

ARTICLE

High vulnerability of juvenile *Nathusius'* pipistrelle bats (*Pipistrellus nathusii*) at wind turbines

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Abstract

Large numbers of bats are killed by wind turbines globally, yet the specific demographic consequences of wind turbine mortality are still unclear. In this study, we compared characteristics of *Nathusius'* pipistrelles (*Pipistrellus nathusii*) killed at wind turbines ($N = 119$) to those observed within the live population ($N = 524$) during the summer migration period in Germany. We used generalized linear mixed-effects modeling to identify demographic groups most vulnerable to wind turbine mortality, including sex (female or male), age (adult or juvenile), and geographic origin (regional or long-distance migrant; depicted by fur stable hydrogen isotope ratios). Juveniles contributed with a higher proportion of carcasses at wind turbines than expected given their frequency in the live population suggesting that juvenile bats may be particularly vulnerable to wind turbine mortality. This effect varied with wind turbine density. Specifically, at low wind turbine densities, representing mostly inland areas with water bodies and forests where *Nathusius'* pipistrelles breed, juveniles were found more often dead beneath turbines than expected based on their abundance in the live population. At high wind turbine densities, representing mostly coastal areas where *Nathusius'* pipistrelles migrate, adults and juveniles were equally vulnerable. We found no evidence of increased vulnerability to wind turbines in either sex, yet we observed a higher proportion of females than males among both carcasses and the live population, which may reflect a female bias in the live population most likely caused by females migrating from their northeastern breeding areas migrating into Germany. A high mortality of females is conservation concern for this migratory bat species because it affects the annual reproduction rate of populations. A distant origin did not influence the likelihood of getting killed at wind turbines. A disproportionately high vulnerability of juveniles to wind turbine mortality may reduce juvenile recruitment, which may limit the resilience of *Nathusius'* pipistrelles to environmental stressors such as climate change or habitat loss. Schemes to mitigate wind turbine mortality, such as elevated cut-in speeds, should be

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implemented throughout Europe to prevent population declines of *Nathusius' pipistrelles* and other migratory bats.

KEYWORDS

bats, females, Germany, hydrogen, juveniles, migration, migratory corridor, *Pipistrellus nathusii*, stable isotopes, wind farms

INTRODUCTION

In an effort to reduce the negative effects of CO₂ emissions on the global climate, many countries have been promoting energy production from renewable sources, such as wind (IRENA, 2020). Although it is considered environmentally friendly, wind energy production may come at significant costs to biodiversity (Saidur et al., 2011; Schuster et al., 2015; Thaker et al., 2018). First, animal populations may suffer from habitat loss during wind turbine constructions in sensitive areas, such as forests or wetlands. Second, some taxa may be killed by operating turbines. Among birds, raptors, gulls, and some songbirds are regularly observed colliding with the rotating blades of wind turbines during daytime (e.g., Barrios & Rodríguez, 2004; Nazir et al., 2020; Smallwood & Bell, 2020). At night, bats are frequently killed by wind turbines either by blunt-force trauma when colliding with blades, or by barotrauma in the tailwind vortices of the spinning blades (Baerwald et al., 2008; Voigt et al., 2015b).

The exact number of bat fatalities at wind turbines is currently unknown. Estimates obtained from systematic environmental impact assessments that control for scavenger removal and searcher inefficiency suggest that a single turbine may lead to 2–30 bat fatalities per year if no mitigation scheme is implemented (Brinkmann et al., 2011; Korner-Nievergelt et al., 2013; Măntoiu et al., 2020). This may add up to hundreds of thousands of bats killed per year in countries with high wind energy production, such as Germany (Fritze et al., 2019; Voigt et al., 2015b) and the United States (Cryan & Barclay, 2009; Hayes, 2013). Migratory bats are most often found dead below wind turbines in the temperate zone (Arnett et al., 2016), suggesting that wind energy infrastructures may impede the connectivity between their summer and wintering habitats (Cryan & Barclay, 2009; Voigt et al., 2015b). Populations may be unable to compensate for the additional losses of individuals at wind turbines since bats have a low reproductive rate, with only one or two offspring per year (Garbino et al., 2021). Recent population trend analyses suggested that some species with high collision risk may be in decline (Frick et al., 2017; Zahn et al., 2014), yet population effects are difficult to monitor in bats because wind turbines can kill migratory bats that originate from both

local and distant populations of unknown location (Lehnert et al., 2014; Voigt et al., 2012).

