






Estimation of spatiotemporal trends in bat abundance from mortality data collected at wind turbines

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Abstract: Renewable energy sources, such as wind energy, are essential tools for reducing the causes of climate change, but wind turbines can pose a collision risk for bats. To date, the population-level effects of wind-related mortality have been estimated for only 1 bat species. To estimate temporal trends in bat abundance, we considered wind turbines as opportunistic sampling tools for flying bats (analogous to fishing nets), where catch per unit effort (carcass abundance per monitored turbine) is a proxy for aerial abundance of bats, after accounting for seasonal variation in activity. We used a large, standardized data set of records of bat carcasses from 594 turbines in southern Ontario, Canada, and corrected these data to account for surveyor efficiency and scavenger removal. We used Bayesian hierarchical models to estimate temporal trends in aerial abundance of bats and to explore the effect of spatial factors, including landscape features associated with bat habitat (e.g., wetlands, croplands, and forested lands), on the number of mortalities for each species. The models showed a rapid decline in the abundance of 4 species in our study area; declines in capture of carcasses over 7 years ranged from 65% (big brown bat [*Eptesicus fuscus*]) to 91% (silver-haired bat [*Lasionycteris noctivagans*]). Estimated declines were independent of the effects of mitigation (increasing wind speed at which turbines begin to generate electricity from 3.5 to 5.5 m/s), which significantly reduced but did not eliminate bat mortality. Late-summer mortality of hoary (*Lasiurus cinereus*), eastern red (*Lasiurus borealis*), and silver-haired bats was predicted by woodland cover, and mortality of big brown bats decreased with increasing elevation. These landscape predictors of bat mortality can inform the siting of future wind energy operations. Our most important result is the apparent decline in abundance of four common species of bat in the airspace, which requires further investigation.

Keywords: aeroconservation, aeroecology, bat mortality, Bayesian hierarchical models population trends, renewable energy, wind energy

Estimación de Tendencias Espacio-Temporales en la Abundancia de Murciélagos a Partir de Datos de Mortalidad Recolectados Alrededor de Turbinas de Viento

Resumen: Las fuentes de energía renovable, como la energía eólica, son herramientas esenciales para la reducción de las causas del cambio climático, aunque las turbinas de viento pueden representar un riesgo de colisión para los murciélagos. A la fecha, los efectos a nivel poblacional de la mortalidad asociada a estas turbinas sólo han sido estimados para una especie de murciélagos. Para estimar las tendencias temporales en la abundancia de murciélagos consideramos a las turbinas de viento como herramientas para el muestreo oportunista de los murciélagos en vuelo (análogo a las redes de pesca), en donde el esfuerzo de captura por unidad (abundancia de cadáveres por turbina monitoreada) es un sustituto para la abundancia aérea de murciélagos, después de

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considerar la variación estacional en la actividad. Utilizamos un conjunto grande de datos estandarizados del registro de cadáveres de murciélagos alrededor de 594 turbinas al sur de Ontario, Canadá, y corregimos estos datos para justificar la eficiencia del muestreador y la extracción por carroñeros. Usamos modelos de jerarquía bayesiana para estimar las tendencias temporales en la abundancia aérea de los murciélagos y para explorar los efectos de los factores espaciales, incluyendo las características del paisaje asociadas con el hábitat de los murciélagos (p. ej.: humedales, tierras de cultivo y bosques), sobre el número de muertes para cada especie. Los modelos mostraron una declinación rápida en la abundancia de cuatro especies dentro de nuestra área de estudio. Las declinaciones en la captura de cadáveres a lo largo de siete años variaron desde el 65% (*Eptesicus fuscus*) hasta el 91% (*Lasionycteris noctivagans*). Las declinaciones estimadas fueron independientes a los efectos de mitigación (el incremento en la velocidad a la cual las turbinas comienzan a generar electricidad de 3.5 a 5.5 m/s), lo cual redujo significativamente la mortalidad de los murciélagos, aunque no llegó a eliminarla. La mortalidad a finales del verano de las especies *Lasiurus cinereus*, *Lasiurus borealis* y *Lasionycteris noctivagans* la pronosticó la cobertura de los lotes boscosos, mientras que la mortalidad de *E. fuscus* disminuyó conforme incrementó la elevación. Estos elementos pronosticadores del paisaje pueden utilizarse para informar al momento de elegir el sitio para la actividad eólica en el futuro y así evitar la mortalidad en murciélagos. Nuestro resultado más importante es la declinación aparente en la abundancia de cuatro especies comunes de murciélagos en el espacio aéreo, lo cual requiere de más investigación.

Palabras Clave: aeroconservación, aerocología, energía eólica, energía renovable, modelos de jerarquía bayesiana, mortalidad en murciélagos, tendencias poblacionales

摘要: 风能等可再生能源是减少气候变化发生的重要工具, 但风力涡轮机可能会给蝙蝠带来碰撞风险。目前, 仅对一种蝙蝠估计了与风有关的死亡的种群水平影响。为了估计蝙蝠丰度的时间趋势, 本研究考虑以风力涡轮机作为飞行蝙蝠的机会抽样工具 (类似于渔网), 在考虑蝙蝠活动的季节性变化的情况下, 利用每单位监测量的捕获量 (即每一监测涡轮机的蝙蝠尸体数量) 来估计飞行蝙蝠的丰度。我们使用了加拿大安大略省南部 594 个涡轮机蝙蝠尸体记录的大量标准化数据集, 并从调查者效率和尸体清除方面对这些数据进行了修正。接下来, 我们用贝叶斯层次模型来估计空中蝙蝠数量的时间趋势, 并探讨空间因素的影响, 包括与蝙蝠栖息地相关的景观特征 (如湿地、农田和林地) 对每种蝙蝠死亡情况的影响。模型显示, 我们研究区域内 4 种物种的丰度发生了急剧下降; 在过去的 7 年中, 捕获动物尸体数量的下降率范围在 65% (大棕蝠 [*Eptesicus fuscus*]) 到 91% (银发蝙蝠 [*Lasionycteris noctivagans*]) 之间。下降率估计值与减缓措施 (将涡轮机开始发电的风力从 3.5 米/秒提高到 5.5 米/秒) 的影响无关, 这一措施显著降低了蝙蝠死亡量, 但没有消除对蝙蝠的致死影响。林地覆盖度可以预测灰蓬毛蝠 (*Lasiurus cinereus*)、红蝠 (*Lasiurus borealis*) 和银发蝙蝠的夏末死亡量, 而大棕蝠的死亡量则随海拔升高而下降。这些蝙蝠死亡量的景观预测因素可以为未来风能发电的选址提供信息。本研究最重要的结果是, 四种空中常见蝙蝠的数量都明显下降, 这需要进一步调查。【翻译: 胡怡思; 审核: 聂永刚】

