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Assessing exposure to wind turbines of a migratory raptor through its annual life cycle across continents

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ABSTRACT

Unsustainable fossil fuel emissions have prompted a global shift towards renewable energy sources, such as wind. This has led to a strong expansion of wind power generation infrastructures, often conflicting with biodiversity conservation. Relatively large flying animals, such as birds and bats, have frequently been reported to collide with wind turbines, resulting in casualties that can depress population size and lead to local extinctions.

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Migratory species that move across continents through their year-round displacements may be especially at risk. We comprehensively assessed wind turbine exposure for a colonial migratory raptor of European conservation interest, the lesser kestrel *Falco naumanni*, based on the distribution and size of >1800 colonies and a large GPS-tracking dataset (>350 individuals) for three distinct biogeographical populations (from Iberian, Italian, and Balkan peninsulas). 26 % of the European population has at least one wind turbine within the foraging areas around colony sites, Italian colonies being most at risk. The main European network of protected areas, the Natura 2000 network, failed to mitigate the potential negative impact of wind turbines on breeding populations. GPS-tracking revealed that exposure was negligible in the African non-breeding areas (Sahel region), particularly high during migration, and lower during breeding for Iberian and Balkan individuals but not for Italian ones. Different countries should prioritize different measures to mitigate collision risk with wind power generation infrastructures. This case study can be leveraged by conservationists and renewable energy stakeholders to mitigate conflicts between biodiversity conservation and expected wind energy infrastructure development in the near future.

1. Introduction

Climate change is impacting our planet at multiple levels, increasingly threatening natural systems and negatively affecting human health and well-being at the same time (Hoegh-Guldberg et al., 2019; Pecl et al., 2017; Romanello et al., 2022). Multiple shreds of evidence from both terrestrial and aquatic realms suggest that current rates of fossil fuel use have an extremely high likelihood of causing catastrophic ecological effects (McGlade and Ekins, 2015). Decarbonisation is thus crucial to secure the long-term stability of global ecosystems, but requires a drastic reduction in carbon dioxide emissions in the next few decades and full-scale adoption of low-carbon sources for energy generation (Delafield et al., 2021; Dunnett et al., 2022b; IPCC, 2018).

This transition is already occurring in a few regions of the world, and it will likely continue and increase on a global scale, mostly involving the solar and wind energy sectors (Dunnett et al., 2022a). However, renewable energy infrastructures require approximately ten times more land than fossil fuel facilities (Rehbein et al., 2020; Trainor et al., 2016), thus likely conflicting with other global priorities, such as food production and biodiversity conservation (IRENA, 2019). This highlights that the "green energy transition" is not exempt from environmental and societal costs (Nazir et al., 2020). A pressing issue related to global sustainability is thus how to balance demands for energy, food production, and biodiversity conservation within a finite land area (Dunnett et al., 2022a).

In Europe, 35 % of energy generation derives from renewable sources, with wind power alone accounting for 16 % (Komusanac et al., 2021). Since the European Commission aims to reach climatic neutrality ("net-zero") by 2050, wind farms are predicted to expand in the next few years (Jung and Schindler, 2022). Compared to conventional energy sources, and even to other renewables, the negative impacts of wind farms on biodiversity are considered relatively small (Saidur et al., 2011). Nevertheless, there are still several drawbacks in wind power generation systems, mainly related to noise, visual, and light pollution, local climate change, electromagnetic interferences, and ecosystem disturbances, e.g. habitat loss, fragmentation, and direct wildlife mortality due to collision (Kati et al., 2021; Sayed et al., 2021). Indeed, there is a rapid increase of studies showing that wind farms have a non-negligible impact on flying animals, mainly related to collisions with turbines of birds and insects and barotrauma in bats (Buchan et al., 2022; Smith and Dwyer, 2016; Thaxter et al., 2017; Voigt, 2021; Wang et al., 2015). These negative impacts are harsher when wind power generation facilities are poorly designed, located or managed (Gauld et al., 2022). Rehbein et al. (2020) have shown considerable overlap between renewable energy (in particular wind) facilities and important conservation areas on a global scale. Over the coming decades, the expected expansion of the protected area network to meet conservation targets will occur alongside the rapid deployment of wind power generation infrastructure to meet emission reduction goals, exacerbating potential conflicts (Dunnett et al., 2022a).

