Mean predictions were also high for Bucerotiformes, Ciconiiformes and Charadriiformes, whereas Galbuliformes and Coraciiformes were among the lowest, and waterbirds such as Anseriformes and Galliformes and Passeriformes songbirds also had smaller than average predictions (figure 2).

For bats, the most vulnerable families containing greater than 10 species/family included Molossidae and Hipposideridae, while Rhinolophidae were among the least vulnerable (figure 3). The largest family, Vespertilionidae, had high collision rates (0.718 ± 0.586 s.d., 294 species) and included

the five bat species most vulnerable to collision (electronic supplementary material, appendix A6).

In total, 57 bird species (including 31 Accipitriformes) were identified as threatened by ‘renewable energy’ [26], of which 43 species (75%) were above the 75% percentile of our collision predictions (electronic supplementary material, table S6). All of the 31 Accipitriformes were above the 75% percentile, and 26 (84%) were ranked above the 90% percentile. After accounting for a significantly greater collision rate for bats than birds ($\chi^2 = 510.30$, $p < 0.001$), there was no residual variation explained by IUCN Red List category ($\chi^2 = 0.63$, $p = 0.73$), or among categories constituting the broader ‘threatened’ category (Vulnerable, Endangered or Critically Endangered) ($\chi^2 = 0.19$, $p = 0.91$, electronic supplementary material, appendix A7).

(f) Relationships between turbine size and mortality

For birds and bats, larger turbines were associated with increased collision rates (figure 1). A greater number of small turbines, however, resulted in higher predicted mortality rates (figure 4) than a smaller number of large turbines per wind farm unit energy output. Using 1000–0.01 MW turbines resulted in the largest estimated number of bird and bat fatalities; thereafter the numbers decreased exponentially up to approximately 1.2 MW, where the relationship for birds continued to decline up to 2.5 MW turbines (posterior means, LCL–UCL 0.8, 0.5–1.1). By contrast, the mortality for bats increased again from 14 (8–21) bats with 1.2 MW turbines, to 24 (12–40) bats with 2.5 MW turbines (figure 4).

(g) Spatial variation in vulnerability to wind energy

The greatest numbers of vulnerable bird species occurred along coastal and migratory pathways in the eastern and southwestern USA, the central American isthmus from Mexico to Panama, Northern Andes, Rift Valley of East Africa and the Himalayas. For bats, the greatest number of collisions was predicted in North America (figure 5).

4. Discussion

Previous studies into the collision risk of birds with terrestrial wind farms have documented a high risk for Accipitriformes (raptors and birds of prey) [41,42]. Further studies have suggested that raptors, migratory soaring birds and waterbirds may be particularly vulnerable [9,43–45].

