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BIOLOGGING

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# Wind turbines cause functional habitat loss for migratory soaring birds

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## Abstract

1. Wind energy production has expanded to meet climate change mitigation goals, but negative impacts of wind turbines have been reported on wildlife. Soaring birds are among the most affected groups with alarming fatality rates by collision with wind turbines and an escalating occupation of their migratory corridors. These birds have been described as changing their flight trajectories to avoid wind turbines, but this behaviour may lead to functional habitat loss, as suitable soaring areas in the proximity of wind turbines will likely be underused.
2. We modelled the displacement effect of wind turbines on black kites (*Milvus migrans*) tracked by GPS. We also evaluated the impact of this effect at the scale of the landscape by estimating how much suitable soaring area was lost to wind turbines.
3. We used state-of-the-art tracking devices to monitor the movements of 130 black kites in an area populated by wind turbines, at the migratory bottleneck of the Strait of Gibraltar. Landscape use by birds was mapped from GPS data using dynamic Brownian bridge movement models, and generalized additive mixed modelling was used to estimate the effect of wind turbine proximity on bird use while accounting for orographic and thermal uplift availability.
4. We found that areas up to approximately 674 m away from the turbines were less used than expected given their uplift potential. Within that distance threshold, bird use decreased with the proximity to wind turbines. We estimated that the footprint of wind turbines affected 3%–14% of the areas suitable for soaring in our study area.

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5. We present evidence that the impacts of wind energy industry on soaring birds are greater than previously acknowledged. In addition to the commonly reported fatalities, the avoidance of turbines by soaring birds causes habitat losses in their movement corridors. Authorities should recognize this further impact of wind energy production and establish new regulations that protect soaring habitat. We also showed that soaring habitat for birds can be modelled at a fine scale using publicly available data. Such an approach can be used to plan low-impact placement of turbines in new wind energy developments.

**KEYWORDS**
aerial habitat, avoidance behaviour, migration, orographic uplift, raptor, thermal uplift, wind farms

## 1 | INTRODUCTION

Wind energy generation has increased immensely over the last decades, and this growth is expected to continue in the forthcoming years, with a predicted annual increase of 5% of the installed capacity until 2020 (GWEC, 2015; IPCC, 2011). Despite the immediate benefits for climate change mitigation, negative interactions between wind energy production and wildlife, mainly birds and bats, have been widely reported (Saidur, Rahim, Islam, & Solangi, 2011). Soaring birds, including most raptors, storks and other large birds, are among the groups of highest concern, as their movement corridors have been populated by wind farms (Cabrera-Cruz & Villegas-Patraca, 2016; Katzner et al., 2012; Martín, Perez-Bacalu, Onrubia, De Lucas, & Ferrer, 2018) leading to high fatality rates through collisions with turbines (e.g., Barrios & Rodriguez, 2004; Ferrer et al., 2012; Smallwood & Thelander, 2008).

Soaring flight allows large birds to travel long distances with a reduced energetic cost (Duriez et al., 2014; Pennycuick, 1975). However, soaring depends on updrafts, which are relatively scarce and scattered across the landscape (Horvitz et al., 2014; Katzner et al., 2015). Two types of updrafts are commonly used by terrestrial soaring birds: (a) orographic uplift that results from the deflection of horizontal winds by sloping terrain and (b) thermal uplift that is formed during the day due to the heating of the land surface by solar radiation (Kerlinger, 1989). Soaring birds use orographic uplift either to gain altitude and glide downwards in a desired direction, or to travel along uplift-rich areas such as mountain ranges (Bohrer et al., 2012; Katzner et al., 2015). Orographic uplift is particularly useful when generated from mountain ranges oriented in the migration direction (Dennhardt, Duerr, Brandes, & Katzner, 2015; Kerlinger, 1989). In the case of thermal uplift, soaring birds typically climb in thermals using a circular trajectory from which they glide linearly towards the next thermal in the desired direction (Katzner et al., 2015; Kerlinger, 1989; Santos et al., 2017). Due to such specific requirements, soaring birds tend to move along areas with high uplift potential, often named corridors (sensu Dennhardt et al., 2015). Besides the physical requirements for soaring, the importance of different corridors may vary dramatically depending on their geographical position relative to migration routes of soaring birds. For example, areas in the vicinity of narrow sea crossings may experience higher traffic during migrations, as soaring birds avoid crossing large bodies of water (Newton, 2008).

Soaring birds and wind energy developments may compete for the same areas both at the local and regional scales. At local scales, wind turbines are frequently installed along the top of mountain ranges, in order to maximize exposure to horizontal winds, and these areas also tend to have high orographic uplift potential for birds (Katzner et al., 2012). At a broader scale, migratory bottlenecks of soaring birds often correspond to narrow sea crossings or mountain passes where the topography favours high wind speeds, thus also well suited for wind-power production (Hilgerloh, Michalik, & Raddatz, 2011; Martín et al., 2018; Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014). Therefore, understanding how wind turbines impact movement corridors of migratory soaring birds is of utmost importance to better reconcile the production of wind power with wildlife conservation.