关键词: 航空保护、, 航空生态、, 蝙蝠死亡量、, 贝叶斯层次模型、, 种群趋势、, 可再生能源、, 风能

Introduction

Renewable energy sources can facilitate divestment from fossil fuels, reducing the rate of climate change (Figueres et al. 2017). Yet climate change is only one threat to human and environmental well-being. Loss of biodiversity and associated ecosystem services also have long-term social, environmental, and economic implications (Oliver et al. 2015; Johnson et al. 2017; Fanin et al. 2018). Renewable energy operations can avoid inadvertent impacts on biodiversity through tools that minimize interactions with wildlife (Arnett et al. 2016; Gibson et al. 2017; Law & Fuller 2018).

Bats experience mortality at wind turbines throughout the world (e.g., Rydell et al. 2010b; Arnett et al. 2016; Thaxter et al. 2017), but mortality varies among species. In eastern North America, long-distance migrants, including hoary bats (*Lasiurus cinereus*), eastern red bats (*L. borealis*), and silver-haired bats (*Lasionycteris noctivagans*) comprise >75% of bat fatal-

ities at wind turbines (Zimmerling & Francis 2016; Frick et al. 2017). High fatality at turbines may be correlated with high activity levels, specific atmospheric conditions, seasonality, and landscape characteristics (Schuster et al. 2015; Hein & Schirmacher 2016). However, the population-level effects of wind-turbine-related mortality have been estimated for only a single species, the hoary bat, and they indicate population declines (Frick et al. 2017). Bayesian modeling of acoustic monitoring data also suggest declining abundance of hoary bats in the Pacific Northwest which coincided with intensification of wind energy infrastructure (Rodhouse et al. 2019).

Many studies have summarized bat mortality counts at wind turbines (O'Shea et al. 2016; Zimmerling & Francis 2016; Lemaitre et al. 2017). However, bat-mortality count data cannot be converted to mortality rates without estimates of population size, which are lacking for most species (Arnett et al. 2016). Therefore, it is difficult to estimate whether the observed bat mortality at wind

turbines threatens species' persistence, although Arnett et al. (2011a) and Frick et al. (2017) circumvented this challenge by modeling a range of scenarios.

Wind turbines can provide a random sampling tool for sampling bats in the airspace suitable for estimating population trends. Such an approach, is similar to the way fishery researchers use capture and bycatch data. Fishery catch per unit effort (CPUE) is used to infer spatial and temporal trends in abundance of target fish species and abundance and distribution of bycatch (i.e. non-target wildlife) (Read et al. 2006; Riskas et al. 2016). If the number of bats killed by turbines is correlated with the abundance of bats moving through the adjacent airspace, it may be possible to track broad-scale temporal trends in the relative abundance of bats given a large enough data set of carcass counts at wind turbines. Global bat populations face a range of threats, including habitat loss, persecution or harvest, and diseases, such as white-nose syndrome (O'Shea et al. 2016; Hammerson et al. 2017). Thus, estimating temporal trends in bat populations from wind mortality data has implications beyond assessing the direct impacts of wind energy itself.

We used a large, standardized data set on bat mortality collected at 594 individual turbines in southern Ontario, Canada. We considered these data in two distinct ways. First, we considered wind turbines opportunistic sampling tools for bats, generating estimated carcass abundance data (carcasses/turbine) that we considered analogous to CPUE data from fisheries (Riskas et al. 2016; Korman & Yard 2017). We used these data to test whether the abundance of bats in the airspace in our study area changed over time. We explicitly controlled for the effects of increasing cut-in speed (wind speed at which turbines begin to generate electricity) from 3.5 to 5.5 m/s (a proxy for capture effort and a common mitigation measure in our study area). Second, we explored spatial predictors of bat mortality at turbines. We estimated species-specific temporal trends in the apparent abundance of four species of insectivorous bats and identified landscape features that predict mortality risk from turbines for these species. These predictors could inform siting of future wind-energy infrastructure to reduce the negative impacts of this important source of renewable energy on biodiversity.

Methods

Estimating Bat Mortality

Wind-energy facilities licensed under Renewable Energy Approvals in Ontario, Canada, conduct standardized mortality monitoring at a subset of turbines for the first three years of operation. Monitoring included carcass counts and field surveys to estimate carcass scavenging rates and searcher efficiency (OMNRF 2011). We extracted these

data from reports submitted to the Ontario Ministry of Natural Resources and Forestry (OMNRF) that described surveys conducted from 1 May 2010 to 31 October 2017 ($n = 594$ individual turbines at 48 facilities [Supporting Information], each surveyed for 1–4 years). Only 1% of carcasses were not identifiable to species. These unidentifiable carcasses were of small bats (*Myotis* or *Perimyotis* species) and therefore did not affect our analyses of hoary, eastern red, silver-haired, or big brown bat mortality.