European *Nathusius' pipistrelles* (*Pipistrellus nathusii*) hold the record for long-distance bat migration, with one individual banded in Latvia and recaptured in Northern Spain, a 2,200-km air-line distance (Alcalde et al., 2021). Populations of *Nathusius' pipistrelles* undergo a seasonal migration from northeastern Europe to western and southern Europe (Hutterer et al., 2005; Meschede et al., 2017; Petersons, 2004). During migration, bats can use flight corridors along coastlines that are also heavily used for wind energy production (Gaultier et al., 2020; Kruszyński et al., 2020; Kurvits et al., 2011). When migrating inland, *Nathusius' pipistrelles* have been observed to use larger water bodies, such as lakes or rivers, for migration and stopovers, preferably in forested areas (Furmankiewicz & Kucharska, 2009). Apart from coastal areas, migration of *Nathusius' pipistrelles* in Germany is not restricted to distinct migratory corridors but instead includes broad, large-scale migratory paths (Meschede et al., 2017). The species ranks second concerning fatality rates at wind turbines in Germany (Rydell et al., 2010). Multiyear recaptures demonstrate site fidelity at summer grounds, maternity roosts, and mating sites (Hutterer et al., 2005), suggesting that a significant proportion of the European population of *Nathusius' pipistrelles* crosses Germany twice each year. Consequently, Germany has an essential responsibility for protecting this and other migratory species due to the country's central location in the flyways of European migratory bats (Voigt et al., 2015b), and its obligations under national and international laws (EU Directive 92/32/CEE – Annexes II and IV; §44 and §7 of the German “Bundesnaturschutzgesetz”; Conservation of Migratory Species of Wild Animals; UNEP/EUROBATS agreement signed Bonn, 1979, and London, 1991).

While wind turbine bat mortality has been clearly documented, the long-term consequences of such mortality are less clear. Previous studies have attempted to identify demographic groups most at risk by sampling carcasses found beneath wind turbines (Baerwald and Barclay 2011, Lehnert et al., 2014, Chipps et al. 2020, Davy et al. 2021). Greater numbers of carcasses from one sex or age group may be evidence of differences in vulnerability to wind turbine mortality. For example, 72% of common noctule bats

(*Nyctalus noctula*) found dead below wind turbines in Germany were of regional origin, whereas 28% of bats were defined as long-distance migrants (Lehnert et al., 2014). However, without corresponding data from the live population at that point in time, it is unclear whether such results are due to unequal ratios of sex, age, and origin in the population or are truly driven by a higher vulnerability in certain demographic groups. To better assess the demographic consequences of wind turbine mortality, we expanded these previous approaches by comparing the sex (males/females), age (juveniles/adults), and origin (regional/distant) of *Nathusius'* pipistrelles found dead beneath wind turbines to bats within the live population.

Identifying demographic groups with higher wind turbine vulnerability will help us better understand the impact of wind turbine fatalities on *Nathusius'* pipistrelles populations. A higher vulnerability of females at wind turbines may lower reproduction in maternity colonies and, thus, the birth rate in source populations. Similarly, the higher mortality risk of juveniles compared to adults may impair juvenile recruitment into the adult population, with negative consequences for population growth and sizes. Additionally, juvenile bats are key for shifting the species' distribution range in response to climate change (Kravchenko et al., 2020). Thus, increased mortality of juvenile bats at wind turbines might constrain a species' ability to respond adequately to global warming. Understanding these potential negative consequences of wind turbines on bats is essential as the prevalence of wind energy will continue to increase.

We predicted that wind turbines would be more likely to kill individuals of distant origin, so-called long-distance migrants, than conspecifics of regional origin. During the migration period, *Nathusius'* pipistrelles are more likely to use corridors (e.g., on the sea coast) with a high density of wind turbines, increasing their vulnerability (Gaultier et al., 2020). Additionally, we expected females to have a higher vulnerability at wind turbines than males, based on the observed attraction of female bats towards wind turbines, that is, search for social partners or roosts for mating at wind turbines (Roeleke et al., 2016). Further, we expected juveniles to have a higher vulnerability at wind turbines than adult conspecifics because they are less experienced around wind turbines and they seem to exhibit a high exploratory behavior (Horn et al., 2008).

METHODS

Sample collection and study area

We used carcasses of *Nathusius'* pipistrelles from the central repository of Brandenburg's Federal Agency for

Environment (Landesumweltamt, Potsdam, Germany), administered at the Vogelschutzwarte Buckow, and the Natural Science Collections of the University Halle-Wittenberg. Carcasses originated from surveys conducted at wind farms between August 2003 and September 2013. Carcasses were kept frozen from the day of collection until fur sampling. In total, we considered 119 *Nathusius'* pipistrelle carcasses as sufficiently fresh (without signs of decomposition from the field) to be included in our study. After thawing, we collected a small tuft of fur from the interscapular region of each carcass from which we estimated geographic origin using stable isotopes. We confirmed the species, age (juvenile or adult), and sex by visual inspection.

We obtained fur samples from 524 live *Nathusius'* pipistrelles that were encountered during routine population surveys conducted as part of official population monitoring schemes between August 2006 and September 2018. We only used samples included in the late summer/early autumn migratory season, ranging from about July 15 to September 31. In *Nathusius'* pipistrelles, molting occurs in the summer habitat prior to the migratory period (Voigt et al., 2016). Samples were obtained from bats encountered during daytime surveys of artificial roosts or mist netting. Surveying experts identified the species and noted the sex and age cohort. In the remainder of this manuscript, we refer to the survey type where we acquired the data from live animals as bat box data (BB) and to those from carcasses as wind turbine data (WT).