In general, birds tend to avoid wind turbines through evasive movements and changes in space use (May, 2015). Empirical evidence published on soaring birds has been showing they change their flight trajectories to avoid turbines (de Lucas, Janss, & Ferrer, 2004; Villegas-Patraca et al., 2014) and that their numbers decrease in the close proximity of the turbines (Barrios & Rodriguez, 2004; Pearce-Higgins, Stephen, Langston, Bainbridge, & Bullman, 2009). Similarly, comparisons between the pre- and post-construction phases showed that soaring birds reduce their use of the areas where turbines are installed and their trajectories become more scattered in nearby areas (Cabrera-Cruz & Villegas-Patraca, 2016; Farfan et al., 2017; Garvin, Jennelle, Drake, & Grodsky, 2011; Johnston, Bradley, & Otter, 2014). While these avoidance behaviours suggest that soaring birds are to some extent able to cope with the presence of wind turbines (Marques et al., 2014), they may also cause functional habitat loss (i.e., loss of aerospace in movement corridors; Diehl, 2013), which is a potentially important, though largely neglected, impact of wind-power generation (Davy, Ford, & Fraser, 2017).

In this study, we investigated the footprint of wind turbines on movement corridors of migratory soaring birds using high-frequency GPS tracking (1-min temporal resolution or higher). GPS tracking is a powerful tool to investigate direct interactions between birds and wind turbines at multiple spatiotemporal scales, but it was only recently introduced in this field of study (e.g., Garthe, Markones, & Corman, 2017; Thaxter et al., 2015, 2018). We tracked 130 black kites (*Milvus migrans*) during the post-breeding migration in an area highly populated by wind turbines in the region of Tarifa, Spain. Black kites and other soaring birds concentrate in this region to cross the Strait of Gibraltar during their migration to Africa (MIGRES, 2009). Birds were captured and tracked during periods of strong cross-winds at the Strait of Gibraltar, which forced them to roam around Tarifa while waiting for conditions favouring the sea crossing. Bird movements were used to map space-use intensity using Brownian bridge movement models. The influence of the wind turbines on the birds' use of the landscape was then modelled taking into account the main predictors of soaring flight, orographic and thermal uplift (Bohrer et al., 2012; Kerlinger, 1989). We hypothesized that (a) birds will use areas with greater uplift (orographic and thermal) more frequently, and (b) the area in the proximity of the wind turbines will be less frequented regardless of its uplift potential.

## 2 | MATERIALS AND METHODS

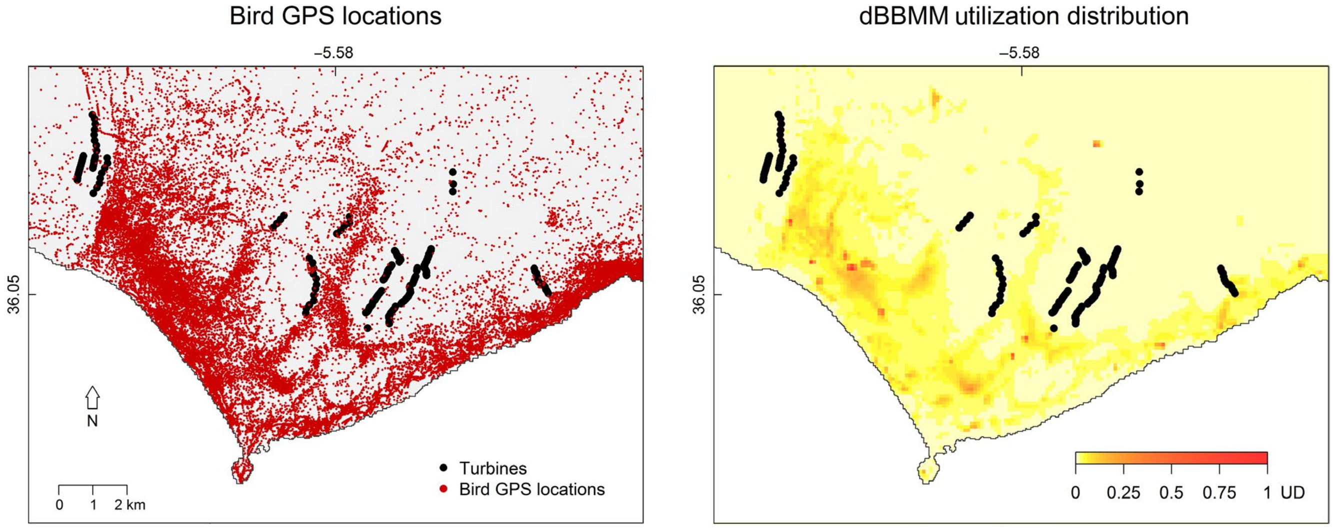
### 2.1 | Study area

This study was conducted in the region of Tarifa (36.0132°N, 5.6027°W), on the Spanish side of the Strait of Gibraltar. The Strait is a narrow sea crossing between Europe and Africa and is the main migration bottleneck for soaring birds travelling along the Western European–West African Flyway (Newton, 2008). The region of Cádiz (that includes Tarifa) is of high importance to the wind energy industry, with ca. 70 wind farms and over 1,300 MW of installed wind-power capacity (IECA, 2015). Our focal area had 160 operating wind turbines on seven wind farms, representing 132 MW of power generation (Figure 1, Supporting Information Table S1). These turbines were mainly arranged in rows from north to south (Figure 1).

### 2.2 | Bird captures and tracking

Our model species, the black kite, is an obligate soaring migrant, and one of the most common soaring species crossing the Strait of Gibraltar during the post-breeding migration (between 100 and 150,000 individuals are counted on an annual basis; Martín, Onrubia, de la Cruz, & Ferrer, 2016). These features make this species susceptible to interactions with wind turbines, and fatalities due to collision with wind turbines have been recorded in earlier studies in this region (Ferrer et al., 2012).