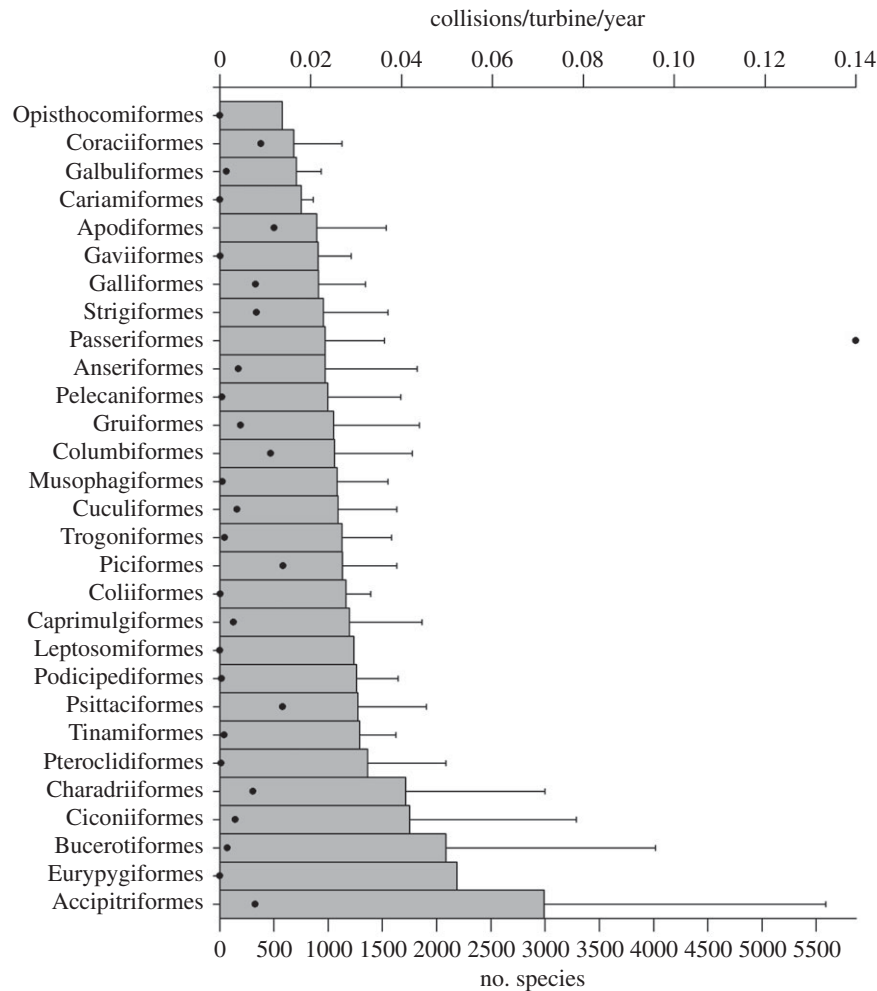


Figure 2. Predictions of mean collisions per turbine (per year) ($\pm$ s.d.) for bird orders (9568 species) from the posterior distributions of MCMCglmm models, ordered by mean predictions; numbers of species per order are shown by black dots.

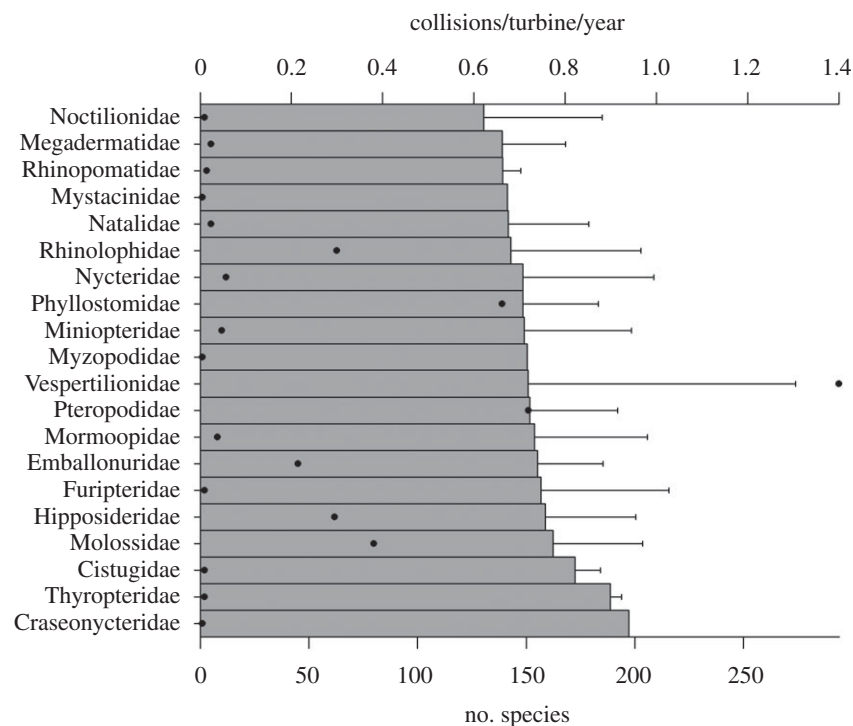


Figure 3. Predictions of mean collisions per turbine (per year) ($\pm$ s.d.) for bat families (888 species) from the posterior distributions of MCMCglmm models, ordered by mean predictions; numbers of species per family are shown by black dots.

