

RESEARCH ARTICLE

Evaluating the sensitivity of raptors to wind turbine collisions: An integrative approach based on GPS tracking

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Abstract

1. Wind energy development leads to an increased mortality of birds due to collisions with wind turbines, especially in raptors. To assess the sensitivity of different bird species to wind turbine collisions, predict collision risk and identify effective mitigation measures, detailed information on flight behaviour is essential, but thus far unavailable for many species.
2. Here, we evaluated the sensitivity of breeding birds of six raptor species—Montagu's Harrier (MoH), Hen Harrier, Marsh Harrier, Common Buzzard (CB), Red Kite (RK) and Short-toed Eagle (STE)—to wind turbine collisions by integrating three aspects of flight behaviour, that is time spent in flight, proportion of flights at risk height and distance travelled from the nest location. We used GPS-tracking data collected in 15 study areas in 6 European countries, comprising 280 individuals, 74,501 individual tracking days and 5786 h of high-frequency flight tracks, providing accurate flight height data.
3. The average time spent in flight ranged from 0.5 (CB) to 3.4 h day⁻¹ (MoH) in females and from 1.0 (CB) to 7.4 h day⁻¹ (MoH) in males. The proportion of flights at risk height (32–200 m above ground level) varied between 12.4% (MoH) and 56.4% (RK). The highest sensitivity index (time spent at risk height per year) was found in RK (1.7–7.4 times higher than in the other species).
4. The mean 90% quantile of distance from nest ranged from 0.7 (CB) to 9.8 km (STE) in females, and from 1.0 (CB) to 5.6 km (MoH) in males. With increasing distance from nest, sensitivity (time spent at risk height per km²) decreased with species-specific slopes.

For affiliations refer to page 11.

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5. *Practical implication:* These results indicate that flight behaviour explains substantial differences in the sensitivity to wind turbine collisions among raptor species. Our integrative approach to assess sensitivity based on flight behaviour regardless of current exposure allows to prioritise species for the selection of wind farm sites and conservation measures, and can be complemented with other aspects, for example extinction risk. Our findings on spatial sensitivity with respect to nest-turbine distances may inform the siting of wind turbines to minimise collision risk.

KEYWORDS

energy transition, flight activity, GPS telemetry, home range size, renewable energy, space use, spatial planning, vulnerability

1 | INTRODUCTION

Wind energy is expanding globally, representing a major component of the decarbonisation of energy production. The global wind energy capacity was expected to surpass 1.000 GW in 2023, a more than 40-fold increase since 2000 (GWEC, 2023). To achieve the objective of net-zero emissions in 2050, another ca. 8-fold increase of the global wind energy capacity is required (IEA, 2021). This expansion, however, should not come at the expense of biodiversity (Pörtner et al., 2021). One negative impact of wind energy is an increased mortality of birds due to collisions with wind turbines (Bellebaum et al., 2013; Schuster et al., 2015). Given the current pace of wind energy expansion, there is an urgent need to improve estimations of collision risk and identify effective mitigation measures reducing the number of collisions.

Conceptually, the vulnerability of a species to an anthropogenic threat can be divided into two components: sensitivity, that is the 'intrinsic aspects of a species' biology that determine its capability to withstand a given threat', and exposure, that is the 'intensity of threat acting against the species', mainly determined by geographic location (Dickinson et al., 2014, p. 1; Green-Tkachenko et al., 2024; May et al., 2015). This division is particularly valuable as it allows comparison between species with different current levels of exposure, including species, which are not yet exposed to the threat in their distribution range, but might be affected in future. Hence, information on species-specific sensitivity is essential for informing collision risk mitigation when developing wind energy projects.

One of the main approaches to investigate wind turbine collision risk in birds has been to record collision fatalities based on carcass searches around wind turbines (Smallwood, 2013; Thaxter et al., 2017). However, this approach does not allow us to distinguish between sensitivity and exposure, as the collision rates are the product of both components. For example, high collision rates in farmland birds could result from high exposure, most wind turbines being installed in agricultural areas, rather than from high sensitivity (Thaxter et al., 2017). Moreover, results from carcass searches are

prone to biases related to carcass persistence, detectability and variation in search protocols (Huso et al., 2017).

An alternative approach which allows to distinguish between sensitivity and exposure is to study the birds' flight behaviour and estimate the expected collision rate using theoretical collision risk models (Masden & Cook, 2016; Schaub et al., 2020; Vasilakis et al., 2016). These models include different aspects of flight behaviour, morphological traits and wind turbine characteristics and thus provide mechanistic insights on how collision risk arises (Band et al., 2007; Masden & Cook, 2016). They also provide the ability to conduct scenario studies for planned wind farms, for example regarding the location and spatial configuration of wind farms and the turbine models used (Schaub et al., 2020; Vasilakis et al., 2016).

Within the framework of collision risk models, different aspects of the birds' flight behaviour affect the expected number of wind turbine collisions in a given area of interest (footprint of an installed or planned wind farm; Figure 1): the extent to which birds are present in the area (expressed as bird density or time spent within the area), the proportion of time spent in flight, the proportion of flights at collision risk height, flight speed and avoidance rate (Band et al., 2007; Masden et al., 2021; Schaub et al., 2020). These aspects vary between species due to differences in ecology and behaviour. For example, reported values for the average amount of time spent in flight per day among raptors (in the broad sense) vary by more than a factor of 30, with <0.3 h in Eagle Owls *Bubo bubo*, a sit-and-wait predator (Grünkorn & Welcker, 2019) and 8.2 h in Montagu's Harriers *Circus pygargus*, which perform extended foraging flights to capture prey (Schaub et al., 2020). Also regarding the proportion of flights at collision risk height, important inter-specific differences have been found, for example 2%–49% among raptor species in southern Africa (albeit based on relatively inaccurate visual observations; McClure et al., 2021). For many species, however, this information is thus far unavailable.