We captured and fitted 130 birds with GPS data loggers during the post-breeding migration (July–September) in 2012 and 2013 (Supporting Information Table S2). Birds were captured during periods of strong Levanter winds (5–15 m/s blowing from the east), which are frequent in the summer (Dorman, Beardsley, & Limeburner, 1995) and are known to prevent the passage of soaring birds to Africa, causing them to congregate around Tarifa for periods up to 1 week (Miller et al., 2016). Birds were captured in a walk-in trap (7 × 7 × 3.5 m) baited with carrion, located 3.5 km north of Tarifa (36.0426°N, 5.6150°W). We captured more birds than those eventually tracked, which enabled us to select similar numbers of adults and juveniles in each capture event. Overall, we tracked 72


Bird GPS locations

dBBMM utilization distribution

**FIGURE 1** Use of the aerospace in the study area (Tarifa, Spain) by the black kites during the post-breeding migration of 2012 and 2013, and the locations of the wind turbines. Left panel: GPS locations of 130 tracked birds. Locations are only shown for birds flying (speed > 1 m/s) during daylight in periods of Levanter wind (blowing from the east), and for the region where the concentration of bird movement was the highest. Right panel: cumulative utilization distribution modelled from dynamic Brownian bridge movement models (dBBMMs). Map grid with 100-m spatial resolution. Black dots in each map are the locations of wind turbines adults and 58 juveniles. Sex ratio was also relatively balanced (69 females, 59 males and 2 unidentified, results from molecular sexing).

Birds were equipped with GPS-GSM data loggers (42 g, TM-202/R9C5 module; Movetech Telemetry, UK, https://www.uea.ac.uk/movetech) attached as backpacks using Teflon ribbon. A weak-link was built in to each harness to allow the loggers to automatically detach. The weak-link was made from rubber band for the birds tagged in 2012 and from biodegradable plastic thread in those tagged in 2013. Previous tests showed that the rubber band breaks within 2–4 weeks when exposed to solar radiation and the biodegradable plastic thread within a year. Birds were released a few hours after capture, immediately after the tagging was completed. Loggers were set to obtain a GPS position at least once a minute. GPS mean error calculated from ca. 1,500 fixes collected by two data loggers left at a fixed known position was 1.4 m in horizontal and 1.5 m in vertical, with maximum errors of 15 m and 31 m, respectively. Data were uploaded to an online server via the GSM network every 2 hr.

The procedures involved in bird trapping and the GPS tagging were approved by the Consejería de Medio Ambiente of the Junta de Andalucía through the licence to Alejandro Onrubia.

## 2.3 | Estimation of orographic and thermal uplift

We used estimates of orographic and thermal uplift to test our first study hypothesis. The orographic and thermal uplift velocities were estimated using a modified version of the methodology employed by Bohrer et al. (2012) and Brandes and Ombalski (2004) for high-resolution spatial data, described in Santos et al. (2017). The estimation of orographic uplift uses parameters from local topography (terrain aspect and slope) and wind (direction and speed). Local topography was obtained from a digital elevation model of 30-m spatial resolution available at http://gdex.cr.usgs.gov/gdex/ (NASA JPL, 2009). Wind direction and speed was obtained at a weather station in Tarifa (36.0138°N, 5.5988°W). Measurements of wind for the whole migration season of black kites (mid-July to mid-September; MIGRES, 2009) during 2012 and 2013 lead to the conclusion that there are two predominant wind conditions: (a) strong Levanter winds (wind direction from 80 to 120°; speed from 4 to 15 m/s) lasting for periods up to a week; and (b) western breeze (wind direction from 270 to 310°; speed from 1 to 6 m/s), typically occurring between Levanters (Supporting Information Figure S1). These wind conditions match with that generically described for the summer at the Strait of Gibraltar (Dorman et al., 1995). In this context, we decided to build three different orographic uplift models, the first representing uplift for average conditions of wind during the collection of our tracking dataset (direction = 97.8°, speed = 8.8 m/s), and the other two models representing the average conditions of Levanter wind (direction = 100°, speed = 7.7 m/s) and western breeze (direction = 290° and speed = 4.1 m/s) observed during the whole migration season of black kites in 2012 and 2013. The uplift estimated from the first model was used as predictor in bird space-use models (described in the section below), while the estimates of the remaining two uplift models were used in the calculation of general scenarios of habitat loss during Levanter wind and western breeze (shown in Figure 5).

The estimation of thermal uplift velocity according to Santos et al. (2017) uses land surface temperature derived from Landsat imagery. In general, satellite images obtained in the same season show high correlation in reflectance values if no major changes of land use are observed (Zhu, 2017). Consequently, high correlation is also expected for thermal uplift models built from those images. Santos et al. (2017) confirmed that uplift models built for the study area in different days during the summers of 2012 and 2013 are highly correlated ($r > 0.77$). Therefore, we decided to build a single thermal uplift model that used land surface temperature estimated from a Landsat 8 OLI/TIRS image acquired on 17 July 2013, available at http://earthexplorer.usgs.gov/ (NASA Landsat Program, 2015). The model was representative of uplift at 225 m height, which is the mean flight height of birds in our tracking dataset, and its spatial resolution was 100 m, corresponding to that of the Landsat 8 OLI/TIRS thermal band.

## 2.4 | Bird movement modelling

Our modelling approach followed the concept of resource utilization function (RUF) proposed by Marzluff, Millspaugh, Hurvitz, and Handcock (2004). RUF uses a two-step analysis, the first that estimates the density or intensity of space use (i.e., utilization distribution; UD) over the geographical domain of interest and the second links the space use to a set of spatially explicit covariates in a regression model (Hooten, Johnson, McClintock, & Morales, 2017).