Similarly, our study showed that Accipitriformes had the highest rates of collision. Among other orders, Buceroti-formes (hornbills and hoopoes), Ciconiiformes (storks and

herons) and some Charadriiformes (shorebirds) were also vulnerable, but notably many waterbirds (e.g. Anseriformes) were not.

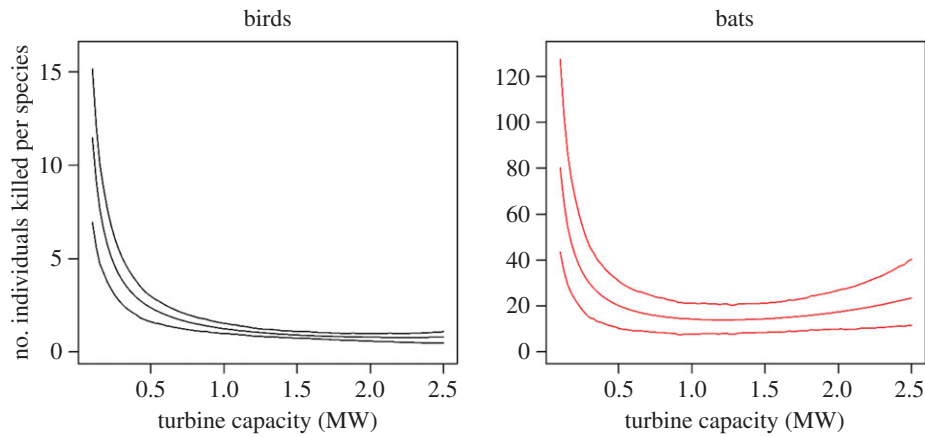


Figure 4. The mean total mortality rate across species for a hypothetical 10 MW wind farm, shown in relation to individual turbine capacities (which in turn require different numbers of wind turbines to meet the same capacity). Lines represent posterior means and 95% upper and lower credible intervals.

Although there was less variation in predicted mortality between bat families (figure 3), a small number of Vespertilionidae species were associated with relatively high rates of collision, as also found in a recent review [8]. Our models predicted higher collision rates for bats than birds, as reported elsewhere [15], which adds to the literature emphasizing the risk that wind farms pose to bat populations [7,8,14].

For birds, vulnerability to collision was related to habitat, migratory status and dispersal distance. High collision rates for species associated with agricultural habitats may reflect the disproportionate number of wind farms from agricultural landscapes in our sample. Species associated with these human-modified habitats, however, may be less likely to avoid wind farms than those occupying natural landscapes [46], while our results suggest that grassland species may also be more vulnerable to collision.

Migratory species are often suggested as being vulnerable to collision with wind farms [44], for which our results are supportive. Previous work has suggested high rates of collision with wind turbines at avian migratory bottlenecks [9,41,42], and for migratory bats in North America [8,47], suggesting migration may outweigh the greater exposure time of residents to wind turbines [41].

Wind farms may have significant meta-population-level impacts [45], for example on species with large home ranges and moderate rates of dispersal [12]. The link, however, between dispersal distance and collision rate across multiple species has not previously been identified, and demonstrates that bird species dispersing short or very long distances may have reduced vulnerability to collision compared with species dispersing intermediate distances. Those species dispersing furthest may exhibit unmeasured traits of flight behaviour, such as flight height rendering them less susceptible to collision, but the large uncertainty in the effect emphasizes that further study is needed. For bats, long-distance dispersers had the highest collision rates, but certainty of behaviour for many species tempers our ability to draw firm conclusions. Tree-roosting bat species were frequently recorded in collision, potentially through attraction mechanisms [48], although this effect was weaker than dispersal. Overall, these findings emphasize the need to consider cumulative impacts of wind farms on populations, particularly for migrants and wide-ranging species.