Sex was recorded in 408 of our samples (119 BB, 299 WT). Age was estimated by visually inspecting the bone density close to the epiphyseal junction of the finger bones. Reliable age estimates were obtained for 186 specimens (118 BB, 68 WT). The majority of samples from both survey types were obtained from eastern parts of Germany and from coastal areas of the North Sea where regional wind energy density is high (Figure 1). Dry fur samples were shipped in plastic vials to the stable isotope laboratory of the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin.

Wind turbine density varies throughout Germany (Lütkehus et al., 2013), which may affect bat mortality. We used data from the renewable power plants in Open Power System Data (OPSD) for Germany to calculate wind turbine density around each sampling site (Figure 1; <https://open-power-system-data.org/>). We counted the number of wind turbines within a 10-km buffer around each sampling site, corresponding to the maximum travel distance of *Nathusius'* pipistrelles per night (Schorcht et al., 2002). We used data from all turbines commissioned between 1983 and 2018 that were still operating when a carcass was found. To illustrate wind energy density in Figure 1, we

used the two-dimensional kernel density estimation provided by the “ggplot2” package in R (Wickham, 2016).

Stable isotope analyses

In our study, we used an isotopic approach to identify the geographical origin of bats. This approach is based on two observations. First, stable hydrogen isotope ratios of precipitation water vary latitudinally across continents following rainfall patterns and ambient temperature (Bowen et al., 2005; Hobson, 1999). Second, body tissues or products, such as hair keratin, are composed of elements that animals consume as water and food. Specifically, stable isotope ratios of fur keratin correlate with those of surface water where molting occurs, usually the summer habitat of migratory bats (Cryan et al., 2004; Lehnert et al., 2018; Popa-Lisseanu et al., 2012; Voigt et al., 2016). Stable hydrogen isotope ratios in fur keratin have been used before to differentiate the origins of bat carcasses observed at wind turbines (Baerwald et al., 2014; Lehnert et al., 2014, 2018; Pylant et al., 2016).

We cleaned the fur from surface oils and contaminants using a 2:1 chloroform-methanol solution and then dried them in an oven for 24 h at 50°C. From each fur sample, we placed a subsample of 0.274 mg (± 0.1 mg) in a silver foil capsule (IVA Analysetechnik e.K. Meerbusch, Germany). The methodological approach in analyzing stable hydrogen isotope ratios in the IZW laboratory has been described in full detail in Kruszynski et al. (2020). Briefly, fur samples were placed in the autosampler (Zero Blank autosampler, Costech Analytical Technologies, Milan, Italy) of the elemental analyzer (HT Elementaranalysator HEKAtech GmbH, Wegberg, Germany). Before combustion, samples were flushed in the autosampler for at least 1 h with chemically pure helium (Linde, Leuna, Germany). We used a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) that was connected via an interface (Finnigan Conflo III, Thermo Fisher Scientific, Bremen, Germany) with the elemental analyzer. For every 10 samples, we included one USGS42 keratin standard (Tibetan Human Hair; U.S. Geological Survey) and three lab keratin standards (powdered sheep hair from Sweden [Kstd.1] and Spain [Kstd.2], and powdered goat hair from