Our modelling dataset included GPS positions of flying birds (i.e., GPS speed > 1 m/s, Supporting Information Figure S2) collected during daylight and in days of Levanter wind (direction: mean = 97.8°, *SD* = 0.22, range = 83.2–116.3°; speed: mean = 8.8 m/s, *SD* = 2.2, range = 4.2–12.7 m/s). Very few tracking data were collected with different wind conditions than Levanter because birds cross the Strait of Gibraltar as soon as the Levanter ceases (Miller et al., 2016). These data were thus excluded from the analysis. We also concentrated the analysis in the area where the concentration of bird movement was the highest (represented in Figure 1).

We used dynamic Brownian bridge movement models (dBBMMs; Kranstauber, Kays, LaPoint, Wikelski, & Safi, 2012) to estimate the UD of each bird in each day on a 100 × 100 m grid. Contrasting to conventional methods of UD estimation, the Brownian bridge movement model quantifies the UD based on the movement path of animals rather than individual points (Horne, Garton, Krone, & Lewis, 2007; Kranstauber et al., 2012). A major advantage of this method is that it accounts for temporal autocorrelation in the data, which is a fundamental problem of tracking data, particularly for GPS data obtained at high frequency (Kranstauber et al., 2012). The dBBMMs were implemented in R (R Core Team, 2016) with the function brownian.bridge.dyn of the package move (Kranstauber, Smolla, & Scharf, 2017), using a window size of 15 locations and a margin of five locations following the recommendations of Kranstauber et al. (2012). The UD calculated for each bird in each day was summed in order to produce a general UD for our study area. This UD was used as a response variable in the models described below.

In order to specifically test our study hypotheses, we fitted a generalized additive mixed model (GAMM) using distance to wind turbines and the orographic and thermal uplift velocities as predictors of bird UD. Orographic and thermal uplift are the most important drivers of soaring flight on land (Kerlinger, 1989), thus we expected bird UD to be fundamentally determined by those factors but potentially affected by the proximity of wind turbines. We selected GAMM as modelling technique because it simultaneously allowed the use of nonlinear predictors and accounting for spatially correlated data (Beale, Lennon, Yearsley, Brewer, & Elston, 2010; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The model was fitted with the function gamm of the R package mgcv (Wood, 2018). Bird UD and all predictors were represented by single values in the 100 × 100 m grid generated in the dBBMM interpolation. We must emphasize that orographic and thermal uplift estimates result from static uplift models, representing the generic conditions for the period of tracking data collection (see section above). We added a Gaussian spatial correlation structure to the model to account for spatial autocorrelation (Beale et al., 2010; Dormann et al., 2007; Wood, 2017). This was done with the function corGaus of the R package mgcv (Wood, 2018) following Zuur et al. (2009). Bird UD was log-transformed to normalize its distribution. No random factors were included in the model. In a first approach, the degree of smoothing of predictors (k) was left free to be optimized by cross-validation (the default method of the gamm function). However, we found that the effects of uplift predictors on bird UD were approximately linear in the regions well supported by data (Supporting Information Figure S3). Therefore, we set these two predictors as linear in our final model. The modelling dataset was restricted to grid cells at distances up to 2 km from wind turbines (i.e., 9,136 grid cells), as the influence of wind turbines on bird UD is expected to dissipate with distance.

A second model was built for grid cells positioned far away from the influence of the wind turbines (1–2 km away from turbines) using only the orographic and the thermal uplift velocities as predictors. We used this model to estimate soaring suitability in the absence of wind turbines (used for the results presented in Figures 4 and 5). This model was a generalized least squares (GLS) since it did not include nonlinear predictors. The model was fitted with the function gls of the R package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2018). As in the GAMM, in this model, we used function corGaus to account for spatial autocorrelation of the data, and the bird UD was log-transformed to normalize its distribution.

Both models were validated through 10-fold cross-validation. The original dataset was randomly split into a training subset with 90% of the data that was used to fit the model, and a testing subset with 10% of the data against which the model is tested. This procedure was repeated 10 times in a way that the training and testing subsets of each run were complementary and cover all the original dataset (Geisser, 1993). The precision and predictive performance of models were evaluated from their normalized root mean square error (nRMSE), defined as the root mean square error divided by the range of the model response variable. The root mean square error (RMSE) is a commonly used metric for regression models accuracy and performance that quantifies model error in the units of the observed data (Kuhn & Johnson, 2013). Normalizing the RMSE facilitates the comparison between models built at different spatial and temporal scales (e.g., Bocinsky & Kohler, 2014; Feilhauer, Asner, Martin, & Schmidtlein, 2010).

For both models, fitting assumptions were checked from diagnostic residual plots of R the packages mgcv and nlme (see Supporting Information Figure S4), and spatial autocorrelation correction was validated from plots of residual autocorrelation generated with the function correlog of the R package ncf (Supporting Information Figure S5, Bjornstad, 2018).

## 3 | RESULTS

We tracked 130 individual black kites for an average of 3 days each, generating ca. 220,000 GPS locations (Figure 1 left panel). Movements were concentrated within a radius of ca. 40 km from Tarifa, with individual birds moving about 120 km on average before they crossed the Strait of Gibraltar (see Supporting Information Figure S6 for examples of tracks). From the original dataset, 77,228 GPS locations were used for modelling purposes (Figure 1 left panel, Supporting Information Table S2; see Materials and Methods for details on data selection).