Our vulnerability estimates may not reflect population-level impacts, to understand which requires further

consideration of population demography and other impact metrics [22,45]. However, our findings may be problematic in terms of species conservation, as the species groups with the greatest rate of collision tended to be *k*-selected species with low fecundity and late ages of maturity, and most sensitive to impacts of additional mortality [49,50], such as Accipitriformes, Bucerotiformes, Ciconiiformes and Charadriiformes for birds, and a range of bat species. Avoiding placement of wind farms in areas with populations or high concentrations of such species, such as coastal areas and migratory flyways (figure 5), would reduce potential impacts of wind farms on biodiversity. Although some passerine families (e.g. Motacillidae) and species (e.g. European starling, *Sturnus vulgaris*) had high predicted rates of collision, their *r*-selected life-histories and relatively high abundances make it less likely that large population-level effects would arise, as population growth rate is less sensitive to reductions in adult survival [49].

Although as comprehensive as possible, our study has some limitations. First, data were largely from well-studied parts of Europe and North America. While our results can be used to infer potential collision risk for species in other parts of the world, uncertainty arises when extrapolating to understudied regions and taxa. This was particularly the case for bats, where studies were exclusively from temperate northern latitudes with low species diversity. More geographically widespread studies, from the tropics and from countries with rapidly growing wind industries (such as India and China), are required to feed into meta-analyses like ours. In the absence of such studies, our estimated collision rates should help indicate vulnerable species in these areas. Second, collision rate data were not available from offshore wind farms. Only 5% of studies recorded collisions with marine species at coastal wind farms, and further work is needed to estimate their vulnerability to offshore wind turbines [51]. Third, trait information for bats was less comprehensive than for birds, meaning it was not possible to extrapolate from a trait-based model globally in the same manner. We also note the strong geographical variation in predicted bat mortality rates between North America and Europe (figure 5), and suggest further work is required to test whether this effect is real. Fourth, although we corrected for data quality, inevitably some variation will not be captured by our classification; for example, corrections for unsearchable portions of the survey area were not always reported. Fifth, our