Concerning the amount of time that birds spend inside a wind farm footprint, an important determinant is the distance from the nest locations (Mammen et al., 2017; Schaub et al., 2020), as the

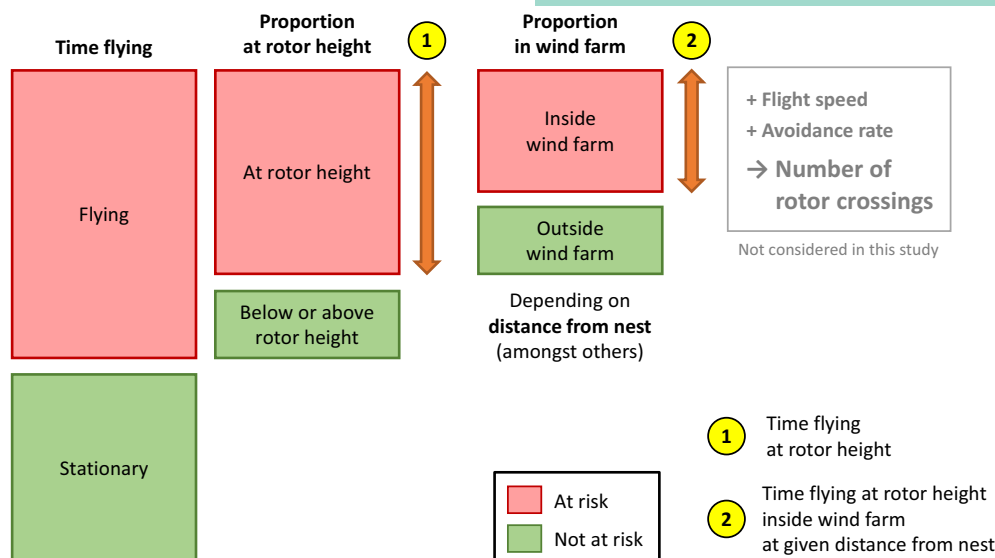


FIGURE 1 Scheme of the conceptual approach adopted in this study. Numbers 1 and 2 indicate the two sensitivity indices calculated. The number of rotor crossings is a main component of collision risk in the Band Collision Risk Model (besides the probability of colliding per rotor crossing; Band et al., 2007). The size of the different compartments in the figure is not based on actual data.

activity of breeding birds is commonly concentrated around the nest, given that food for the mate and chicks has to be transported to the nest regularly (central-place foraging; Bell, 1990). Therefore, the distances travelled from the nest can be used to characterise the general 'spatial sensitivity' of breeding birds to wind turbine collisions and provide indications for recommended distances that should be kept between wind turbines and nests (LAG VSW, 2014).

Among the flight parameters of interest, flight height is particularly challenging to study. Conventional methods such as visual observations and GPS tracking suffer from substantial inaccuracy in the vertical dimension (Johnston et al., 2014; Péron et al., 2020), which may bias the derived proportion of flights at collision risk height (Schaub et al., 2023). Novel methods providing more accurate height data such as high-frequency GPS tracking or barometric altimetry are available (Schaub et al., 2023), but these have not been widely applied yet.

In this comparative study, we analysed the sensitivity to wind turbine collisions in six species of raptors, a bird order found to be particularly collision-prone (Perold et al., 2020; Thaxter et al., 2017), during the stay in the breeding areas. For this assessment, we applied an integrative approach based on three aspects of flight behaviour, that is (1) the time spent in flight, (2) the proportion of flights at collision risk height and (3) the distance travelled from the nest location, which we studied using GPS-tracking data from 15 study areas across Europe. Regarding flight height, we relied on an extensive dataset of high-frequency flight tracks (ca. 5800h), providing accurate height data.

Based on the time spent in flight and the proportion of flights at risk height, we estimated the time spent at collision risk height per year per species and sex (Figure 1), serving as a general indication of the species-specific sensitivity to wind turbine collisions. In addition, we assessed the relationship of the intensity of area use with

distance from nest (Figure 1), and determined 50% and 90% quantiles of distance from nest per species and sex, providing an indication for the spatial sensitivity. To verify whether the results can be transferred between regions, we assessed the differences between study areas throughout.

2 | MATERIALS AND METHODS

2.1 | Data collection

GPS-tracking data of breeding birds of 6 raptor species were collected using solar-powered GPS tags deployed on 280 individuals (Montagu's Harrier [MoH; $n=101$], Hen Harrier *Circus cyaneus* [HH; $n=54$], Marsh Harrier *Circus aeruginosus* [MaH; $n=31$], Common Buzzard *Buteo buteo* [CB; $n=31$], Red Kite *Milvus milvus* [RK; $n=61$] and Short-toed Eagle *Circus gallicus* [STE; $n=2$]) in 15 study areas in France, Belgium, Luxembourg, The Netherlands, Germany and Sweden between 2009 and 2023 (see Appendix S1 for details). Twelve different GPS tag models (Table S1.2) from the manufacturers Milsar, Ornitela and UvA-BiTS (Bouten et al., 2013) were mounted as backpacks using a thoracic cross-strap harness (Anderson et al., 2020) made from Teflon ribbon. Tags including harness weighed 12.2–30.4g (1.6%–7.7% of body weight; median: 3.8%). GPS tagging was approved by the responsible authorities in each country (Appendix S3).

In spring and summer, the basic setting for the GPS fix interval was 5 min (MoH, MaH, RK, STE) or 15 min (CB and most HH) during daytime, and 1–4h at night. During autumn and winter, periods of bad weather, and incubation periods in females, the fix interval was increased to 1–12h to preserve battery voltage. In addition to this basic data collection scheme ('low-frequency

data'), 'high-frequency data' were collected using an interval of 3 s in *Ornitela* and *UvA-BITS* tags and 2–3 s in *Milsar* tags to obtain more accurate flight height data (GPS operating in continuous mode; Bouten et al., 2013; Schaub et al., 2023). These were collected mostly during manually set blocks of 1–4 h per day, and to a lesser extent using automatic geofences around areas of interest such as wind farms. Due to the high-energy demand of the continuous GPS mode, high-frequency data were mainly available from spring and summer (94.8% of positions from March to August; Appendix S1: Figure S1.2; Table S1.2). By manually setting the periods of high-frequency data collection, we unlinked data collection from the immediate charging conditions as much as possible, which ensured a relatively even sampling across the course of the day and different weather conditions.