We verified turbine locations provided in facility reports based on a geospatial database of all turbines constructed in Ontario compiled by the OMNRF. Study facilities were in agricultural fields and contained 1–140 turbines (mean = 57). Twelve facilities reported estimated fatality of ≥ 10 bats/turbine/year (1 in year 2 of monitoring; the other 11 in year 1). These facilities implemented operational mitigation in subsequent years, increasing cut-in speeds from 3.5 to 5.5 m/s from 15 July to 30 September (late-summer migratory season when bat mortality at turbines is highest [Baerwald et al. 2009; Arnett et al. 2016]). Data from these facilities include estimates made before mitigation and estimates from ≤ 3 years of mitigation. Thus, our data set included turbines that did not require mitigation (survey data available for 1–3 years/turbine; median of 2 years/turbine) and turbines that did (data available for 1–4 years/turbine; median = 3 years/turbine).

Reports submitted to OMNRF followed current Ontario guidelines for monitoring bat mortality at wind turbines and applied the OMNRF estimator, which is based on the Winkelman or Meyer estimator (Meyer 1978). We extracted the raw data from each report and derived corrections for scavenging rates, observer efficiency, and surveyed proportion of search areas with the Korner-Nievergelt mortality estimator (first equation in Korner-Nievergelt et al. [2011]). The Korner-Nievergelt estimator has relatively low bias compared with other estimators (Péron 2018). It produces lower estimates than the OMNRF estimator, but the magnitude of the estimate is irrelevant in our study design. Our aim was to leverage consistent data collection and apply consistent statistical treatment among turbines (Conkling et al. 2020) to estimate the magnitude of potential trends, not to compare estimates of absolute mortality.

Corrections were applied separately for counts made during the spring (May and June) and during the mitigation window (15 July to 20 September). We divided each corrected estimate by the surveyed proportion of search areas (50-m radius from turbine bases) to generate the final carcass abundance (estimated carcasses per turbine) for each species. Carcass counts should be corrected for the proportions of bats expected to fall into areas searched because bats do not fall uniformly around turbine bases (Huso & Dalthorp 2014). However, we analyzed data from 36 of the facilities in this

Table 1. Variables used to test spatial predictors of bat mortality at wind energy facilities in Ontario.

<i>Model Component</i>	<i>Data Source</i>	<i>Details</i>
Response variable bat mortality	natural heritage assessment reports *—total carcass counts per turbine per wind facility	counts corrected for area searched, carcass scavenging, and searcher efficiency ^a
Predictor variable temporal (year)		
spatial (region)		wind facilities clustered within latitudinal or longitudinal bands
wind facility turbine	facility mortality reports * facility mortality reports *, GIS analysis	number of turbines turbine hub height, northward turbine position relative to other turbines, density of other turbines within 1.5 km
bat habitat	GIS analysis	distance to and amount of surrounding potential bat habitat (per turbine): woods, wetlands, buildings, roads, ponds, streams, rivers, large lakes, urban areas; these variables used to derive amount of water and cropland
topographic	GIS analysis	elevation, proximity to valleys or cliffs, proximity to a Great Lake shoreline

*Information extracted directly from facility mortality reports (compiled by qualified consultants) and assumed accurate.

study where areas searched exceeded 95% (2031 carcasses) and found that proportions of carcasses varied by only 10% across distance bands around turbine bases (lowest 0–10 m, 19% of carcasses, highest 20–30 m, 24% of carcasses). Mortality estimates per turbine corrected for the variation in carcass density differed from estimates corrected for area searched by only 0.15 on average.

Compiling Spatial Predictors

We compiled spatial variables that we hypothesized would influence bat mortality based on information in reports on facility mortality and data in a geographic information system (GIS) (Table 1). We retrieved spatial data layers for the locations of buildings, roads, woodlots, wetlands, hydrological features (streams, rivers, ponds, lakes), urban centers, and topography (digital elevation model [DEM]) from Land Information Ontario (www.ontario.ca/page/land-information-ontario). We added a 5-m buffer to linear features (roads and streams) before calculating area. We also calculated area covered by more generalized land cover: water (wetlands and hydrological features) and cropland (area not covered by other features). We calculated area around turbines covered by each feature within 11 radii (350, 400, 450, 600, 900, 1,500, 3,000, 6,000, 9,000, 12,000, and 18,000 m).

We calculated turbine density (turbines within 1.5 km) and tested whether it correlated with carcass abundance. To test whether late-summer mortality of long-distance migrants was higher where south-migrating bats first encounter turbines, we related carcass abundance to whether turbines were positioned along the northern perimeter of facilities. To test whether mortality was associated with topographic features that migrating bats

may use for orientation, we mapped valleys and cliffs from a DEM with spatial analysis tools in ArcGIS and calculated proximity of turbines to valleys and cliffs and to shorelines of the Great Lakes. Spatial predictors were standardized (mean [SD] = 0 [1]). We also reran models with unstandardized values to extract estimates of effect size in interpretable units.

Statistical Modeling

We used Bayesian hierarchical models with a log link to relate carcass abundance (per species and for all species) to year, turbine, and land-cover features and to estimate posterior distributions for parameters with Bayesian inference. Hierarchical model structure allowed estimation of a trend in carcass abundance on year for each turbine, nested within each facility. Models were fit with the R package brms (Bürkner 2017). For each parameter estimate, we ran 4 sampling chains (2000 iterations; warm-up of 1000 iterations). We used Gaussian priors (mean [SD] = 0 [1]) for parameters of population-level effects (fixed effects in frequentist language) because these were estimated from standardized spatial predictors. We used the default weakly informative half Student's *t* distribution for the SDs of random effects (mean = 0, df = 3, scale parameter > 10). Model convergence was assessed using Rhat < 1.1 and visual assessment of chain mixing (Bürkner 2017). The resulting population-level effect of year estimated from the model was the trend in carcass abundance averaged across facilities in the study with the variation in trend across individual turbines and facilities incorporated.