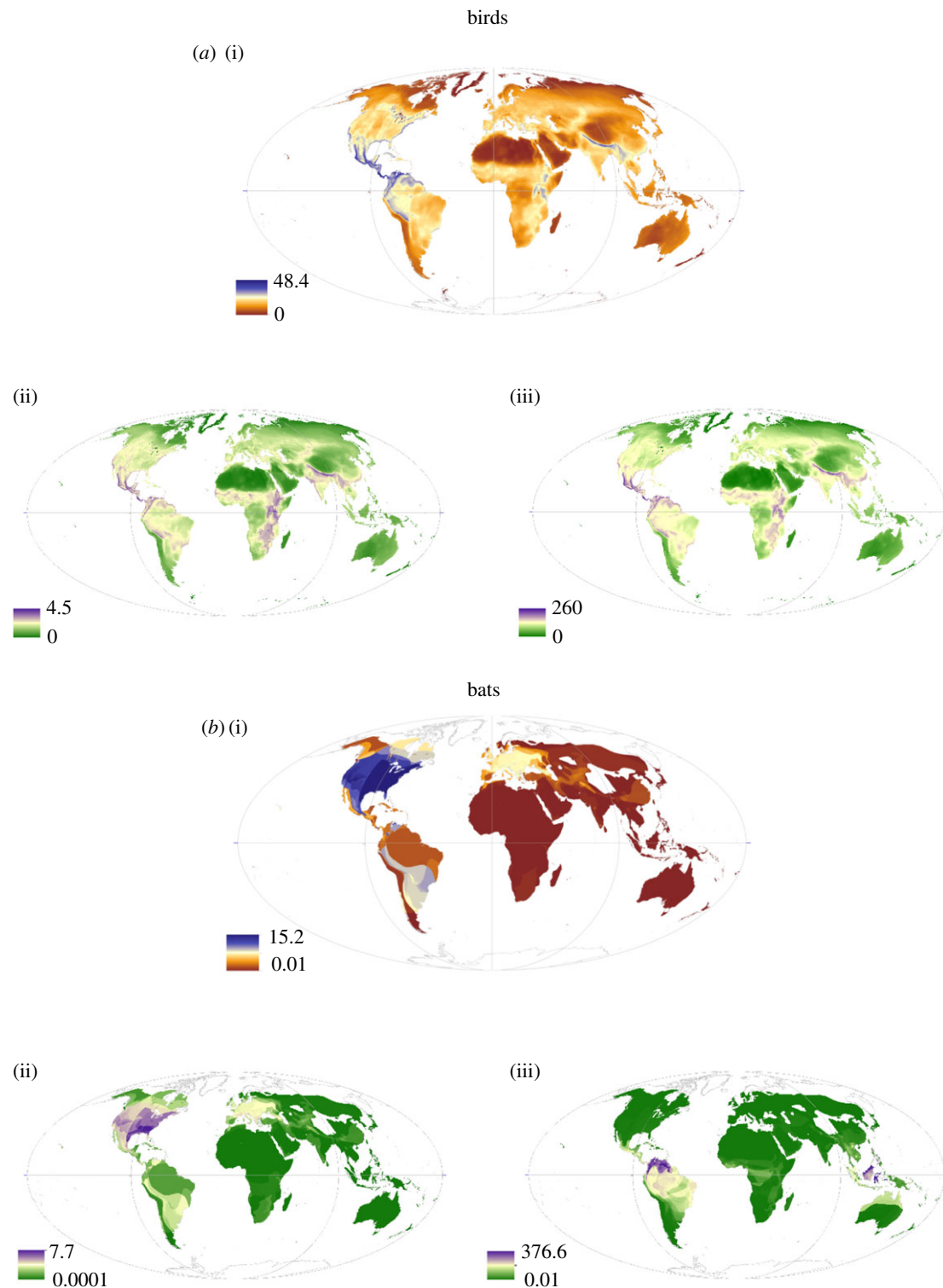


Figure 5. Worldwide distribution of $(a(i)–iii)$ bird and $(b(i)–iii)$ bat species' vulnerability to wind farm collisions, based on summing vulnerability of each species that occurs at each point, according to species range maps for $(a(i), b(i))$ mean across species, and lower and upper $(a(ii), b(ii))$ and $(a(iii), b(iii))$ credible intervals from MCMCglmm models (for details of data manipulation and calculations behind these maps, see methods).

study metric focused on a measured impact after collision with turbines, reflecting both initial sensitivity and current exposure. Our study, however, did not include future potential to habituate (adaptability), necessitating caution when translating our findings more broadly. Finally, our list of species putatively present at a wind farm was derived from broad-scale distribution polygons, and so may have included false negatives [27].

Given the recent dramatic increases in wind energy generating capacity in parts of the world where wind farms

have not previously been deployed [52], and probably continued increases to meet climate change mitigation targets, wind farms pose an increasing threat to bird and bat species worldwide. Our study can be used to mitigate this risk in two ways. First, although uncertain, our species-level predictions of collision rates provide a useful starting point for scoping potential impacts of wind farms on species where collision risk has not been studied. New wind developments should preferably be in areas with low concentrations of species vulnerable to collision. Our results can help identify locations

based on the distribution of vulnerable species, which alongside habitat restrictions on wind farm development, such as in forested areas, can be used to minimize the risk of negative biodiversity impact. Although country and regional maps [53,54] should be developed to help identify local hotspots, our global vulnerability maps (figure 5) are a useful starting point, suggesting key areas and migratory pathways where collision may occur. The agreement between our predictions and species classified by the IUCN Red List as being threatened by 'renewable energy' suggests an emerging consensus for key taxa.

Second, there was a strong positive relationship between wind turbine capacity and collision rate per turbine. The strength of this relationship, however, was insufficient to offset the reduced number of turbines required per unit energy generation with larger turbines, at least for birds. Therefore, to minimize bird collisions, wind farm electricity generation capacity should be met through deploying fewer, large turbines, rather than many smaller ones, supporting suggestions for marine birds [16]. For bats, an optimum turbine size of approximately 1.25 MW may minimize collision risk, with the largest turbines associated with a disproportionately high collision rate, but we again caution that model certainty for bats was low for the reasons outlined. More research is required to understand the relationship between collision risk and turbine size for larger (and more efficient) turbines, and how this may vary between habitats.