The study was restricted to breeding birds, with breeding status assigned per calendar year (data retained from combinations of individual and year [hereafter termed 'individual-years'] during which at least one breeding attempt was made). Information on the nest location, timing and success of breeding attempts were collected based on field observations or based on data from the GPS tags (see Appendix S1).

The dataset was restricted to 15 defined study areas (Figure S1.1), which are used for breeding by the study species. CB were year-round residents within the study areas, while all tagged MoH, MaH and STE (trans-Saharan migrants) and most tagged HH and RK (partial migrants) left the study areas outside the breeding season.

The density of wind turbines varied among study areas and individuals (Table S1.1). As there was no clear evidence for effects of wind turbine density on the aspects of flight behaviour of interest for this study (Appendix S4), data were included irrespective of wind turbine density.

2.2 | Data processing and analysis

All data processing and analyses were performed in R 4.3.1 (R Core Team, 2023). As all six study species are known to be diurnal, data were restricted to daytime, applying solar depression angles of 6° (MoH, HH, MaH, CB), 4° (RK) and 0° (STE) as thresholds (see Appendix S1). Throughout the study, to obtain confidence intervals, hierarchical bootstrapping was used (resampling 1000 times among individuals, individual-years or individual-year-nest combinations with replacement; see Appendix S1). The 2.5% and 97.5% quantiles of the 1000 bootstrap replicates were used as limits of the 95% confidence interval. We considered groups to be significantly different if their confidence intervals did not overlap. We used bootstrapping instead of mixed modelling because (a) the dataset was unbalanced in different regards (e.g. data from only one sex in some species and species–area combinations); (b) the nonlinear seasonal pattern of time spent in flight was difficult to include in mixed models, as it was species- and sex-specific (Appendix S2: Figures S2.1 and S2.2); and (c) bootstrapping

allowed to derive combined confidence intervals when multiplying the outcomes on the three considered aspects of flight behaviour (see below).

2.2.1 | Time spent in flight

To obtain a dataset with more homogeneous GPS fix intervals for the analysis of the time spent in flight, the GPS-tracking data were subsampled to a minimum interval of 15 min. To account for inter-specific variation in the time spent in the study areas per year and in the duration and timing of the breeding season, we considered three different time periods (Figure 2). Period A covered the whole calendar year; Period B was the period when all species were present in the study areas, defined as 1 May to 8 August (100 days), allowing comparison of flight behaviour between species under the same conditions (e.g. weather, day length); and Period C was the period with active nests, which was determined per individual-year as the time between (1) 7 days before the estimated date of the onset of egg-laying and (2) 7 days after the estimated fledging date of the first chick, or, if applicable, the estimated date of nest failure. Note that for Periods A and B, data after nest failure were retained within the dataset.

We distinguished between in-flight and stationary GPS positions using the GPS-based ground speed measurements provided along every position. The distribution of speed values typically shows two modes associated with stationary and flight positions, respectively. We used the location of the minimum between the two modes as a threshold, separately for low-frequency and high-frequency data for

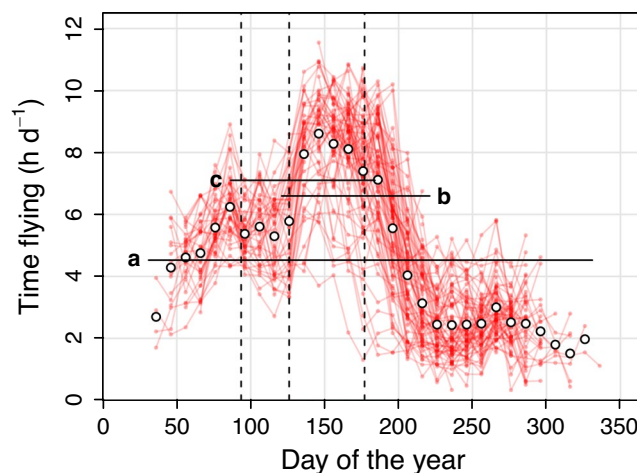


FIGURE 2 Illustration of the applied approach to derive the mean time spent in flight per day corrected for uneven seasonal sampling (example for male Red Kites). Red points and lines: Data per 10-day period for individual-years ($n = 74$; from 32 individuals); white points: Means across individual years per 10-day period; vertical dashed lines: Median laying, hatching and fledging dates; horizontal black lines: Corrected means for three time periods (a: whole year; b: period of shared presence in the breeding area [May–August]; c: period with active nests [determined per individual-year]).

each combination of species and tag manufacturer ($0.75\text{--}3.75\text{ m s}^{-1}$; Table S1.4). Nine individuals, for which we suspected unusually large error in the low-frequency speed data, were removed for the analyses on time spent in flight and distance from nest (see Appendix S1). The dataset for time Period A comprised 271 individuals, 524 individual-years and 3,302,242 GPS positions (see Table S1.5 for Periods B and C).

Our objective was to obtain the mean time spent in flight per day across the three time periods mentioned above. To correct for uneven seasonal sampling, among others due to seasonal variation in the GPS fix interval (see above), the calendar year was divided into 10-day periods (TDP). For each combination of TDP, individual and year, the proportion of flight positions during daytime was determined, only considering combinations with ≥ 30 GPS positions ($n=7487$). The time spent in flight per day was derived by multiplying the proportion of positions in flight during daytime with the average day length in the given TDP at the location of the given individual. We then calculated the mean across individual-years per TDP per combination of species and sex (Figure 2; only considering TDP with data from ≥ 2 individual-years). Finally, to obtain the overall average, the mean across the means per TDP was calculated. The same approach was applied for each combination of species, sex and study area with ≥ 10 combinations of TDP, individual and year with ≥ 30 GPS positions.