To account for potential overdispersion in models of late-summer carcass abundance, we compared global models fit with the Poisson error distribution and

with the negative binomial distribution. Because of the frequency with which no carcasses were counted, late-summer little brown bat carcasses and all spring carcasses were additionally fitted to zero-inflated Poisson and zero-inflated negative binomial models. We compared these distributions with the leave-one-out-cross-validation information criterion (LOOIC) (Gelman et al. 2014; Vehtari et al. 2016). The negative binomial model was the best-fitting for late-summer carcass abundance of all species except little brown bats, for which the zero-inflated Poisson model fit better. The zero-inflated Poisson was the best-fitting for spring mortality of all species. We used these distributions to compare late-summer carcass models with and without an interaction term (mitigation status \times year) to test whether mitigation affected carcass trend. For all species, we chose the model without the interaction term because 95% Bayesian credible intervals (BCI) for all interaction terms overlapped 1 (Supporting Information).

We used these base models to build a candidate set of 58 models, representing different hypotheses regarding effects of spatial variables on bat mortality. First, we calculated variance-inflation factors (VIF) and used VIF < 3 to ensure models were not constructed from multicollinear variables (Zuur et al. 2010). We compared 11 base models for each species, differing only in spatial scale. We then used the spatial scale that resulted in the lowest LOOIC to represent the land-cover feature in the candidate set. Spatial scales for wetland and wooded cover were chosen from the next lowest LOOIC for silver-haired bats in late summer, big brown bats in spring, and all species combined in both seasons to avoid collinearity. We chose the simplest model of nested models within 2 LOOIC of the model with the lowest LOOIC and considered variables within it to be informative if 95% BCI did not overlap one (Arnold 2010; Harrison et al. 2018). The use of the LOOIC for model selection among a large number of models can result in biased model selection, but this problem seems primarily limited to small data sets (Piironen & Vehtari 2016; Vehtari et al. 2016). We compared the 58 models with the base spring (random intercepts and slopes on year) and null models (60 models total) and with base late-summer model (fixed-effect of mitigation and random intercepts and slopes on year), null model, base model without mitigation, and base model with a year \times mitigation interaction (62 models total).

After selecting the best fitting late-summer model, we considered whether spatial patterns in mortality influenced temporal trends in carcass abundance. If turbines in mortality hotspots were sampled more often in earlier or later study years, estimated carcass trends could reflect post hoc study design, rather than ecological conditions. We defined *hotspots* as grid cells with average mortality > 80 th percentile. Turbines were categorized as in or out of hotspots, and we mapped late-summer hotspots

with GIS analysis by calculating average carcasses per turbine across all species within 4×4 km grid cells over the study area. In the first half of the study (2010–2013), the proportion of turbines in hotspots varied from 32% to 100%. Turbines in hotspots were sampled less frequently (6% to 30%) in the latter half of the study (2014–2017). Thus, we compared the population-level effect of year resulting from the best model for each species fit for the whole study duration to data from the last half of the study.

Finally, we explored whether estimated trends in mortality counts might be an artefact of bats learning to avoid areas with turbines, which could drive declining carcass counts. Using a random effect for facility, we reran our models with only the first year of mortality data from each facility. We hypothesized that if bats learn to avoid facilities, then mortality should be similar among facilities in the first year of operation. Conversely, the hypothesis of regional declines in bat abundance predicts a temporal decline in mortality among facilities even when considering only their first year of data.

Results

More bats were killed in late summer than spring: average late-summer carcass abundance ranged from 17 times higher than spring for eastern red bats to 3.6 times higher for big brown bats (Supporting Information). Annual trends and effects of mitigation and spatial predictors could not be reliably estimated for little brown bat mortality, likely due to low sample size (Tables 2 and 3).

Spatial Predictors of Spring Bat Mortality

Comparison of models of spring carcasses identified ≤ 3 competing models per species (Supporting Information), but few informative predictors. Spring carcass abundance of eastern red bats decreased as distance to Great Lake shorelines increased, and carcass abundance of big brown bats decreased as elevation increased (Table 2) (study site elevation range 71–551 m). No spatial predictors were informative for hoary bats, silver-haired bats, or for all species combined.

Spatial Predictors of Late-Summer Bat Mortality

Comparison of late-summer carcass abundance models identified ≤ 5 competing models for migratory tree bats (eastern red, hoary, and silver-haired bats) and for all species combined, each contained woodlot cover as the only informative parameter (Supporting Information; Table 3; Fig. 1). Expected carcass abundance of migratory tree bats increased with the amount of woodlot cover within 1.5 km of turbine bases (95% probability)

Table 2. Parameter means (response scale) and 95% Bayesian credible intervals (BCI) from the best fitting hierarchical models of spring mortality of bats at wind energy facilities in southern Ontario (2011–2017) with zero-inflated Poisson error distribution.

	Mean	Lower 95% BCI	Upper 95% BCI	Change/year (%)
Eastern red bat				
distance to Great Lakes*	0.39	0.17	0.95	
distance to river valleys	0.61	0.34	1.04	
elevation	0.44	0.17	1.05	
year*	0.72	0.55	0.93	–28
Hoary bat				
wetlands (400 m)	1.06	0.83	1.34	
wetlands amount in landscape	1.75	0.78	3.85	
year*	0.67	0.55	0.85	–33
Silver-haired bat				
wetlands (450 m)	1.15	0.94	1.40	
ponds (600 m)	0.60	0.35	1.03	
streams (350 m)	0.90	0.77	1.05	
year	0.89	0.70	1.07	
Big brown bat				
elevation*	0.43	0.326	0.87	
turbine hub height	0.87	0.39	1.34	
year*	0.64	0.43	0.93	–36
Little brown bat				
turbine hub height	0.55	0.25	1.15	
elevation	1.80	0.90	3.00	
year	0.99	0.65	1.58	
All species				
elevation	0.87	0.73	1.03	
turbine hub height	1.05	0.84	1.32	
turbine density	0.99	0.88	1.12	
year*	0.79	0.70	0.88	–21

*Informative predictor.