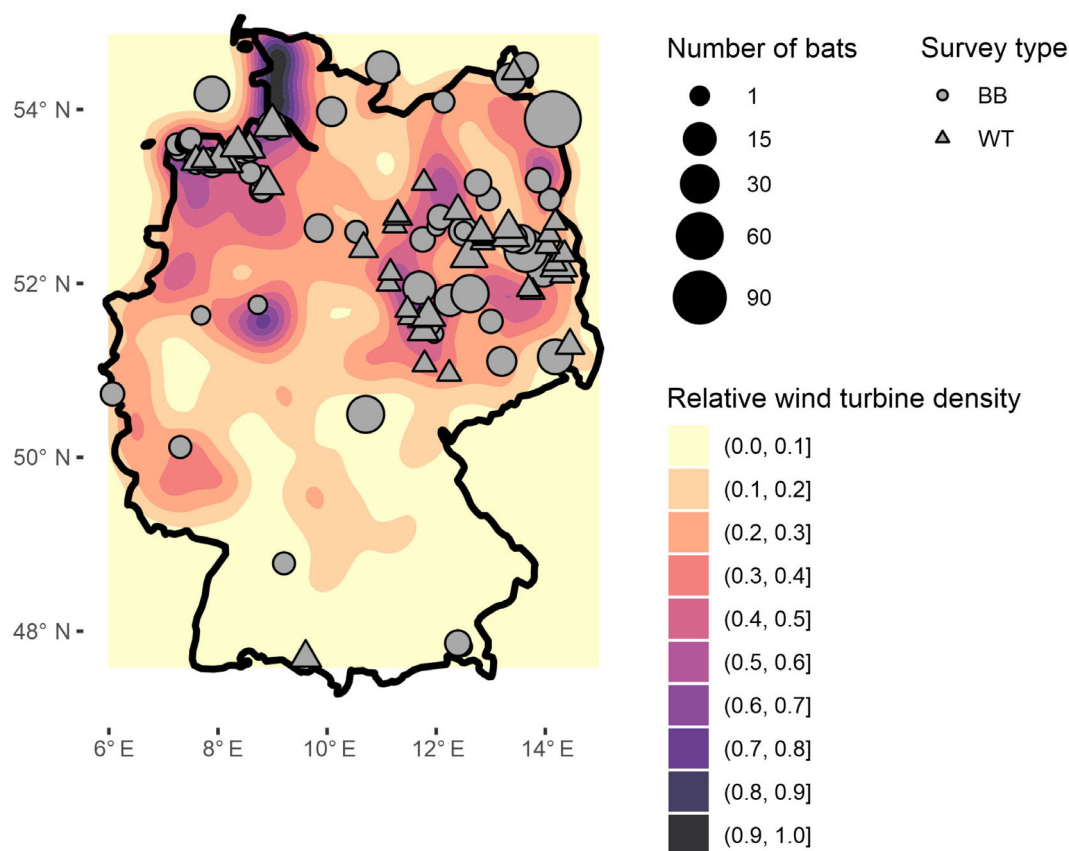


FIGURE 1 Sampling locations in Germany from which material was obtained in relation to wind turbine densities (in shades of yellow to black, indicating absence/low density and high density of wind turbines scaled from 0 to 1, respectively). Turbine density was calculated by counting the number of turbines within a 10-km buffer around the location where carcasses were found. The survey type from which data for Nathusius’ pipistrelles originated is indicated by triangles for animals found dead below wind turbines (WT) and by circles for live animals from artificial daytime roosts, so-called bat boxes (BB). The sizes of triangles and circles indicate the number of samples collected per location

Tanzania [Kstd.3]). Stable hydrogen isotope ratios of samples were normalized to the stable isotope ratio of the non-exchangeable portion of hydrogen in standard material following Soto et al. (2017). All values are given in the δ notation as parts per mill (‰) deviation from the international standard V-SMOW. The $\delta^2\text{H}$ values of keratin standards equaled $-73.1\% \pm 0.5\%$ for USGS42, -167.3% for Kstd.1, -110.02% for Kstd.2, and -65.5% for Kstd.3. Analytical precision based on the repeated analyses of stable hydrogen ratios in laboratory keratin standards was always better than 1.3% (one standard deviation). Twenty-nine samples were used in another publication (Kruszynski et al., 2020) and they are referenced in Kruszynski et al. (2021).

Estimating migratory status based on keratin $\delta^2\text{H}$ values

We used the package IsoriX (Courtiol et al., 2019) to classify individuals as either long-distance or regional migrants. The approach uses the Global Network of Isotopes in Precipitation (GNIP) annual data (from 1960 to 2018) from the International Atomic Energy Agency (IAEA, Vienna, Austria). We used a transfer function for regressing $\delta^2\text{H}$ values based on 458 data points from *Nathusius'* pipistrelles during the non-migration period against mapped $\delta^2\text{H}$ values of mean annual precipitation

(Kruszynski et al., 2020). With this function, we established a $\delta^2\text{H}$ isoscape map with predicted sample values. This isoscape map was then used to assign every individual a P value within each grid cell to test the putative origin (Courtiol et al., 2019). Individuals were classified as being long-distance migrants when the sampling location was not considered a possible origin location (i.e., $P \leq 0.05$). All other animals were considered as being of regional origin (Kruszynski et al., 2020). This is a conservative approach in the case of *Nathusius'* pipistrelles given the relative imprecision of the species' transfer function (Kruszynski et al., 2020), which limits the predictive power of the regression function when used in isoscape origin models. The probability maps of long-distance migrants were plotted separately for bats of the WT and BB population and males and females (Figure 2). The probability maps were calculated by overlaying P values > 0.5 of individuals in each aforementioned group.

Statistical models

Demographic differences in wind turbine mortality

We fitted generalized linear mixed effects logistic regression models for each of the three response variables: (1) probability to sample a female, (2) a juvenile, and