2.2.2 | Proportion of flights at risk height

As low-frequency GPS height data are subject to large error, which may lead to biases (Péron et al., 2020), we relied exclusively on the more accurate high-frequency data to determine the proportion of flights at risk height (Schaub et al., 2023). Furthermore, the data were restricted to flight positions and to individuals with at least 5 h of recorded flights. The resulting dataset comprised 162 individuals and 7,013,897 in-flight GPS positions, that is 5786.1 h of recorded flights (Table S1.6). We transformed the altitude above mean sea level obtained from the GPS tags into height above ground level (a.g.l.) by applying the *Shuttle Radar Topography Mission* global digital elevation model with a resolution of 30 m (NASA JPL, 2013). See Appendix S1 for additional information on the processing of the GPS height data. The collision risk height range was set to 32–200 m a.g.l., encompassing the rotors of 75% of the wind turbines installed in the six study countries since 2015 (determined based on The Wind Power (2022, 2023)). For this part of the analysis, we did not distinguish between sexes, as little high-frequency data from females were available.

2.2.3 | Time spent at risk height

The total time spent at risk height within the study areas per species–sex combination ('sensitivity index 1'; Figure 1) was

calculated for the whole calendar year (Period A) and for the period of shared presence (Period B, see above), by multiplying the average time spent in flight per day with the proportion of flights at risk height and the length of the time period in days (for Period A: average number of days present within the study areas per year, determined per species [see Appendix S1 for details]; for Period B: 100 days).

2.2.4 | Distance from nest

To assess the spatial distribution of flight movements, we analysed the distance of in-flight positions from the nests. The dataset was subsampled to a minimum interval of 15 min and restricted to the period with active nests (Period C) and to completely recorded successful breeding seasons. A breeding season was defined to be complete if a minimum number of TDP with ≥ 30 positions was available from the period during which the given nest was active (e.g. ≥ 7 TDP in MoH and ≥ 13 TDP in STE; Table S1.3). The dataset comprised 169 individual-year-nest combinations from 111 individuals and 230,943 in-flight GPS positions (Table S1.7).

To correct for the potential bias brought by heterogeneous GPS intervals across the breeding season (e.g. reduced number of positions during the incubation period in females), for each TDP, we determined the average time spent in flight per day and resampled the in-flight GPS positions to achieve the number of flight positions expected with a 15-min GPS fix interval. This resampled dataset was used to derive 50% and 90% quantiles of distance from nest for each individual-year-nest combination.

To estimate the intensity of space use as a function of distance from nest, we applied concentric distance bands of 0.5 km around the nest location and divided the proportion of positions within each band by the band's area size. Furthermore, the proportion of positions per area for each distance band was multiplied by the average time spent in flight per day and the proportion of flights at risk height to obtain the time spent at risk height per area as a function of distance from nest ('sensitivity index 2'; Figure 1).

3 | RESULTS

3.1 | Time spent in flight

The mean time spent in flight across the calendar year was higher in males than in females in all five species with data available from both sexes (males flying on average 1.5–2.2 times more than females; Figure 3a,d; Table S2.1). Time spent in flight per day varied greatly between species, ranging from 0.5 (CB) to 3.4 (MoH) h in females and from 1.0 (CB) to 7.4 (MoH) h in males (Figure 3; Table 1). When considering only the period of shared presence in the breeding areas (May–August) or periods with active nests, the differences

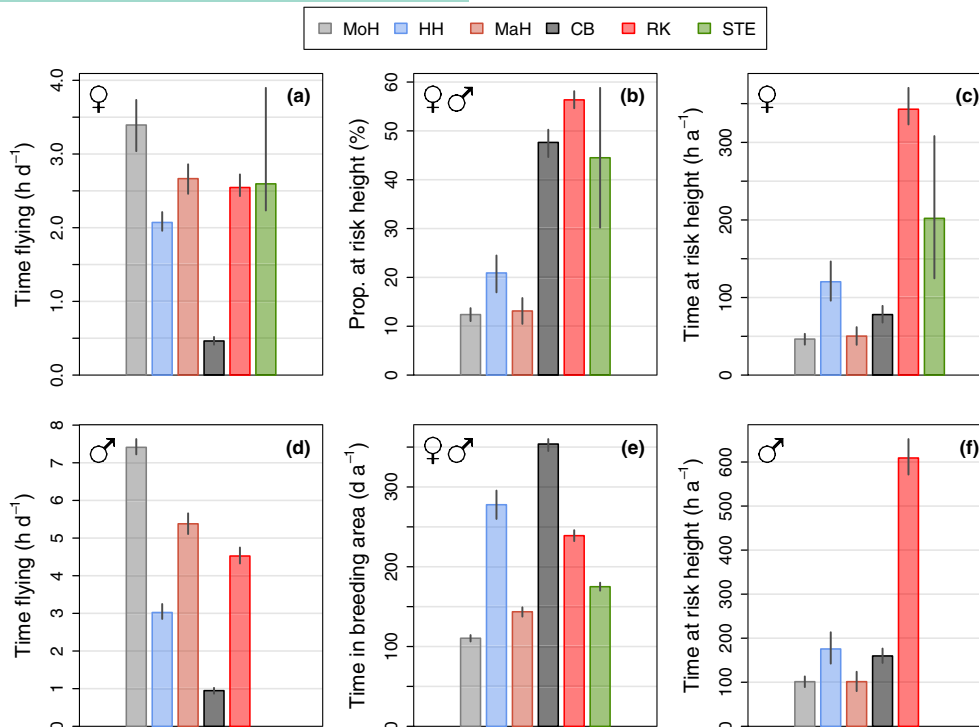


FIGURE 3 Time spent in flight per day (a, d), proportion of flight positions at risk height (b), time spent within the breeding area (e) and time spent at risk height within the breeding area per year (i.e. the product of the three previous aspects; c, f) for six raptor species (means and 95% confidence intervals from bootstrapping). Note different y-axis scales between females and males. Sexes were lumped in (b) and (e). See [Appendix S2: Tables S2.1, S2.3 and S2.5](#) for sample sizes, and [Figure S2.3](#) for corresponding results for the period of shared presence in the breeding area (May–August). CB, Common Buzzard; HH, Hen Harrier; MaH, Marsh Harrier; MoH, Montagu's Harrier; RK, Red Kite; STE, Short-toed Eagle.