(Table 3). The effect of woodlot cover was largest for eastern red bats and smallest for silver-haired bats. Mortality increased by 1.04 (95% BCI: 1.02–1.05) and 1.01 (1.00–1.02) times for every 1 ha increase in cover within 400 and 900 m of turbine bases, respectively.

Elevation was the only informative predictor within 2 competing models of late-summer carcasses of big brown bats (Supporting Information); predicted carcass abundance declined by 0.7%/m of elevation (95% BCI: 0.2–0.9).

Effects of Mitigation on Late-Summer Bat Mortality

Average carcass abundance during the mitigation window was highest for hoary bats (Supporting Information). Mitigation reduced average predicted carcass abundance by 59% (95% BCI: 35–72) for eastern red bats, 72% (60–80) for hoary bats, 58% (39–72) for silver-haired bats, and 68% (47–81) for big brown bats (Table 3, Fig. 2). Refitting the model to include only facilities with pre- and postmitigation data yielded similar estimates: eastern red bats, 64% reduction in mortality after mitigation (95% BCI 34–81); hoary bats, 81% (70–88); silver-haired, 74% (51–85); and big brown bats, 69% (31–86).

Annual Trends in Bat Mortality at Turbines

Spring and late-summer carcass abundance of eastern red bats declined by 28%/year ($[0.73 - 1] \times 100 = 27\%$) (Tables 2 & 3). Hoary bat carcass abundance declined by 33%/year (95% BCI: 15–54) in spring (Table 2) and 21%/year (10–30) in late-summer (Table 3). Decline in spring carcass abundance (36%/year [95% BCI: 7 – 57]) (Table 2) of big brown bats was more than twice that of the late-summer decline (14%/year [1–29]) (Table 3). The 95% BCI for spring carcass abundance for silver-haired overlapped 1 (Table 2), but late-summer carcass abundance for this species declined by 29%/year (95% BCI: 19–37) (Table 2). Cumulative estimated declines in late-summer carcass abundance over 7 years ranged from 68% (big brown bats) to 91% (silver-haired bats) (Table 3 & Fig. 3).

Nonmitigating and mitigating facilities exhibited similar yearly trends in late-summer carcass abundance (95% BCI for interaction term overlapped 1). Trends (95% BCI) for nonmitigating versus mitigating facilities were as follows: eastern red, 0.73 (95% BCI: 0.66–0.80) versus 0.64 (95% BCI: 0.52–0.80); hoary bat, 0.79 (95% BCI: 0.70–0.90) versus 0.81 (95% BCI: 0.67–0.98); silver-haired bat, 0.71 (95% BCI: 0.63–0.81) versus 0.64 (95% BCI:

Table 3. Parameter means (response scale) and Bayesian credible intervals (BCI) from the best fitting hierarchical models of late-summer mortality of bats at wind energy facilities in southern Ontario (2010–2017) with negative binomial (eastern red bat, hoary bat, silver-haired bat, big brown bat, all species) or zero-inflated Poisson error distribution (little brown bat).

	Mean	Lower 95% BCI	Upper 95% BCI	Change/year (%)
Eastern red bat				
woods (400 m)*	1.25	1.11	1.40	
wetlands (12 km)	0.65	0.54	1.02	
year*	0.73	0.66	0.80	–27
mitigating—yes versus no*	0.41	0.28	0.65	
Hoary bat				
woods (1500 m)*	1.21	1.08	1.35	
wetlands (18 km)	0.99	0.83	1.18	
buildings (1500 m)	0.96	0.89	1.03	
roads (18 km)	1.21	0.93	1.38	
year*	0.79	0.70	0.90	–21
mitigating—yes vs no*	0.28	0.20	0.40	
Silver-haired bat				
woods (900 m)*	1.16	1.04	1.34	
distance to Great Lakes	1.19	0.98	1.43	
buildings (18 km)	1.00	1.00	1.00	
distance to valleys	1.09	0.90	1.30	
year*	0.71	0.63	0.81	–29
mitigating—yes vs no*	0.42	0.28	0.61	
Big brown bat				
elevation*	0.56	0.44	0.73	
roads (3 km)	1.06	0.95	1.19	
buildings (350 m)	0.86	0.73	1.02	
urban (9 km)	1.19	0.96	1.34	
year*	0.86	0.71	1.00	–14
mitigating—yes vs no*	0.32	0.19	0.53	
Little brown bat				
year	0.32	0.56	1.27	
mitigating—yes vs no	0.62	0.13	1.26	
All species				
woods (450 m)*	1.12	1.06	1.20	
roads (18 km)	1.13	0.96	1.32	
buildings (18 km)	1.00	1.00	1.00	
year*	0.78	0.71	0.85	–22
mitigating - yes vs no*	0.33	0.26	0.43	

*Informative predictor.

0.51–0.79); and big brown bat, 0.85 (95% BCI: 0.73–0.88) versus 0.64 (95% BCI: 0.51–0.92).