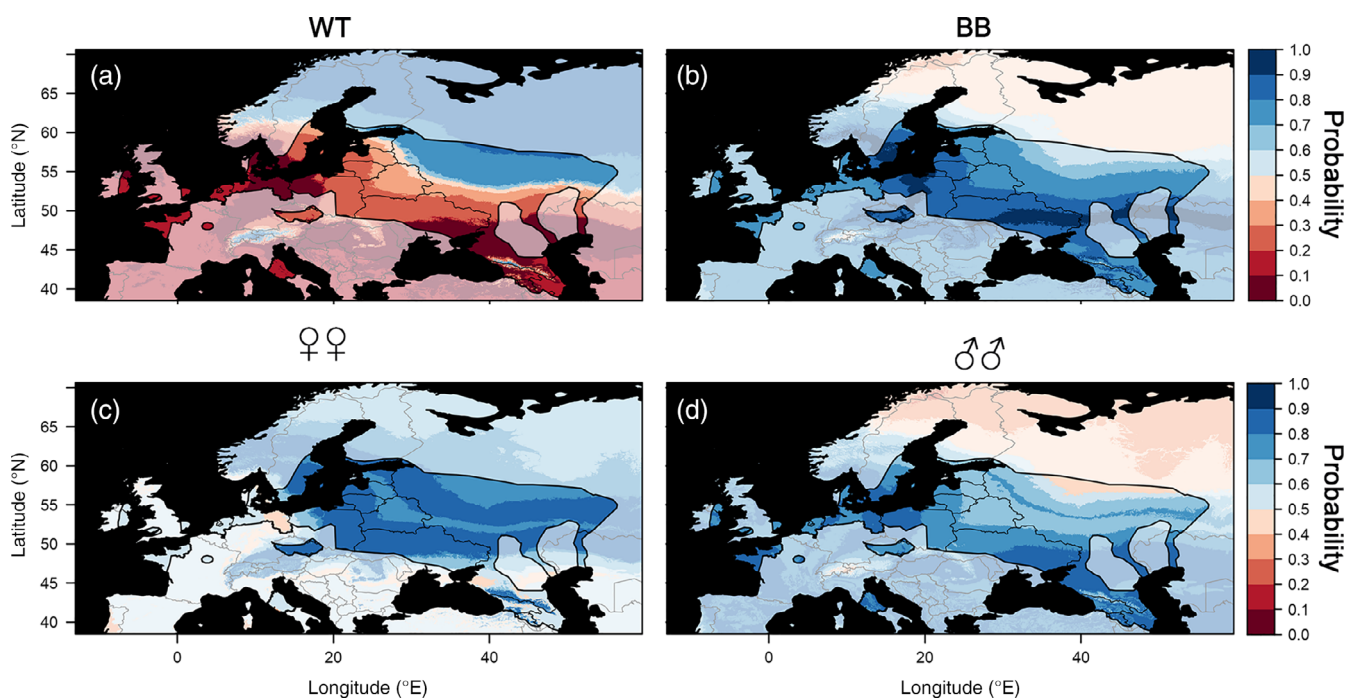


FIGURE 2 Probability maps for the likely origin of long-distance migrating *Nathusius'* pipistrelles found (a) dead below wind turbines ($n = 8$) or (b) live in bat boxes ($n = 49$), and (c) females ($n = 23$) and (d) males ($n = 33$). Probabilities were calculated by overlaying $P > 0.5$ of migratory bats in each category. The highlighted polygon represents the current breeding range of *Nathusius'* pipistrelles (Kruszynski et al., 2020)

(3) a long-distance migrant. For each response variable, we used a subset of our data that had complete information for the target response, that is, we excluded all data that did not have the information on the variable being tested. We use “y” in the model descriptions below to cover these three response variables. For each response variable, we compared three model structures using Akaike information criterion corrected for sample size (AICc) model selection. These models are as follows:

1. Model 1: No effect of survey type (WT/BB) on the response variable. Neither demographic group is particularly vulnerable to wind turbine mortality

$$\text{Mod1} = y \sim 1 + (1|\text{location}).$$

2. Model 2: Effect of survey type (WT/BB) on the response variable. One demographic group is more vulnerable to wind turbine mortality

$$\text{Mod2} = y \sim \text{survey type} + (1|\text{location}).$$

3. Model 3: Effect of survey type (WT/BB) on the response variable. One demographic group is more vulnerable to mortality. The effect of wind turbine survey type differs with wind turbine density. The variance in wind turbine density around bat boxes was set to zero, therefore, the interaction between BB and wind turbine density was excluded during the process of model fitting

$$\text{Mod3} = y \sim \text{survey type} + \text{survey type} : \text{number of wind turbines} + (1|\text{location}).$$

In order to account for the uncertainty in the models, we presented coefficients from each model individually and model-averaged coefficients using the MuMIn package in R (Barton, 2020).

Isotopic differences between demographic groups

We fitted a generalized linear mixed model to test the influence of sex (male/female), age (juvenile/adult), and the interaction between survey type (WT or BB) and origin (regional/distant) on $\delta^2\text{H}$ values, with sampling site (unique locations where bats were collected) as a random effect to account for potential spatial autocorrelation. We did not consider samples with unknown sex or age in this analysis.

All analyses were conducted in R (R Core Team, 2020).

RESULTS

Models

We obtained data from 119 carcasses (WT; 59 females, 50 males, 10 individuals of unknown sex) of *Nathusius' pipistrelles* found dead below wind turbines and from 524 live conspecifics of local populations (BB; 164, 135, 225) in Germany (Figure 1). For analysis of each response variable, we used a subset of data that had comprehensive information for the target response. Sample sizes for each model are reported in Table 1.