TABLE 1 Proportion of significant pairwise comparisons between species, and between study areas within species, in relation to the total number of pairs for different aspects of flight behaviour. For time flying and nest distance, only pairwise comparisons within the same sex were considered (sexes lumped for proportion at risk height).

Aspect	Between species	Between areas (within species)
Time flying		
Period A	21/25	5/64
Period B	17/25	—
Period C	15/25	—
Prop. at risk height	12/15	3/35
Time at risk height		
Whole year	21/25	—
Shared presence	13/25	—
Nest distance		
Median	15/25	7/28
Q90	18/25	7/28

Abbreviation: Prop., proportion.

between species remained substantial ([Table S2.1](#)). The variation in time spent in flight between study areas, however, was relatively small ([Figure 4a,b](#); [Table S2.2](#)).

3.2 | Proportion of flights at risk height

The proportion of flight positions at collision risk height (32–200 m a.g.l.) varied between 12.4% (MoH) and 56.4% (RK; [Figure 3b](#)). Twelve out of 15 pairwise comparisons between species were significant ([Table 1](#)), but note the large CI in STE ([Figure 3b](#); [Table S2.3](#)). Again, variation between study areas was small relative to the variation between species ([Table 1](#); [Figure 4c](#); but note significant differences between some study areas in MoH and RK; [Table S2.4](#)).

3.3 | Time spent at risk height

As a result of the found differences in time spent flying, proportion at risk height and the number of days spent in the breeding area ([Figure 3e](#); [Table S2.5](#)), the time spent at risk height within the breeding areas across the whole calendar year varied significantly between species ([Figure 3c,f](#); [Table S2.6](#)). It was highest in RK, both in females (342 h a⁻¹; 1.7–7.4 times more than in the other species) and males (609 h a⁻¹; 3.5–6.0 times more than in the other species). STE had the second highest mean in females (202 h a⁻¹), but note the large confidence interval (125–308 h a⁻¹). When restricting the comparison to the period of shared presence in the breeding areas (May–August), RK still stood out compared to MoH, HH, MaH and CB (3.8–6.4 times more in RK females; 3.6–4.6 times more in RK males; [Figure S2.3](#); [Table S2.6](#)).

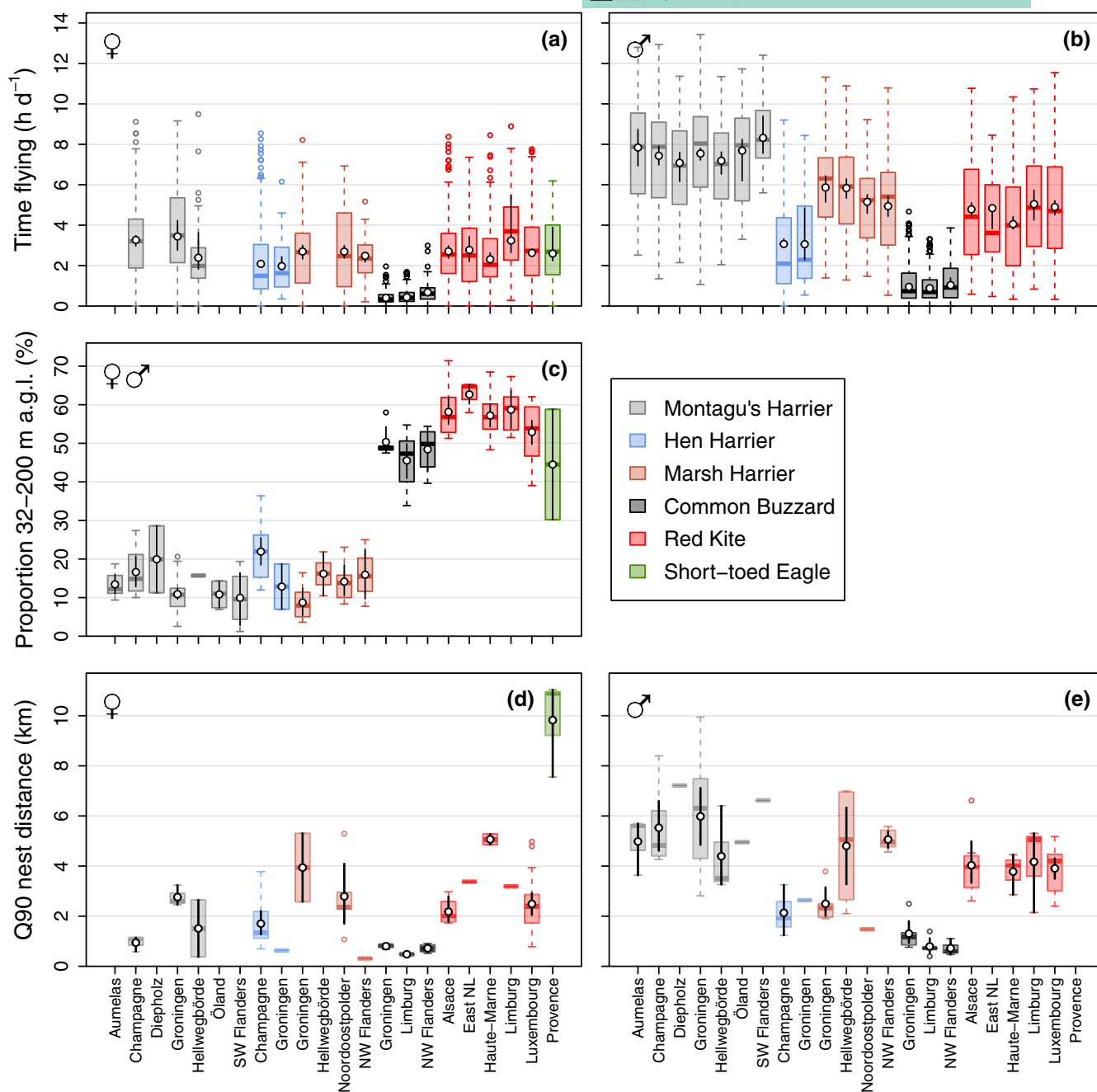


FIGURE 4 Variation between study areas in three aspects of flight behaviour for breeding birds of six raptor species. (a, b) Time spent in flight per day during the whole calendar year ('Period A'); boxplots: Data per 10-day period per individual-year (including seasonal variation); overlaid points: Means corrected for unbalanced seasonal sampling. (c) Proportion of flight positions at risk height (females and males lumped); boxplots: Data per individual. (d, e) 90% quantile of distance from nest for complete successful breeding seasons; boxplots: Data per combination of individual-year and nest. In all panels, overlaid points and vertical black lines indicate means and 95% confidence intervals from bootstrapping. See [Appendix S2: Tables S2.2, S2.4 and S2.8](#) for sample sizes.