Limiting the analysis to the latter half of the study duration yielded similar trend estimates for late-summer carcass abundance versus year: eastern red, 0.71 (95% BCI: 0.59–0.85); hoary, 0.72 (95% BCI: 0.61–0.84); silver-haired, 0.63 (95% BCI: 53–75); and big brown bat, 0.76 (95% BCI: 0.61–0.95) (Table 3). Thus, we found no evidence that a higher prevalence of hotspots early in the study resulted in the observed declines. Re-fitting the late-summer model with only the first year of data from each facility supported the hypothesis of declining abundance of bats, rather than bats learning to avoid new facilities after the first year. This model estimated a 25% (95% BCI: 13–35) decline per year for eastern red bats, 16% (95% BCI: 5–25) for hoary bats, and 11% (95% BCI: 1–25) for big brown bats; the 95% BCI for the trend estimate for silver-haired bats overlapped 1 (Fig. 3 & Supporting Information).

Discussion

The airspace provides essential habitat for insectivorous bats and other flying wildlife (Diehl 2013; Roeleke et al. 2016; Davy et al. 2017; Voigt et al. 2018), but monitoring the abundance and distribution of aerial wildlife is challenging. We used estimated bat captures per turbine to infer rapid declines in the abundance of four bat species in southern Ontario, which is somewhat alarming as none of these species are currently considered at risk of extinction. Increasing cut-in speed reduced mortality but did not prevent it, and we identified woodlot cover and elevation as predictors of bat mortality for migratory tree bats and big brown bats, respectively. We assumed wind turbines strike a random sample of individuals from each bat species, but this assumption has several caveats (see below). Nevertheless, declining abundance of bats in the airspace appeared the most likely explanation for the estimated trends.

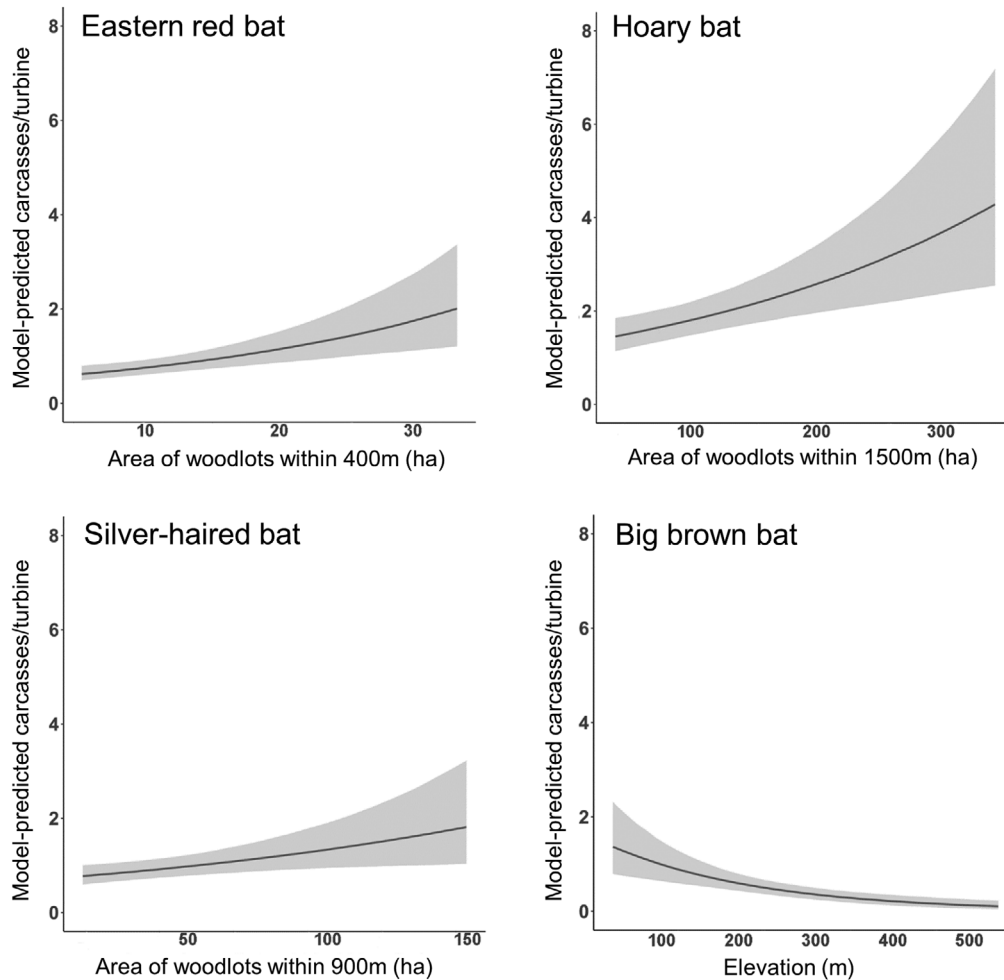


Figure 1. Model-predicted relationship between habitat and topography around wind-energy turbines and late-summer bat carcass abundance (estimated number of carcasses/turbine; mean of the posterior distribution and 95% Bayesian credible intervals) for eastern red bats, hoary bats, silver-haired bats, and big brown bats at 48 facilities in southern Ontario, Canada.

Our data could not be used to isolate the causes of the trends we observed, and wind energy is not the only source of anthropogenic mortality for our study species (O’Shea et al. 2016). Nevertheless, a precautionary approach to bat conservation would minimize mortality of bats at wind turbines (Rydell et al. 2010b; Zimmerling & Francis 2016; Thompson et al. 2017). Increasing cut-in speed of turbines decreased the number of bats killed by turbines in our study, consistent with previous studies (Baerwald et al. 2009; Arnett et al. 2011b, 2016; Martin et al. 2017), but did not prevent mortality. Mitigation was least effective for silver-haired bats (58% reduction in carcass abundance), which also exhibited the highest estimated temporal declines (91% over 7 years). Even big brown bats (a common and ubiquitous species) exhibited a 68% decline in model-predicted carcass abundance over 7 years. This result presents a classic challenge for “keeping common species common” (Ellison 2019), par-

ticularly because the exact causes of the apparent decline are unclear.