Model 3 (effect of survey type and interaction with wind turbine density) best explained variation in age patterns (Table 1). At low wind turbine densities, model 3 showed juvenile bats were found dead beneath wind turbines more often (19 out of 68; 27.9%) than expected based on their abundance in the live population (14 out of 118; 11.8%). The probability to encounter juveniles dead below wind turbines decreased with increasing wind turbine density (Table 2). Due to model selection uncertainty, we cannot definitively exclude alternative models 1 and 2 ($\Delta\text{AICc} < 2$), therefore we also presented model-averaged coefficients and standard errors (Table 2). Model average coefficients showed qualitatively similar results to our top model, although model-averaged confidence intervals overlapped with 0.

For sex and migratory status, Model 1 (intercept-only model) had the lowest AICc (Table 1), suggesting no effect of survey type or wind turbine density on the sex or migratory status of sampled individuals at wind turbines. Females were observed more often than males both beneath wind turbines and in the live population (54.6%; Table 2), while regional migrants were more common than long-distance migrants both in the carcass and live population (91.1%; Table 2).

Stable isotope data and general statistics

$\delta^2\text{H}$ values of male bats were higher ($-112.2\% \pm 19.1\%$) than those of females ($-115.0\% \pm 17.9\%$; $\beta_{\text{SEX}} = 5.27$, $\text{df} = 165.6$, $t = 2.34$, $P = 0.02$), yet the difference between sexes was small. We did not find any difference in $\delta^2\text{H}$ values between adults ($-113.9\% \pm 18.1\%$) and juveniles ($-118.6\% \pm 26.8\%$; $\beta_{\text{AGE}} = -0.83$, $\text{df} = 178.5$, $t = -0.25$, $P = 0.7$).

Eight out of 119 *Nathusius' pipistrelle* bats (6.7%) killed by wind turbines were classified as long-distance migrants, compared to 49 out of 524 (9.3%) of bats from the live population. Migrants of distant origin from the live population had higher $\delta^2\text{H}$ values ($-114.4\% \pm 27.1\%$) than those found dead below wind

TABLE 1 Model comparison to test the effects of the independent variables (age, sex, and migratory status) for the mortality risk *Nathusius'* pipistrelles at wind turbines

Variable, <i>N</i> (BB/WT), model	Parameter ^a	AICc	ΔAICc	Weight
Age, 118/68				
3	survey type + survey type:nrwt + (1 location)	159.8	0	0.507
1	1 + (1 location)	161	1.21	0.277
2	survey type + (1 location)	161.5	1.71	0.216
Sex, 299/109				
1	1 + (1 location)	574.2	0	0.604
2	survey type + (1 location)	575.8	1.6	0.271
3	survey type + survey type:nrwt + (1 location)	577.4	3.16	0.124
Status, 524/119				
1	1 + (1 location)	158.9	0	0.551
2	survey type + (1 location)	160.1	1.17	0.306
3	survey type + survey type:nrwt + (1 location)	161.6	2.71	0.142

Notes: In addition to the AICc values (Akaike information criterion corrected for sample size), sample sizes (*N*), Akaike weights, and ΔAICc (the difference in AICc between this model and the best model) are also presented. Model 3 presents an interaction between survey type and wind turbine density, however, the variance around bat boxes was set to zero, therefore, this effect at the bat boxes was excluded during model fitting.

^aVariables are survey type, wind turbine (WT) or bat boxes (BB); location, sampling sites; nrwt, number of wind turbines inside a 10-km buffer around the sampling site.

turbines ($-169.7\% \pm 48\%$; $\beta_{\text{SAMPLE_LOCATION}} = -39.13$, $\text{df} = 91.53$, $t = -4.08$, $P < 0.001$). $\delta^2\text{H}$ values of regional *Nathusius'* pipistrelles were higher than conspecifics of distant origin for both BB and WT populations (regional BB, $-111.6\% \pm 12.6\%$; regional WT, $-117.7\% \pm 14.9\%$; $\beta_{\text{STATUS}} = 24.42$, $\text{df} = 84.48$, $t = 3.34$, $P = 0.001$), although this effect was greater in bats from the WT than from those of the BB population ($\beta_{\text{STATUS: SAMPLE_LOCATION}} = 33.9$, $\text{df} = 129.25$, $t = 3.4$, $P < 0.001$, Appendix S1: Figure S1).

Long-distance migrants from the WT population were assigned to more northeastern areas in Europe, such as Russia and Finland (Figure 2a), than long-distance migrants from the live population (Figure 2b). Within long-distance migrants, females had the most likely origin in eastern and central Europe (Figure 2c) whereas males had most likely originated from western areas in Europe (Figure 2d).