3.4 | Distance from nest

Both the 50% and 90% quantiles of distance from nest were smaller in females than in males (Figure 5; e.g. 1.8 vs. 5.6 km for the mean 90% quantile for female and male MoH), but the difference was not significant in all cases for the 90% quantile (HH, MaH and CB; Table S2.7). Individual variation was large (e.g. 90%

quantile ranging between 2.8 and 9.9 km in MoH males), resulting in relatively wide confidence intervals (Figure 5; Table S2.7). In females, the mean 90% quantile varied between 0.7 (CB) and 9.8 km (STE); and in males between 1.0 (CB) and 5.6 km (MoH). There was more variation between study areas than for the other two studied aspects of flight behaviour (Table 1; Figure 4d,e; Figure S2.4; Table S2.8).

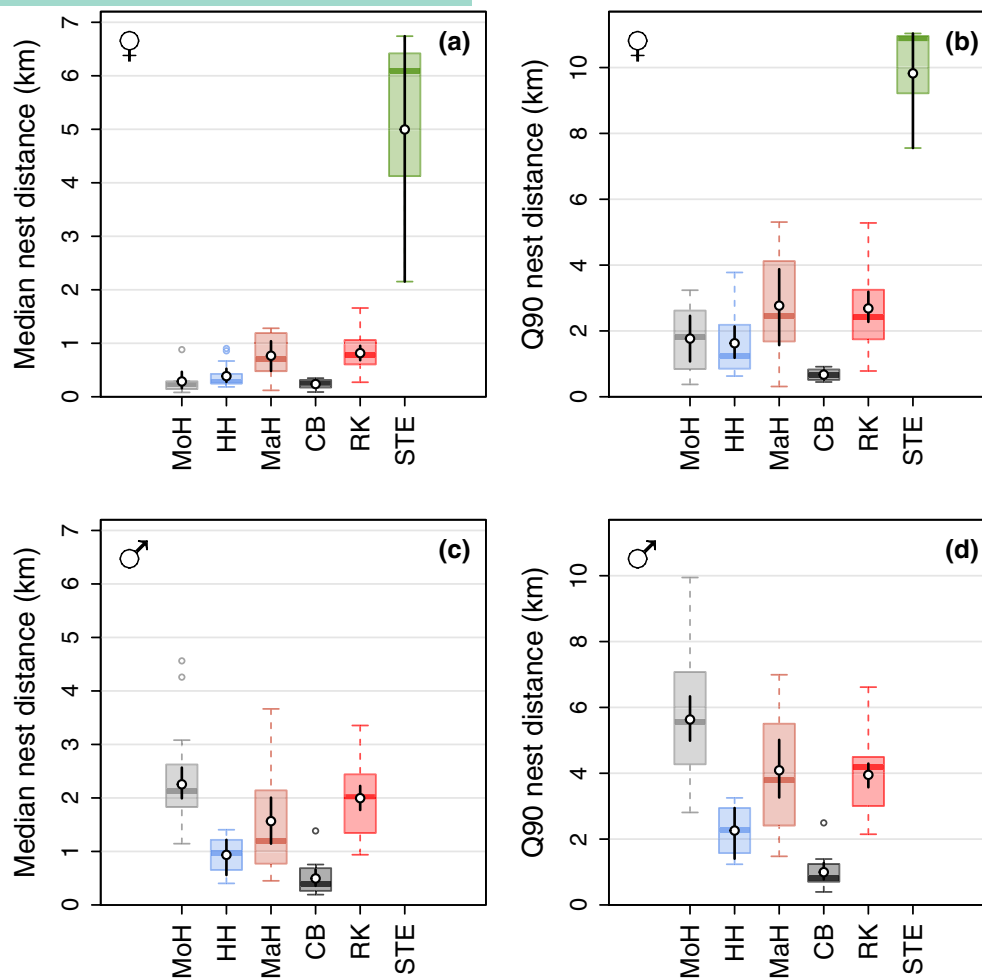


FIGURE 5 Median (Panels a and c) and 90% quantile (Q90; Panels b and d) of distance from nest for complete successful breeding seasons. Overlaid white points: Means; vertical black lines: 95% confidence intervals from bootstrapping. See [Appendix S2: Table S2.7](#) for sample sizes, and [Figure 3](#) for species abbreviations.

Overall, the proportion of positions in distance bands of 0.5 km decreased with increasing distance from nest, while the slopes differed between species and sexes ([Figure S2.5](#); see [Figures S2.6](#) and [S2.7](#) for individual variation). When considering the proportion of positions per km², the decrease with distance was even more pronounced, especially between the 0.0–0.5 and the 0.5–1.0 km distance band (e.g. 98.6% km⁻² in the first vs. 8.2% km⁻² in the second band in CB females; [Figure S2.5](#)).

Consequently, the time at risk height per km² also decreased with increasing distance from nest in all species and in both sexes, while the ranking of species changed along the distance scale ([Figure 6](#)). In females, between 0 and 2.5 km, the amount of time at risk height per km² was greatest in RK, while above 2.5 km, it was greatest in STE. In males, RK had the highest value in all distance bands until 6.5 km, with MoH taking over at higher distances. CB males spent on average nearly as much time at risk height as RK in the smallest distance band (0.0–0.5 km), but much less at higher distances (e.g. time at risk height 9.3 times larger in RK than in CB at 1–1.5 km, and 21.8 times larger at 1.5–2 km; [Figure 6](#)).