Results of our species-specific analyses revealed trends that were undetected in the pooled data (i.e., all bats). Some previous studies of wind-related bat mortality pooled bat species to achieve robust sample sizes (Thaxter et al. 2017; Thompson et al. 2017; MacGregor & Lemaître 2020), but the effects of turbines on each species are independent and should be considered independently where possible. The effect of individual mortality increases as populations decline. Thus, even low bat mortality at turbines may be unsustainable if the affected population is small (Tellería 2009; Graham & Hudak 2011), and that effect is not offset by greater mortalities of other species. If hoary bats became extirpated from our study area, but no other species declined in abundance, the total number of bat carcasses detected under Ontario turbines would drop dramatically.

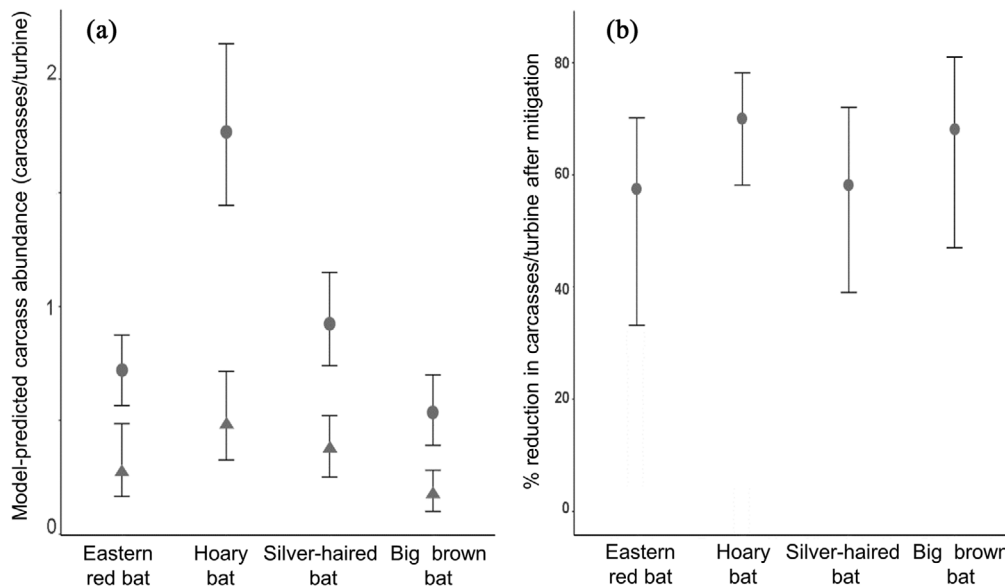


Figure 2. (a) Model-predicted bat carcass abundance under wind turbines after a 3.5 m/s cut (circles) in turbine speed (mean posterior distribution) and after a 5.5 m/s cut (triangles) in speed (circles and triangles, mean posterior distribution; bars, 95% Bayesian credible intervals [BCI]). Model output not shown for little brown bats because credible intervals were too wide to detect an effect. (b) Estimated percent reduction in carcass abundance (95% BCI) following mitigation (i.e., turbine speed reduction) for each species.

Observed mortality counts might appear acceptably low, yet the impact of turbine-related mortality on each remaining species' populations would remain the same (Arnett et al. 2011a).

We assumed wind turbines sample bats randomly at each turbine, but bats are not distributed randomly in 3-dimensional airspace. Male and female bats use the airspace differently and may exhibit different migratory strategies, reflecting sex-specific energetic trade-offs (Jonasson & Guglielmo 2016; Roeleke et al. 2016; Fraser et al. 2017). Some bats may be attracted to turbines by conspecifics for mating purposes (Cryan & Barclay 2009; Cryan et al. 2014) or by the weather-dependent aggregations of insects that can accumulate there (Rydell et al. 2010a, but see Reimer et al. 2018). Bats may also track the convective boundary layer as migratory insects move through it (Nguyen et al. 2019), bringing them into the rotor-swept zone (RSZ) of tall turbines.

We interpreted spatial predictors of carcasses as indicators of relative bat abundance near particular landscape features. The apparent increase in relative abundance of migratory tree bats near woodlots could reflect their importance both for summer roosting and as potential stop-over sites during late-summer migrations (Arnett et al. 2016). Woodlots may have particular significance for tree bats in largely deforested, agricultural landscapes, like our study area (Put et al. 2019). However, the observed spatial associations could also reflect increased risk of collision with turbines associated with particular features. If bats adjust their flight altitude

relative to perceived ground level, they may fly lower over agricultural fields but increase altitude over woodlots to maintain an equivalent perceived height relative to the canopy. Some bats follow ridges and hilltops for ascending flights, which likely reduces energetic costs of ascent (Roeleke et al. 2018), and we speculate that bats may use woodlot edges in the same way in flat landscapes, like our study area. These altitudinal shifts could increase encounters with turbines near woodlots. Fortunately, these potential confounding factors are not expected to vary continuously among years and are unlikely to affect our estimates of temporal trends in carcass abundance.

Bats almost certainly learn to avoid turbines to some extent, and the role of learning in turbine collision risk deserves further study. Unfortunately, the estimated temporal decline in carcass abundance among facilities when analyzing only the first year of survey data per facility suggests that the observed decline in mortality over the study period is not driven by bats learning to avoid turbines (Fig. 3 & Supporting Information). The learning hypothesis also predicts a greater or equal proportion of juvenile (i.e., naïve) carcasses under turbines. We were unable to test this prediction with our data, but other studies with robust sample sizes do not show high proportions of juvenile carcasses (Hull & Cawthen 2013; Arnett et al. 2016; Hein & Schirmacher 2016).