The UD estimated from dBBMMs showed an uneven spatial pattern, with reasonably defined areas of concentration of movement (Figure 1 right panel). Higher intensity of movement was observed along two central areas aligned approximately north–south and along the coastline (Figure 1 right panel).

The estimates of uplift showed highly heterogeneous distributions (Figure 2). The highest orographic uplift velocities during the period of data collection were estimated along the east-facing mountain slopes in the most western and eastern regions of the study area (Figure 2 left panel). In contrast, the highest estimates of thermal uplift were concentrated in a valley located in the centre of the study area (Figure 2 right panel). Orographic uplift was spatially more concentrated with more extreme velocities than thermal uplift, but the latter showed higher values on average (orographic uplift velocity: mean of grid cell values = 0.35 m/s, *SD* = 0.72, range = 0–6.18 m/s; thermal uplift velocity: mean of grid cell values = 1.69 m/s, *SD* = 0.26, range = 0.10–2.19 m/s).

Generalized additive mixed model results showed that bird UD was significantly affected by the distance to wind turbines and the two types of uplift (Table 1, Figure 3). A negative effect of wind turbine proximity on bird UD was observed up to a distance of approximately 674 m (i.e., the maximum of the curve of Figure 3 left panel), which dissipates beyond that. However, it should be noted that there was a slight drop of bird UD after the 674 m. Both orographic and thermal uplift velocities had a positive effect on bird UD (Table 1, Figure 3).

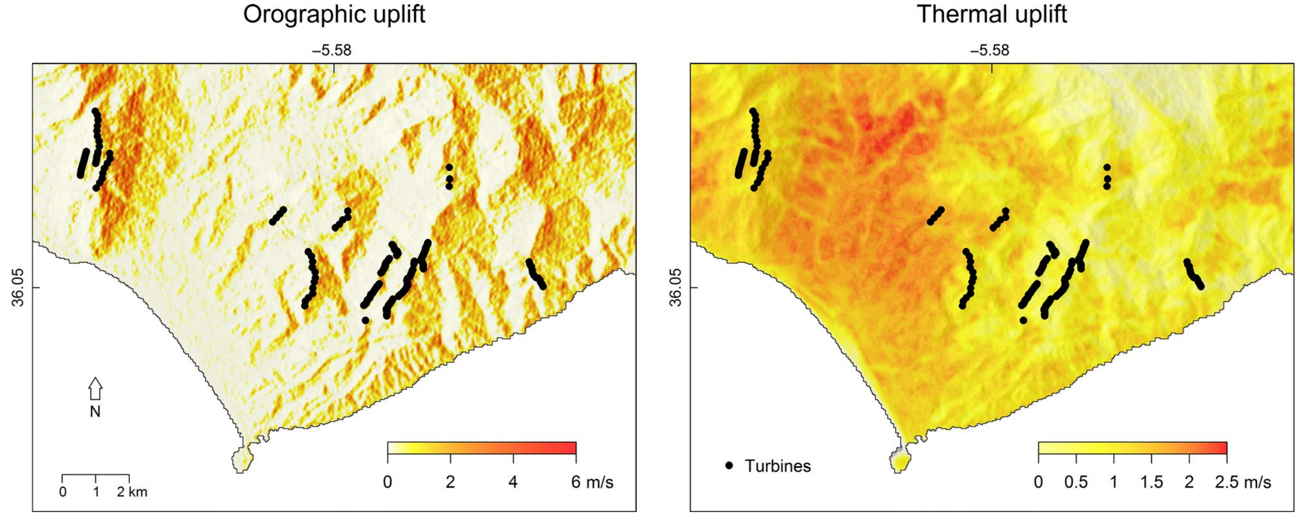


**FIGURE 2** Estimated orographic (left) and thermal (right) uplift velocities in the study area. Orographic uplift represents deflected Levanter winds during the period of bird tracking (wind direction: mean = 97.8°, *SD* = 0.22, range = 83.2–116.3°; wind speed: mean = 8.8 m/s, *SD* = 2.2, range = 4.2–12.7 m/s). Thermal uplift velocity was modelled for 225 m height (mean flight height of birds) using land surface temperature estimated from a Landsat 8 OLI/TIRS image acquired on 17 July 2013 (NASA Landsat Program, 2015) (available at the USGS archive, http://earthexplorer.usgs.gov/). Light hill shading was added to illustrate interaction between topography and uplift. Black dots represent wind turbines

**TABLE 1** Summary statistics for the two models explaining black kite utilization distribution (UD). The first model tested the effect of wind turbines on bird UD while accounting for the effects of uplift. The model was a generalized additive mixed model (GAMM) fitted with grid cell data at distances up to 2 km from wind turbines, and included the distance to the wind turbines, the orographic and the thermal uplift velocities as predictors. The second model was designed to evaluate soaring suitability of grid cells independently of the effect of wind turbines. The model was a generalized least squares (GLS) fitted with data obtained far from the influence of wind turbines (between 1 and 2 km distance) and used only orographic and thermal uplift velocities as predictors. Both models were corrected for spatial autocorrelation (see Materials and Methods for details). Fitting and cross-validation normalized root mean square error ($nRMSE_{fit}$ and $nRMSE_{cv}$) are shown for the evaluation of precision and predictive performance of the models, respectively. For $nRMSE_{cv}$, we show the range of the nRMSE calculated for the 10 models produced in the cross-validation procedure (see Materials and Methods for further details)