4 | DISCUSSION

Our study of flight behaviour in six raptor species based on extensive GPS-tracking data, including high-frequency data providing high vertical accuracy, illustrates how variation in the time spent in flight, the proportion of flights at risk height (i.e. within the height range of wind turbine rotors) and the distances travelled from the nest site translates into interspecific and spatial variation in the sensitivity to wind turbines collisions. This integrative approach improves our understanding of wind turbine collision risk and allows to compare the species-specific sensitivity irrespective of current exposure, which may ultimately help to reconcile wind energy development with bird conservation.

4.1 | Sensitivity based on time spent in flight and proportion of flights at risk height

We found that both the time spent in flight and the proportion of flights at risk height varied considerably between species, with profound

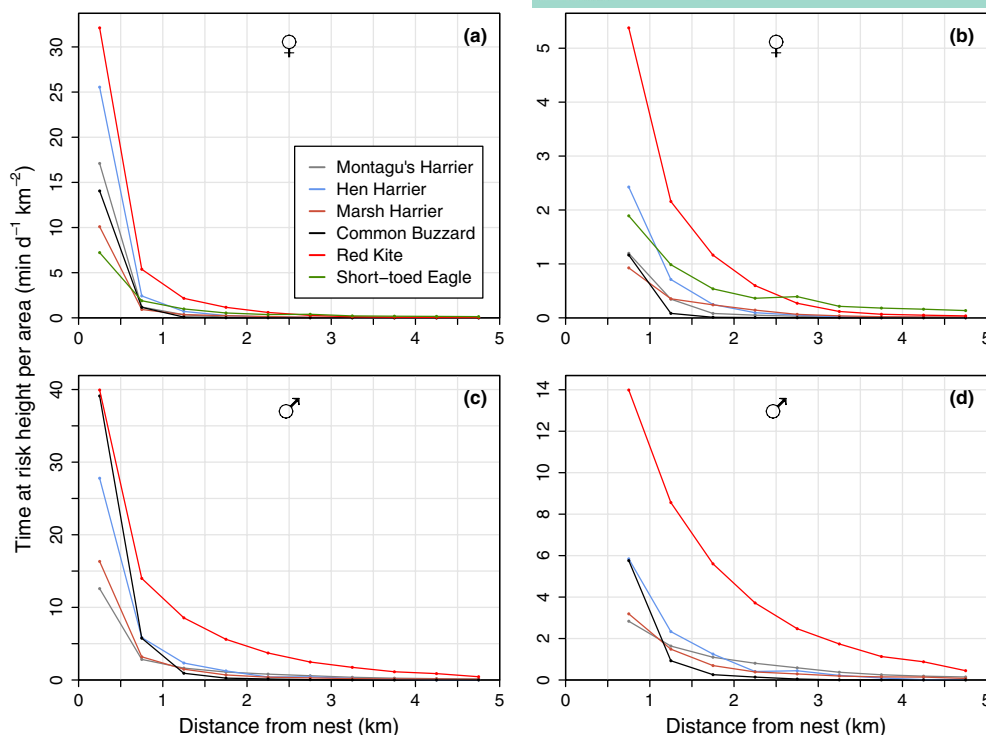


FIGURE 6 Time spent at risk height (32–200 m a.g.l.) per km² as a function of distance from nest for complete successful breeding seasons (distance bins of 0.5 km; means across individual breeding seasons). Panels (b) and (d) are zoomed-in versions of (a) and (c) with shortened y-axis (distance bin 0.0–0.5 km excluded). Note different y-axis scales between females and males.

effects on the sensitivity to wind turbine collisions. The comparison between species highlighted that sensitivity is determined by the interaction of both aspects: for example, the sensitivity (time spent at risk height per year) for both MoH and CB was relatively low. However, in MoH, this was the result of flying much in combination with a low proportion of flights at risk height, whereas CB flew little, but with a high proportion at risk height. By contrast, RK were found to both fly relatively much, and often at risk height, resulting in a notably high relative sensitivity. This matches the general perception of RK being a particularly collision-prone species. For example, RK features the second-highest number of reported fatalities in Germany (Dürr, 2025) and the number of fatalities divided by the national population size (Gedeon et al., 2014) is about seven times higher in RK than in CB (but note that this comparison does not involve corrections for potential biases related to e.g. geographical distribution of search effort or differences in reporting probability between species).

Overall, the time spent in flight and the proportion of flights at risk height varied much more between species than between study areas. This implies that these aspects of flight behaviour can be considered as relatively fixed characteristics of a species, closely related to its morphology, behaviour and ecology. Even though variation may be larger when considering regions with very different characteristics concerning, for example, topography or climate (i.e. factors affecting the energy landscape; Péron et al., 2017), we can reasonably expect it to be small compared to interspecific variation. As our study focussed on the stay in the breeding areas, it would be valuable to apply a year-round perspective on the time spent in flight

and the proportion of flights at risk height in future studies, also covering the migration period and the stay on the wintering grounds (if applicable).

Besides interspecific variation, our results show large differences in time spent in flight between sexes in all five species for which data on both sexes were available, with males flying about twice as much as females when considering the entire period of presence in the study areas (range of 1.5–2.2 among species). This is in line with the fact that in all five species, the duties of incubation and brooding are predominantly fulfilled by the females, while the males hunt and supply prey (del Hoyo et al., 1994). As a consequence of the larger amount of time spent in flight, we found a higher sensitivity to wind turbine collisions in males than in females. Indeed, in MoH, there are indications of a higher collision risk in males than in females based on carcass searches (Gitenet & Bouzin, 2014). However, it should be noted that we did not consider sex-specific variation in the proportion of flights at risk height, which could modulate the differences in sensitivity between sexes. For example, a higher proportion of flights at risk height in female MaH compared to males was reported in earlier studies (Buij et al., 2022; Grande, 2018), whereas no sex-specific differences in mean flight height were found in RK (Pfeiffer & Meyburg, 2022).