Another potential explanation for reduced carcass abundance during our study period is consistent, yearly altitudinal increase or decrease in insect abundance that

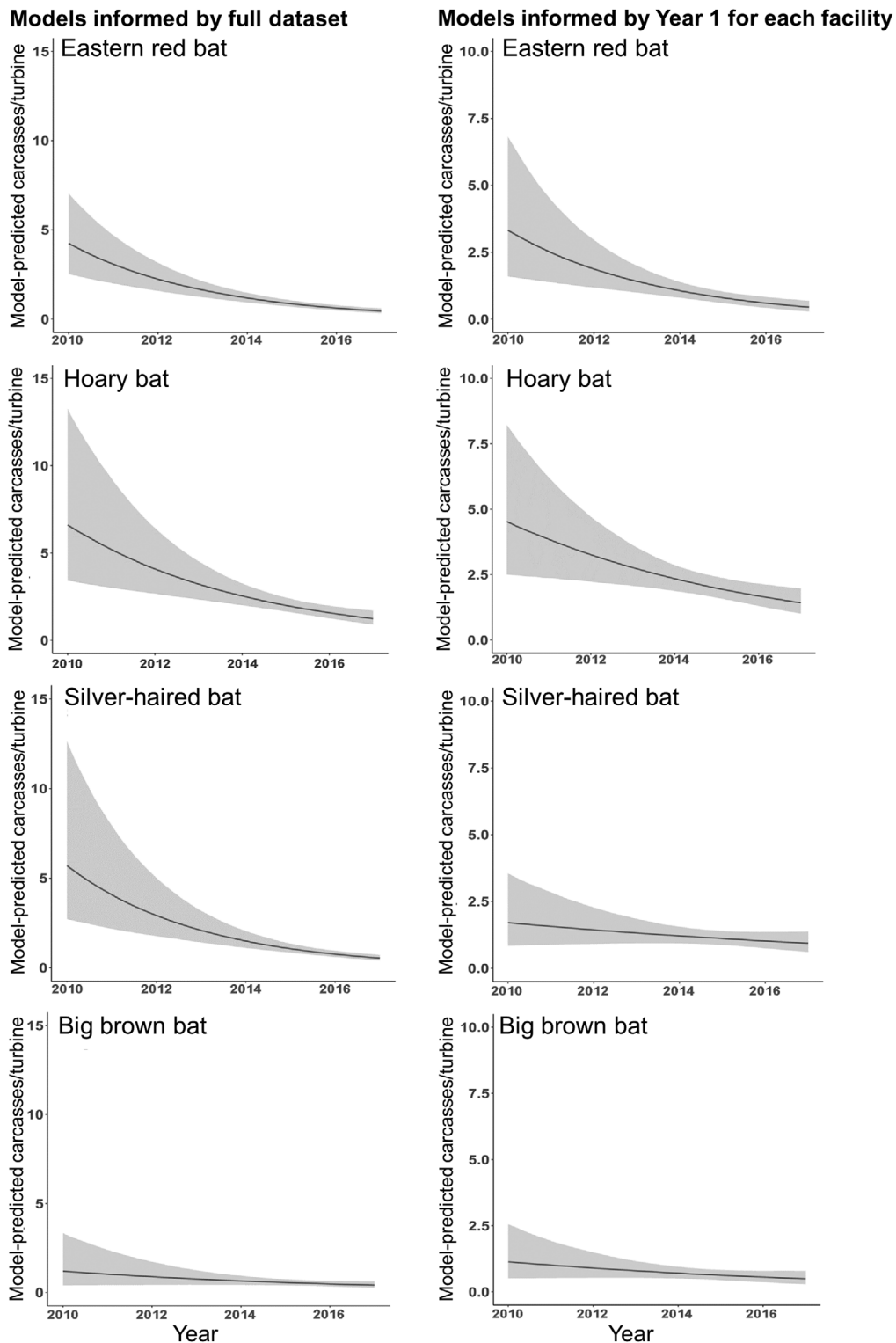


Figure 3. Model-predicted yearly late-summer carcass abundance of bats at 48 wind facilities in southern Ontario ($n = 48$) across 8 years (2010 - 2017). On the left, results for models informed by the full data set. On the right, models informed by only the first year of data from each facility based on model output presented in Table 3 (left) and Supporting Information (right) (lines, trend of average yearly estimates [mean of posterior distribution]; shading, 95% Bayesian credible intervals). Model output not shown for little brown bats because credible intervals were too wide to detect a trend in carcasses.

could entice foraging bats above or below the RSZ (Rydell et al. 2010a; Krauel et al. 2018; Nguyen et al. 2019). Climate change could potentially cause altitudinal movements of the boundary layer and associated insect activity, and wind farms themselves can actually push the boundary layer upward (Lu & Porté-Agel 2015). Turbine hub height did not predict mortality in our study, as would be expected if insect and bat activity were increasing or decreasing in altitude, but the range of turbine hub height in our study (83–110 m) may be too low to detect this effect, and the altitude of the RSZ is also affected by blade length. Further study of the effects of turbine design on bat mortality should incorporate data from a wider range of turbine models.

Our results strongly suggest decreased abundance of bats in the airspace over seven years, which is consistent with other recent evidence of declining bat abundance (Rodhouse et al. 2019). We encourage the operators of wind energy facilities to take a precautionary approach to mitigating bat mortality at their sites to avoid inadvertently increasing the rate of the estimated declines. Biodiversity loss and the climate crisis are equally urgent threats (Oliver et al. 2015; Figueres et al. 2017; Fanin et al. 2018). Meeting these challenges requires collaboration among renewable energy operators and conservation scientists—after all, most bat mortality at wind turbines can be avoided completely through careful timing of operations.

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Supporting Information

Locations of the wind-energy facilities (Appendix S1), estimated average carcasses/turbine (Appendix S2), and notes on interpretation of raw data and hypotheses (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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