| | Estimate | *SE* | *t* | *edf* | *F* | *p*-Value | $nRMSE_{fit}$ (%) | $nRMSE_{cv}$ (%) |
|---|---|---|---|---|---|---|---|---|
| Model: effect of wind turbines | | | | | | | 13.7 | 13.6–16.5 |
| Intercept | −10.59 | 0.26 | −41.33 | | | | | |
| s(distance to turbines) | | | | 5.22 | 12.95 | <0.001 | | |
| Orographic uplift | 0.11 | 0.01 | 8.03 | | | <0.001 | | |
| Thermal uplift | 2.70 | 0.15 | 18.17 | | | <0.001 | | |
| Model: soaring suitability | | | | | | | 14.5 | 14.8–17.9 |
| Intercept | −10.42 | 0.36 | −28.74 | | | | | |
| Orographic uplift | 0.12 | 0.02 | 5.96 | | | <0.001 | | |
| Thermal uplift | 2.62 | 0.21 | 12.68 | | | <0.001 | | |

*Note*. edf, estimated degrees of freedom; *F*, *F* statistics; *SE*, standard error; *t*, *T* statistics.

The GLS model, fitted with data obtained beyond the influence of the wind turbines (i.e., 1–2 km from wind turbines), showed effects of orographic and thermal uplift velocities on bird UD similar to those of the GAMM (Table 1, Supporting Information Figure S7). Predictions of the GLS model applied to areas up to 674 m from the wind turbines were significantly higher than the dBBMM estimates for the same areas (Figure 4). This indicates that birds used areas close to turbines less than expected based on their soaring suitability. After extrapolating this model to the entire study area, we found that between 3% and 14% of the area suitable for soaring was within the area of influence of wind turbines (i.e., within 674 m of wind turbines), these being similar during Levanter wind (4%–14%) and western breeze (3%–14%; Figure 5).

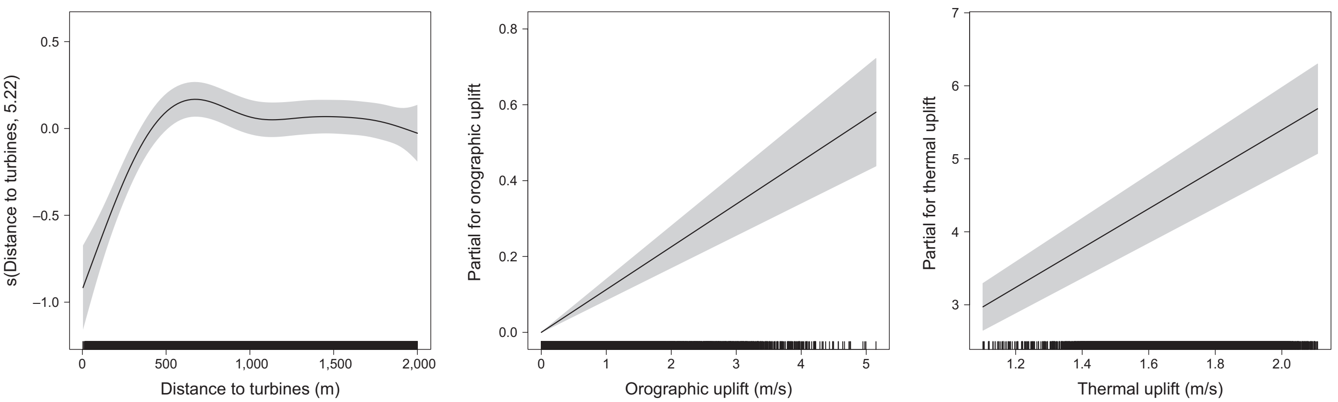


**FIGURE 3** Generalized additive mixed model partial effects of distance to turbines, orographic uplift and thermal uplift on black kite utilization distribution. Shaded areas represent 95% confidence intervals. Modelling dataset includes grid cells up to 2 km from wind turbines

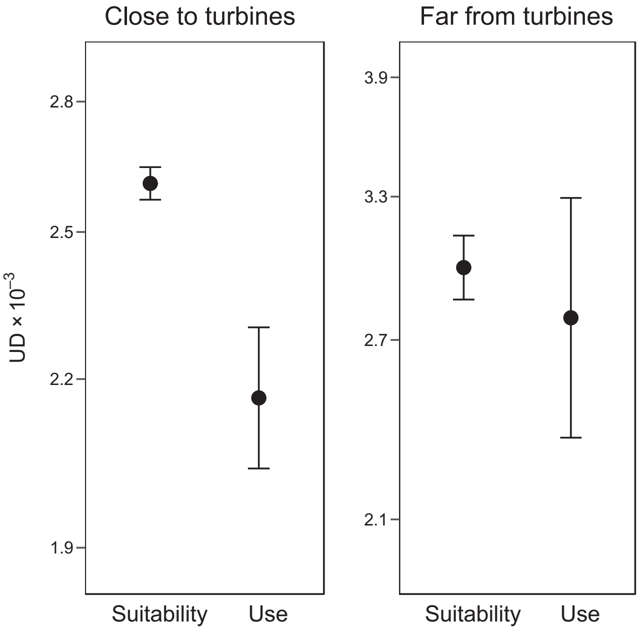


**FIGURE 4** Comparison between soaring suitability and the use by black kites of the areas close to wind turbines (up to 674 m of distance) and far from wind turbines (located at 1–2 km distance from the closest turbine). Bird use corresponds to the utilization distribution (UD) obtained directly from the dynamic Brownian bridge movement model (dBBMM), and the soaring suitability is the UD predicted from a generalized least squares (GLS) fitted with orographic and thermal uplift velocities as predictors and the dBBMM UD as response variable (see Materials and Methods for further details). The GLS model was fitted with data of grid cells placed far away from the influence of wind turbines (between 1 and 2 km distance of the closest turbine). These data were randomly divided into two datasets, the first was used to fit the GLS model (with 90% of the data) and the second was used to represent bird use far from turbines in the plot (with 10% of the data). Error bars in the plot represent 95% confidence intervals