It should be noted that our approach does not provide a complete account of sensitivity to wind turbine collisions. Additional factors might modify the ranking of species, such as avoidance behaviour, morphology (e.g. bird size) and extinction risk, the latter depending on population size and demography, amongst others (larger

effects of increased mortality on population growth in species with low pace of reproduction; Diffendorfer et al., 2021). Earlier studies attempting to produce comprehensive sensitivity estimates mostly relied on crude information on flight behaviour (Beston et al., 2016; Green-Tkacenko et al., 2024). Thus, incorporating results based on GPS tracking as we present here would be an important step forward for such assessments.

Avoidance behaviour on different spatial scales is expected to vary between species (NatureScot, 2025; Sassi et al., 2024; Schaub et al., 2020), but clear evidence is still scarce, especially for the smallest spatial scale (last-second escape). Concerning RK, it has been suggested that the high perceived sensitivity was due to a lack of avoidance behaviour (Hötter, 2017), but recent studies have shown a substantial degree of wind turbine avoidance in RK (Mercker et al., 2023; Reichenbach et al., 2023). Here, we show that a high sensitivity in RK compared to other raptor species could 'simply' result from basic aspects of flight behaviour, that is time spent in flight and proportion of flights at risk height.

4.2 | Spatial sensitivity

We found that the proportion of time spent in a given area, and consequently the sensitivity to wind turbines collisions, decreased with increasing distance from nest in all species. Similar results have been obtained in earlier studies (Eichhorn et al., 2012; Rasran et al., 2017; Schaub et al., 2020; Tikkanen et al., 2018). With our comparative approach, we showed that the sensitivity ranking of species changed over distance. For example, despite of a much lower overall amount of time spent in flight, CB males were on average nearly as sensitive to collisions as RK males at lowest distance from the nest (0–500 m; but much less sensitive at larger distances). This illustrates how the interplay of the three considered aspects of flight behaviour shapes sensitivity to wind turbine collisions. Note that we did not account for a potential effect of distance from nest on the proportion of flights at risk height, which would be a valuable improvement for future studies. For example, certain flight behaviour may predominantly be performed in the vicinity of the nest site (e.g. display or guarding flights), which could affect the proportion at risk height.

Regarding distance from nest, we found more variation between study areas than for the two other aspects of flight behaviour. However, regional variation is difficult to tear apart from individual variation here, as sample sizes (number of complete successful breeding seasons) per combination of species, sex and study area were small. It can be expected that regional and/or individual variation in distance from nest is driven by factors like general habitat quality (including prey density) and the spatial distribution of suitable habitats. Also in seabirds, a considerable amount of regional and individual variation in foraging distances from the breeding colony was found (Cleasby et al., 2023).

4.3 | Implications for management

In this study, we provide a framework to assess the sensitivity of bird species to wind turbine collisions irrespective of current exposure by integrating several aspects of flight behaviour and space use. Information on species-specific sensitivity is essential to prioritise species in the wind energy planning process with respect to site selection and the mitigation measures to apply. Sensitivity maps from the regional up to the global scale, allowing to identify sites for wind energy development leading to the lowest overall impact on birds, can be produced by combining the sensitivity index values for the bird species present in each area, alongside estimations of abundance (BirdLife International, 2025).

Concerning wind turbine siting on the local scale, our study quantitatively underpins the common-sense assumption that an increasing distance between wind turbines and nest sites reduces the collision risk of breeding birds, and that it should especially be avoided to construct wind turbines in close vicinity to nests. The species-specific relationships of collision risk with distance from nests (Figure 6) can be used to compare scenarios of wind turbine development in a given area with varying wind turbine locations. A publicly available online tool allowing project developers and other stakeholders to perform these scenario comparisons has been developed (Schaub et al., 2025). It should, however, be noted that distance from nests only gives a first indication of the expected intensity of use of a given area of interest, as other factors such as habitat type or topography may also play an important role (Heuck et al., 2019; Tikkanen et al., 2018). For example, high habitat quality can lead to an intensity of use which is higher than expected based on distance from nests alone. Within environmental impact assessments for planned wind energy projects, these additional aspects should be considered in combination with general considerations based on nest-turbine distances.

The quantiles of distance from nest we provided can serve as first indications for the distances to keep between wind turbines and nest sites for each species. The 90% quantile could be applied to be 'on the safe side'. However, defining a threshold is not straightforward: as sensitivity differs between species, it appears sensible to apply different quantiles as a threshold (e.g. larger quantile for species with high overall sensitivity such as RK). Ideally, a threshold should be based on a complete assessment of sensitivity, accounting for the species-specific extinction risk (e.g. larger threshold for slowly reproducing species).

Our finding that regional variation in flight behaviour was limited, at least concerning time spent in flight and proportion of flights at risk height, has practical implications for pre-construction impact assessments. Conducting a GPS-tracking study for each wind farm project is unfeasible and undesirable from an ethical viewpoint. Our results suggest that it is generally possible to transfer species-specific results between regions to inform wind energy planning.

5 | CONCLUSIONS

Our study demonstrates that variation in key aspects of flight behaviour translates into highly variable sensitivity to wind turbine collisions among raptor species. Assessing time spent in flight and proportion of flights at risk height, which we found to be well-conserved across regions for a given species, provides a general account of species-specific sensitivity. On the local scale, results on distance from nest allow to compare the expected collision risk among alternative wind turbine locations. Thus, our approach based on GPS-tracking data—which are becoming available for a growing number of bird species—provides valuable information for the spatial planning for wind energy development from the global to the local scale, enabling to optimise the siting of wind farms and wind turbines to reduce the collision risk of birds.

AUTHOR CONTRIBUTIONS

TS, RHGK, CDZ and AMil conceptualised the study. TS, RHGK, PA, J-LB, RB, CG, HI, KJ, AK, SL, AMio, GM, SR, JR, GS, BVH, JW and AMil organised the local GPS tracking projects and did fieldwork. TS performed data processing and data analysis. TS, RHGK and AMil wrote the first draft. All authors contributed to subsequent drafts and approved the final manuscript.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The dataset supporting the results of this article is available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.n8pk0p398>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Additional materials and methods.

Appendix S2. Additional results.

Appendix S3. Information on the local GPS-tracking projects.

Appendix S4. Additional analysis on the effect of wind turbine density on flight behaviour.

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