5. Conclusion

This study is the first global quantitative assessment from the published literature of the relative vulnerability of different

species groups to wind farms. Wind farms have the potential to benefit biodiversity through their contribution to climate change mitigation, but our results emphasize the global nature of the potential risks to biodiversity involved, which needs to be accounted for through appropriate wind turbine design and planning, if those risks are to be minimized.

Data accessibility. Supporting data are available on the Dryad Digital Repository: The collision rate data for bird and bat species obtained from the literature is available at: <http://dx.doi.org/10.5061/dryad.h9s55> [55].

Authors' contributions. C.B.T., J.W.P.-H., G.M.B., J.C., S.H.M.B., T.N. and R.E.G. conceived and designed the study. C.B.T. conducted the literature review and carried out the meta-analysis, J.C., S.H.M.B. and J.A.T. extracted and provided data for analysis, and G.M.B. produced mapped outputs from statistical models. C.B.T. and J.W.P.-H. drafted the manuscript, and conceived appropriate testing and statistical procedures, under the guidance of all authors, and an independent project advisory group, including W.B.F. and S.O'B. All authors edited the manuscript and gave their approval for publication.

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References

- IPCC. 2014 *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change* (eds Core Writing Team, RK Pachauri, LA Meyer), 151 pp. Geneva, Switzerland: IPCC.
- UNFCCC. 2015 Adoption of the Paris Agreement. FCCC/CP/2015/10/Add.1.
- Schleussner C-F *et al.* 2016 Science and policy characteristics of the Paris agreement temperature goal. *Nat. Clim. Change* **6**, 827–835. (doi:10.1038/nclimate3096)
- Kumar Y, Ringenberg J, Depuru SS, Devabhaktuni VK, Lee JW, Nikolaidis E, Andersen B, Afjeh, A. 2016 Wind energy: trends and enabling technologies. *Renew. Sustain. Energy Rev.* **53**, 209–224. (doi:10.1016/j.rser.2015.07.200)
- Schuster E, Bulling L, Köppel J. 2015 Consolidating the state of knowledge: a synoptical review of wind energy/ wildlife effects. *Environ. Manage.* **56**, 300–331. (doi:10.1007/s00267-015-0501-5)
- Drewitt A, Langston RHW. 2006 Assessing the impacts of wind farms on birds. *Ibis* **148**, 29–42. (doi:10.1111/j.1474-919X.2006.00516.x)
- Hayes MA. 2013 Bats killed in large numbers at United States wind energy facilities. *BioScience* **63**, 975–979. (doi:10.1525/bio.2013.63.12.10)
- Zimmerling JR, Francis CM. 2016 Bat mortality due to wind turbines in Canada. *J. Wildl. Manage.* **80**, 1360–1369. (doi:10.1002/jwmg.21128)
- Pearce-Higgins JW, Green RE. 2014 *Birds and climate change: impacts and conservation responses*. Cambridge, UK: Cambridge University Press, www.cambridge.org/bacc.
- Frick WF *et al.* 2017 Fatalities at wind turbines may threaten population viability of a migratory bat. *Biol. Conserv.* **209**, 172–177. (doi:10.1016/j.biocon.2017.02.023)
- Martin GR, Portugal SJ, Murn CP. 2012 Visual fields, foraging and collision vulnerability in *Gyps* vultures. *Ibis* **154**, 626–631. (doi:10.1111/j.1474-919X.2012.01227.x)
- Carrete M, Sanchez-Zapata JA, Benitez JR, Lobon M, Donazar JA. 2009 Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biol. Conserv.* **142**, 2954–2961. (doi:10.1016/j.biocon.2009.07.027)
- Dahl EL, Bevanger K, Nygard T, Roskaft E, Stokke BG. 2012 Reduced breeding success in white-tailed eagles at Smola windfarm, western Norway, is caused by mortality and displacement. *Biol. Conserv.* **145**, 79–85. (doi:10.1016/j.biocon.2011.10.012)
- Voigt CC, Popa-Lisseanu AG, Niermann I, Kramer-Schadt S. 2012 The catchment area of wind farms for European bats: a plea for international regulations. *Biol. Conserv.* **153**, 80–86. (doi:10.1016/j.biocon.2012.04.027)
- Barclay RMR, Baerwald EF, Gruver JC. 2007 Variation in bat and bird fatalities at wind energy facilities: assessing the effects of rotor size and tower height. *Can. J. Zool.* **85**, 381–387. (doi:10.1139/Z07-011)
- Johnston A, Cook ASCP, Wright LJ, Humphreys EM, Burton NHK. 2014 Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *J. Appl. Ecol.* **51**, 31–41. (doi:10.1111/1365-2664.12191)
- Bartholomé E, Belward AS. 2005 GLC2000: a new approach to global land cover mapping from Earth observation data. *Int. J. Remote Sens.* **26**, 1959–1977. (dx.doi.org/10.1080/01431160412331291297)
- Smallwood KS. 2013 Comparing bird and bat fatality-rate estimates among North American wind-energy projects. *Wildl. Soc. Bull.* **37**, 19–33. (doi:10.1002/wsb.260)
- Huso MMP, Dalthorp D. 2014 Accounting for unsearched areas in estimating wind turbine-caused fatality. *J. Wildl. Manage.* **78**, 347–358. (doi:10.1002/jwmg.663)