## 4 | DISCUSSION

We found that wind turbines affect a large area of potentially suitable soaring habitat around them. GPS-tracked black kites showed a reduced use of the areas up to approximately 674 m away from the wind turbines (corresponding to an area of ca. 143 ha around each turbine), this effect being stronger at shorter distances (Figure 3), which proves our second study hypothesis. We also demonstrated that areas within 674 m of the wind turbines had suitable uplift conditions for soaring flight but they were used less than expected by the black kites (Figure 4). Interestingly, there was a slight peak of bird use at areas near the 674 m threshold (Figure 3) that might have been a consequence of birds changing direction to avoid entering the areas adjacent to the turbines (Cabrera-Cruz & Villegas-Patraca, 2016; Villegas-Patraca et al., 2014). Additionally, we showed clear increasing relationships between orographic and thermal uplift and bird UD (Figure 3 and Supporting Information Figure S5), proving the first hypothesis of this study.

We must emphasize that our models include some level of error (see Table 1), likely because that were other environmental variables influencing the movement of the birds that were not included as predictors. However, that amount of error is comparable to that found in previous studies linking bird soaring behaviour to uplift proxies (Bohrer et al., 2012; Dodge et al., 2014; Hernandez-Pliego, Rodriguez, & Bustamante, 2015; Santos et al., 2017; Sapir et al., 2011). The fact that uplift predictors were estimated for a single generic circumstance in time may also have added inaccuracy to our models. Tracking data used in the models were collected in highly uniform conditions of wind direction; therefore, we do not expect the areas with orographic uplift potential to change spatially in time. However, the variation observed in wind speed may have affected overall uplift intensity of those areas. This could potentially have influenced the birds' trade-off in using orographic uplift or thermal uplift in nearby areas. Regarding the thermal uplift, a considerable temporal variation is expected within a day and between days mostly due to the amount of solar radiation heating the earth surface (Stull, 1988). As in the case of orographic uplift, we do not expect such variation to promote spatial changes in uplift but some intensity variation is expected that could represent a trade-off in the use of alternative sources of uplift.