DISCUSSION

Wind energy production has been endorsed worldwide as a CO₂-free renewable energy source; however, wind energy production comes at high ecological costs since turbines kill large numbers of bats and birds when no mitigation measures are practiced (Cryan & Barclay, 2009; Hayes, 2013; Nazir et al., 2020; Smallwood & Bell, 2020; Voigt et al., 2015b). To improve our understanding of how wind turbines might cause

population declines (Frick et al., 2020; Zahn et al., 2014), we studied the European long-distance migratory bat species *Nathusius'* pipistrelles (*Pipistrellus nathusii*). We assessed whether individual characteristics (sex, age, migratory origin) affected vulnerability to wind turbine mortality, that is, whether certain individuals are killed more than would be predicted based on their relative proportion in the live population. To this end, we compared demographic and isotopic data of live *Nathusius'* pipistrelles encountered during mist-netting and surveys of artificial daytime roosts (so-called bat boxes, also referred to as bats from the live population) with data from conspecifics found dead beneath wind turbines, during the late summer/early autumn migration season. Model selection suggested juveniles were more likely to die at wind turbines than expected given their abundance in the live population, yet this pattern varied with wind turbine density. An elevated fatality rate of juvenile bats was most apparent where wind turbine density was low. At high wind turbine densities, juvenile *Nathusius'* pipistrelles were as likely to collide with wind turbines as adult bats. The underlying reason for this pattern remains unclear. There was no evidence of increased vulnerability of either sex. However, we observed a higher proportion of females than males in the population, which could be derived from females migrating south from maternity colonies in northeastern Europe. Finally, geographic origin (regional/distant) did not explain the likelihood of getting killed at wind turbines.

TABLE 2 Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of the models for Nathusius' pipistrelles

Variable, model, and parameter ^a	Estimate	Conditional SE	<i>t</i>	Lower 95% CI	Upper 95% CI
Age					
1					
Intercept	−1.57	0.45	−3.44	−2.8	−0.70
2					
Intercept	−2.23	0.72	−3.06	−4.13	−0.93
Survey type (wt)	1.06	0.84	1.26	−0.48	3.12
3					
Intercept	−2.23	0.73	−3.05	−4.38	−0.95
Survey type (wt)	1.74	0.93	1.86	0.07	3.89
Survey type = “wt”:nrwt	−0.04	0.02	−1.63	−1.14	−0.006
Average					
Intercept	2.05			−3.48	−0.61
Survey type (wt)	1.11			−0.35	3.44
Survey type = “wt”:nrwt	−0.02			−0.09	0.009
Sex					
1					
Intercept	0.2	0.15	1.32	−0.11	0.48
2					
Intercept	0.13	0.17	0.76	−0.2	0.48
Survey type (wt)	0.20	0.32	0.65	−0.42	0.8
3					
Intercept	0.13	0.17	0.77	−0.22	0.48
Survey type (wt)	0.05	0.39	0.12	−0.73	0.84
Survey type = “wt”:nrwt	0.006	0.009	0.68	−0.01	0.02
Average					
Intercept	0.17			−0.14	0.49
Survey type (wt)	0.06			−0.53	0.85
Survey type = “wt”:nrwt	0.0008			−0.01	0.02
Status					
1					
Intercept	−7.38	2.02	−3.65	−26.0	−4.87
2					
Intercept	−8.06	2.4	−3.34	−29.42	−5.11
Survey type (wt)	1.23	1.37	0.89	−2.54	6.26
3					
Intercept	−8.41	2.74	−3.06	−29.94	−5.23
Survey type (wt)	1.9	1.75	1.08	−2.71	13.73
Survey type = “wt”:nrwt	−0.03	0.05	−0.63	−37.43	0.09
Average					
Intercept	−7.73			−12.24	−3.22
Survey type (wt)	0.65			−1.56	4.46
Survey type = “wt”:nrwt	−0.004			−0.13	0.06

Note: The interaction between survey type and wind turbine density is not considering the variance around bat boxes because it was set to 0, therefore, this effect at the bat boxes was excluded during model fitting.

^aVariable abbreviations are survey type (wt), survey type on WT; nrwt, number of wind turbines inside a 10-km buffer around the sampling site.

Most of the sampled carcasses used for this study were collected in high wind turbine density areas along the German North Sea coastline (Figure 1), that is, within the coastal migration corridors of *Nathusius' pipistrelles* (Kurvits et al., 2011, Gaultier et al., 2020, Kruszynski et al., 2020,). Additionally, we received carcass data from another area with high wind turbine density close to the river Oder (at the border between Germany and Poland), which is also known to function as a migration corridor for *Nathusius' pipistrelles* (Furmankiewicz & Kucharska, 2009). Within these migration corridors, our analysis suggested that the relative risk for *Nathusius' pipistrelles* to collide with wind turbines was independent of age. In these corridors, adults and juveniles are flying at speeds of about 25 km/h (Troxell et al., 2019), most likely during continuous flights of several hours. As both sexes and all age groups migrate in the same manner, we would expect similar vulnerability for all migrating individuals. Outside migration corridors, predominantly in northeastern Germany where wind turbines occur at lower densities (Figure 1), the risk for *Nathusius' pipistrelles* appeared to be unevenly distributed. The region is dominated by large forests and several larger lakes areas. In this region, juvenile *Nathusius' pipistrelles* were more likely to die at wind turbines than are adult conspecifics. Outside the migration corridors, adult *Nathusius' pipistrelles* may pause migration at stopover sites where they court and mate (Voigt-Heucke et al., 2016). Yet, juveniles may still be attracted to the tall structures of wind turbines because of an increased exploratory behavior (Horn et al., 2008) and a lack of experience in responding to environmental cues, such as the Earth's magnetic field for orientation, during the first southward journey when their navigation system has not yet fully developed (Lindecke et al. 2019). Without behavioral data from bats in areas of both high and low wind turbine density, it is difficult to provide a mechanistic explanation for our results with certainty. Future studies are needed to address in more detail why juvenile *Nathusius' pipistrelles* appear to be more vulnerable at wind turbines at low densities, and it would be important to understand whether wind turbines present a similarly high risk for juveniles of other migratory bat species.