20. Loss SR, Will T, Marra PP. 2013 Estimates of bird collision mortality at wind facilities in the contiguous United States. *Biol. Conserv.* **168**, 201–209. (doi:10.1016/j.biocon.2013.10.007)
21. Smallwood KS. 2017. Long search intervals underestimate bird and bat fatalities caused by wind turbines. *J. Wildl. Manage.* **41**, 224–230. (doi:10.1002/wsb.774)
22. Erickson WP, Wolfe MM, Bay KJ, Johnson DH, Gehring JL. 2014 A comprehensive analysis of small-passerine fatalities from collision with turbines at wind energy facilities. *PLoS ONE* **9**, e107491. (doi:10.1371/journal.pone.0107491)
23. Birdlife International. 2016 Birdlife datzone. See <http://www.birdlife.org/datzone> (accessed 19 Oct 2016).
24. Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, Barlow J, Tobias JA. 2016 Using avian functional traits to quantify the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. B* **283**, 20161289. (doi:10.1098/rspb.2016.1289)
25. Baldwin MW, Winkler H, Organ CL, Helm B. 2010 Wing pointedness associated with migratory distance in common garden and comparative studies of stonechats (*Saxicola torquata*). *J. Evol. Biol.* **23**, 1050–1063. (doi:10.1111/j.1420-9101.2010.01975.x)
26. IUCN. 2016 The IUCN Red List of Threatened Species, 2016-2. ISSN 2307-8235. See <http://www.iucnredlist.org/> (accessed 20 Oct 2016).
27. Beresford AE, Buchanan GM, Donald PF, Butchart SHM, Fishpool LDC, Rondinini C. 2011 Poor overlap between the distribution of protected areas and globally threatened birds in Africa. *Anim. Conserv.* **14**, 99–107. (doi:10.1111/j.1469-1795.2010.00398.x)
28. Jones KE *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648. (doi:10.1890/08-1494.1)
29. Kissling WD, Dalby L, Fløjgaard C, Lenoir J, Sandel B, Sandom C, Trøjelsgaard K, Svenning J-C. 2014 Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecol. Evol.* **4**, 2913–2930. (doi:10.1002/ece3.1136)
30. Dietz C, Kiefer A. 2016 *Bats of Britain and Europe*. London, UK: Bloomsbury Publishing.
31. Animal Diversity Web. 2017 The Animal Diversity Web (ADW), Musuem of Zoology, University of Michigan. See <http://animaldiversity.org/> (accessed 06 July 2017).
32. Barova S, Streit A. 2016 Action plan for the conservation of bat species in the European Union—2016–2021: DRAFT. Inf.EUROBATS.AC21.5. European Commission & UNEP Eurobats.
33. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
34. Rubolini D, Liker A, Garamszegi LZ, Møller AP, Saino N. 2015 Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Curr. Zool.* **61**, 959–965. (doi:10.1093/czoolo/61.6.959)
35. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
36. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Soft.* **33**, 1–22. (doi:10.18637/jss.v033.i02)
37. Hadfield JD. 2016 Package ‘MCMCglmm’, Version 2.22.1. See <https://cran.r-project.org/web/packages/MCMCglmm/MCMCglmm.pdf> (accessed 12 Dec 2016).
38. Dale J, Dey CJ, Delhey K, Kempnaers B, Valcu M. 2015 The effects of life history and sexual selection on male and female plumage colouration. *Nature* **527**, 367–370. (doi:10.1038/nature15509)
39. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining *R* from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
40. R Core Team. 2016 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
41. Barrios L, Rodriguez A. 2004 Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *J. Appl. Ecol.* **41**, 72–81. (doi:10.1111/j.1365-2664.2004.00876.x)
42. Smallwood KS, Thelander C. 2008 Bird mortality in the altamont pass wind resource area, California. *J. Wildl. Manage.* **72**, 215–223. (doi:10.2193/2007-032)
43. Steward GB, Pullin AS, Coles CF. 2007 Poor evidence-base for assessment of windfarm impacts on birds. *Environ. Conserv.* **34**, 1–11. (doi:10.1017/S0376892907003554)
44. Desholm M. 2009 Avian sensitivity to mortality: prioritising migratory species for assessment at proposed wind farms. *J. Environ. Manage.* **90**, 2672–2679. (doi:10.1016/j.jenvman.2009.02.005)
45. Beston JA, Diffendorfer J, Loss SR, Johnson DH. 2016 Prioritizing avian species for their risk of population level consequences from wind energy development. *PLoS ONE* **11**, e0150813. (doi:10.1371/journal.pone.0150813)
46. Pearce-Higgins JW, Stephen L, Langston RHW, Bainbridge IP, Bullman R. 2009 The distribution of breeding birds around upland wind farms. *J. Appl. Ecol.* **46**, 1323–1331. (doi:10.1111/j.1365-2664.2009.01715.x)
47. Voigt CC, Lehnert LS, Petersons G, Adorf F, Bach L. 2015 Wildlife and renewable energy: German politics cross migratory bats. *Eur. J. Wildl. Res.* **61**, 213–219. (doi:10.1007/s10344-015-0903-y)
48. Cryan PM *et al.* 2014 Behavior of bats at wind turbines. *Proc. Natl Acad. Sci. USA* **111**, 15 126–15 131. (doi:10.1073/pnas.1406672111)
49. Sæther B-E, Bakke Ø. 2000 Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653. (doi:10.1890/0012-9658(2000)081[0642:ALHVC]2.0.CO;2)
50. Niel C, Lebreton J-D. 2005 Using demographic invariants to detect overharvested bird populations from incomplete data. *Conserv. Biol.* **19**, 826–835. (doi:10.1111/j.1523-1739.2005.00310.x)
51. Newton I, Little B. 2009 Assessment of wind-farm and other bird casualties from carcasses found on a Northumbrian beach over an 11-year period. *Bird Study* **56**, 158–167. (doi:10.1080/00063650902787767)
52. Ahmed S, Mahmood A, Hasan A, Sidhu GAS, Butt MFU. 2016 A comparative review of China, India and Pakistan renewable energy sectors and sharing opportunities. *Renew. Sustain. Energy Rev.* **57**, 216–225. (doi:10.1016/j.rser.2015.12.191)
53. Bright JA, Langston RHW, Bullman R, Evans RJ, Gardner S, Pearce-Higgins JW, Wilson E. 2008 Map of bird sensitivities to wind farms in Scotland: a tool to aid planning and conservation. *Biol. Conserv.* **141**, 2342–2356. (doi:10.1016/j.biocon.2008.06.029)
54. BirdLife International. 2016 Soaring bird sensitivity mapping tool. See <https://maps.birdlife.org/MSBtool/> (accessed 15 Dec 2016).
55. Thaxter CB *et al.* 2017 Data from: Bird and bat species’ global vulnerability to collision mortality with wind farms revealed through a trait-based assessment. Dryad Digital Repository. (<http://dx.doi.org/10.5061/dryad.h9s55>)