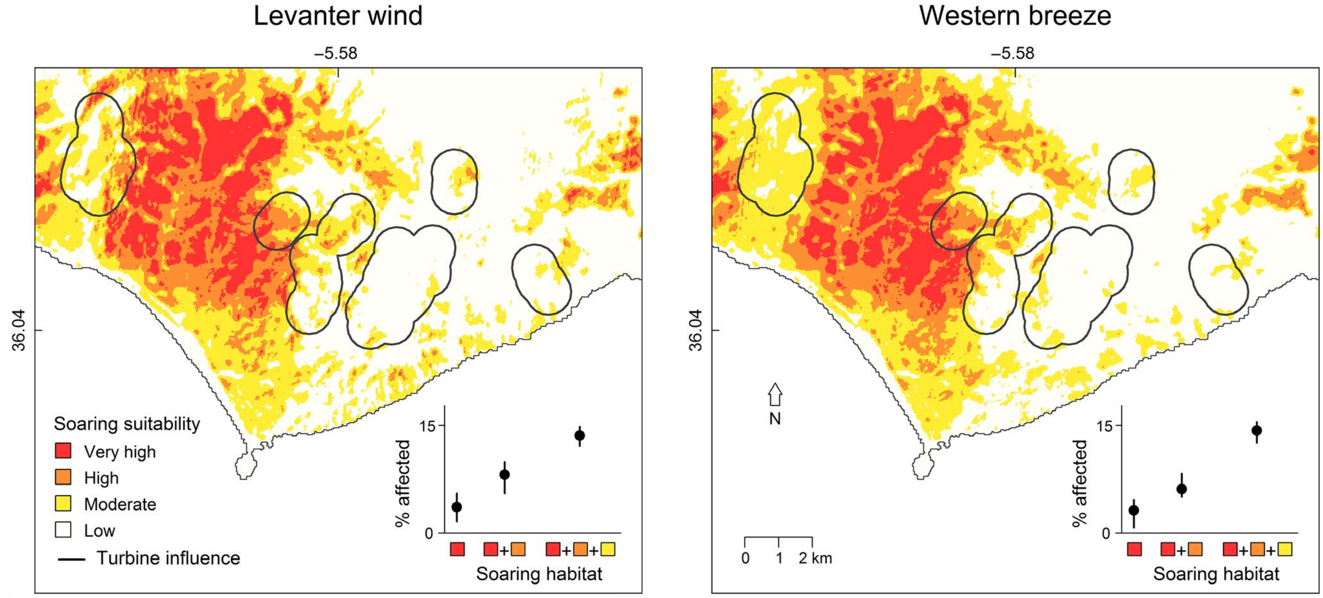


**FIGURE 5** Soaring habitat affected by wind turbines for average conditions of Levanter wind (blowing from the east) and western breeze observed during the migration seasons of the black kites in 2012 and 2013. Wind turbine influence is represented by circles of 674 m radius around each turbine (this distance resulted from the generalized additive mixed model (GAMM) shown in Table 1 and Figure 3). Soaring suitability resulted from predictions of a generalized least squares (GLS) model (detailed in Table 1 and Supporting Information Figure S7) using thermal and orographic uplift estimates for the whole study area and for the two sorts of wind observed during the migration seasons of the black kites in 2012 and 2013. The utilization distribution (UD) predictions produced from the GLS model were simplified in soaring suitability categories: very high suitability—are the 10% highest UD values; high suitability—are the following highest 15% UD values; moderate suitability—are the following highest 25% UD values; and low suitability—are the lowest 50% UD values. The inset plot shows the percentage of area under the influence of wind turbines considering different scenarios of soaring suitability. Confidence intervals in the plot result from confidence intervals of fitted values of GLS model predictions

The displacement effects of wind-power plants have been demonstrated in earlier studies for soaring birds (Barrios & Rodriguez, 2004; Cabrera-Cruz & Villegas-Patraca, 2016; Garvin et al., 2011; Johnston et al., 2014; de Lucas et al., 2004; Pearce-Higgins et al., 2009; Villegas-Patraca et al., 2014). However, to the current date, only a single study quantified the extent of the area affected by this phenomenon (Pearce-Higgins et al., 2009). That study reports lower densities of two species of raptors during their breeding season in areas up to 800 m from turbines, coarsely matching the estimates of our model. Our study is the first attempt to quantify the proportion of soaring habitat lost or negatively affected by the presence of wind farms. We estimated that 3%–14% of the areas suitable for soaring in our study area were impacted by wind energy production, this estimate being similar for Levanter winds and western breeze (Figure 5). These two sorts of wind comprise most wind conditions found in Tarifa during the migration season of black kites (Supporting Information Figure S1). The magnitude of this impact is likely similar in other critical areas for migratory soaring birds where new large wind-power projects are being constructed, such as the Gulf of Suez in Egypt (Hilgerloh et al., 2011) or the Isthmus of Tehuantepec in Mexico (Villegas-Patraca et al., 2014). It should be emphasized that soaring birds are restricted to fly in soaring corridors (e.g., Leshem & Yom-Tov, 1998; Santos et al., 2017; Shamoun-Baranes, Leshem, Yom-Tov, & Liechti, 2003); thus, small losses of suitable area may have large constraints for their vital activities. Losses in movement corridors may be particularly important during migrations, as soaring birds already experience considerable mortality while overcoming natural barriers, such as deserts and sea stretches (Bildstein, Bechard, Farmer, & Newcomb, 2009; Klaassen et al., 2014; Strandberg, Klaassen, Hake, & Alerstam, 2010). Suboptimal soaring conditions may force birds to delay or suspend migration or to use flapping flight, which is energetically unsustainable for most species (Newton, 2008).

The reason why migratory soaring birds avoid wind turbines is still unclear. The fact that birds are displaced far beyond the areas occupied by the physical infrastructure of wind-power plants could be a consequence of neophobia, as turbines do not belong to their natural environment (Walters, Kosciuch, & Jones, 2014), but it could also be a consequence of earlier negative experiences, such as birds being caught in the airflow around turbines, or even witnessing fatalities of conspecifics. In addition, the functioning of wind turbines disturbs local airflow regimes (e.g., Magnusson & Smedman, 1999; Sorensen et al., 2015), which may compromise uplift generation. However, this is expected to affect only the areas downwind the turbine rotors (e.g., Magnusson & Smedman, 1999; Sorensen et al., 2015). We should also recognize that the avoidance of turbines varies considerably among soaring species, their life stage and their annual cycle (May, 2015); thus, the range of influence of wind turbines found in this study is not necessary replicable in other contexts.

Our findings indicate that the negative effects of wind-power developments on soaring birds may be far more extensive than the commonly reported mortality caused by collision (Marques et al., 2014). Avoidance behaviour may suggest that soaring birds, as well as other birds, are partly able to cope with the existence of wind turbines (Marques et al., 2014). However, our results make clear that this is a simplistic interpretation and may lead to the underestimation of the real impacts of wind-power generation. We recommend that the authorities responsible for wildlife protection and wind industry regulations recognize the loss of aerial habitat caused by wind turbines and the potential associated negative impacts on soaring birds. It becomes clear from our results that individual turbines greatly differ on their impact depending on their geographical position (Figure 5); thus, it is possible to significantly reduce overall impact of wind-power production with adequate planning. The method we used to map updrafts uses only data that is publicly available (Santos et al., 2017) and can be used in environmental impact assessment studies to guide the selection of low-impact locations for new wind turbines. We are convinced that wind energy production is necessary to face global warming, but the accelerating increase of wind-power developments needs to be accompanied by science-based solutions to minimize its impacts on wildlife.

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## AUTHORS' CONTRIBUTIONS

A.T.M., C.D.S., J.P.S., J.P., F.M. and M.W. designed the study; C.D.S., A.-R.M., A.O. and J.P.S. collected the data; A.T.M., C.D.S. and F.H. analysed the data; A.T.M. and C.D.S. wrote the manuscript. All authors discussed the results and commented on the manuscript.

## DATA ACCESSIBILITY

The tracking data used in this study are available at Movebank Data Repository https://doi.org/10.5441/001/1.q23p1t84 (Marques, 2019).

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## SUPPORTING INFORMATION

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

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