The sex ratio of *Nathusius' pipistrelles* populations is known to vary across Europe during the migratory season (Boshamer & Bekker, 2008; Flaquer et al., 2009; Gukasova et al., 2011; Petersons, 2004). Our results from both the live population and the carcasses from wind turbines suggested a female-biased sex ratio in Germany. Germany is a major pathway and stopover site for bats migrating southward, and we expect many of the sampled females would be moving from northern maternity colonies (Alcalde et al., 2021; Hutterer et al., 2005; Kurvits et al., 2011). Wind turbine mortality in Germany

during the migratory season may therefore be particularly problematic as it could include higher numbers of deaths for reproductively active females. A female sex ratio bias has also been reported in other species with northern maternity colonies (*Nyctalus noctula*; Lehnert et al., 2014), suggesting that the risks posed by wind turbines in Germany may extend beyond *Nathusius' pipistrelles* and should therefore be a focus for future mitigation actions.

Based on the results of our study, we perceive three possible consequences of wind turbine mortality for *Nathusius' pipistrelles* source populations. First, mortality of females at wind turbines during the migratory season could lead to declining numbers of maternity colonies and may lead to the eventual extirpation of local populations (Frick et al., 2017; Zahn et al., 2014). Second, a disproportionately higher vulnerability of juvenile *Nathusius' pipistrelles* at wind turbines may affect the recruitment of juveniles, which may lead to population declines. Third, the elevated mortality risk of juvenile bats might reduce the dispersal of juveniles to novel breeding or wintering areas. Adult *Nathusius' pipistrelles* show high site fidelity in their wintering and summer areas (Lehnert et al., 2018), making dispersal of juveniles a key driver of northward range shifts in response to climate change (Kravchenko et al., 2020). The so-called “generational shift” that is responsible for the northward range expansion of bats might be impaired when juveniles are killed by wind turbines during their first journeys, and thus limiting the ability of the species to adequately respond to a warming climate.

Our ability to distinguish between regional and long-distance migrants, and to identify differing vulnerability in either group, may have been impeded by the weak isotopic transfer function available for *Nathusius' pipistrelles*. This function aims to regress $\delta^2\text{H}$ values of the likely place of molt based on $\delta^2\text{H}$ values in fur keratin of focal animals. The transfer function is relatively imprecise for *Nathusius' pipistrelles* compared to transfer functions of other species such as common noctule bats (Lehnert et al., 2018). The imprecision yields large areas of more than 1000 km across latitude and longitude as likely places of origin for this species (Kruszynski et al., 2020). This imprecision may be a result of *Nathusius' pipistrelles* foraging between limnic and terrestrial food webs (Voigt et al., 2015a), and because of an age effect on $\delta^2\text{H}$ values. $\delta^2\text{H}$ values of juvenile bats were shown to be lower than those of corresponding mothers, most likely because of the consumption of deuterium-depleted fat-rich milk by juveniles (Kravchenko et al., 2019). This further complicates the geographic assignment of juveniles based on stable isotopes (Kravchenko et al., 2019).

This is one of the first studies to account for demographic characteristics in the live population when studying bat wind turbine mortality. Without this comparison,

it is impossible to disentangle whether demographic data from carcasses represent true differences in vulnerability or simply biased demographic ratios within the studied population. However, our analysis relies on observational data collected with inconsistent effort and thus our results should be seen only as a first step towards understanding the uneven impact of wind turbines on bats. Systematic data collection that includes both consistent effort sampling below wind turbines and live population surveys within close proximity to wind turbine sites would provide us with a more robust test of the results presented here. Such systematic effort should also focus on areas with different levels of wind turbine densities to better understand how juvenile mortality may vary with turbine density.

In this study, we demonstrated that the threat of wind turbines can be uneven across bat populations. The higher vulnerability of juveniles to wind turbine mortality may lead to population declines of migratory species and to an impaired ability of populations to respond adequately to warming global temperatures. This calls for more robust mitigation measures, such as curtailment speeds (Arnett et al., 2011), to reduce the number of fatalities of bats at wind turbines. Furthermore, wind turbine construction should be limited in sensitive areas for bats, such as forested areas with large water bodies. Understanding and mitigating the effects of wind turbine mortality on bats will be an important conservation challenge for the future as countries transition to renewable energy.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Supplementary data (Kruszyński et al., 2021) is provided in Zenodo: <https://doi.org/10.5281/zenodo.4557292>.

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