In this study, we provided a cross-continental-scale assessment of the exposure to onshore wind turbines of a trans-Saharan migratory raptor, the lesser kestrel *Falco naumanni*, throughout its annual cycle. An analysis of wind turbine exposure in this taxon may be of broader significance because: 1) it is a species of European conservation interest [listed in Annex I of the "Birds Directive" (2009/147/EC) and Annex II of Bonn Convention] that suffered steep population declines and range contraction in the second half of the 20th century, from which it has yet to recover (BirdLife International, 2017; Iñigo and Barov, 2010); 2) it is a migratory species that moves across continents, requiring a trans-national approach to conservation (Lopez-Ricaurte et al., 2021; Sarà et al., 2019); 3) it is a colonial species, implying that large aggregations of individuals (largest colonies can host up to 1000 breeding pairs) can be exposed to the same local threat, often occurring in restricted areas (Cecere et al., 2018; Di Maggio et al., 2015; Morinay et al., 2023); 4) due to its flight mode and behaviour (see Materials and Methods), it is a relatively frequent victim of wind turbines, which may threaten the persistence of local populations (Thaxter et al., 2017; Duriez et al., 2023); 5) it is a flagship species for biodiversity conservation in agro-ecosystems (Assandri et al., 2023); 6) its size is large enough to allow tracking with GPS tags, providing valuable information about both small- and large-scale movements which may result in spatial and temporal variability in exposure to wind turbines.

Among the complex causes of lesser kestrel decline, climate warming is predicted to negatively affect the species at both breeding grounds in Southern Europe and non-breeding grounds in sub-Saharan Africa (Catry et al., 2015; Corregidor-Castro et al., 2023; Mihoub et al., 2010, 2012; Rodríguez and Bustamante, 2003), while at the same time promoting expansion to more northern cooler regions (Morganti et al., 2017). It is thus relevant to understand if the transition to renewable energies, like wind energy, is compatible with the conservation of this species. To date, relatively little evidence exists on the effects of wind power generation infrastructure on lesser kestrel populations. Yet, a recent meta-analysis showed that it is among the most sensitive bird species to wind turbine collisions, with an estimated 0.15 collisions/turbine/year (Thaxter et al., 2017). In Spain, out of 1746 lesser kestrels admitted to wildlife recovery centres during 2008–2018, 120 (6.8 %) were due to direct collisions with wind turbines and 536 (31 %) were due to collisions with power lines, often associated with wind power generation infrastructure (García Tapia and López-Jiménez, 2023). Moreover, a recent study conducted in southern France (Duriez et al., 2023) shed light on how additive mortality induced by collisions with wind turbines affects demography, ultimately threatening local population persistence in the long term.

We compiled a comprehensive dataset of breeding colonies (including location and size) from the whole European distribution of the species. We then assessed the proportion of the European lesser kestrel breeding population potentially exposed to collision with onshore wind turbines and identify areas of higher exposure for the three main European biogeographical populations (i.e., Iberian, Italian, and Balkan; Sarà et al., 2019). We further assessed whether the exposure to wind power generation infrastructures during breeding was mitigated

by the Natura 2000 Network (hereafter N2k). N2k is a pan-European network of protected areas established to preserve threatened and/or ecologically important habitats and species, including those listed in Annex I of the Birds Directive. Hence, we might expect that breeding lesser kestrels exploiting foraging areas surrounding colony sites (mostly within 5–10 km from the breeding site; see Materials and Methods) that are more extensively designated as N2k protected land should be less exposed to collision than others, i.e. the number of turbines within colony's foraging areas should be lower the more a colony is surrounded by N2k protected land.

Furthermore, we gathered a large GPS-tracking dataset consisting of 354 individuals breeding in four countries, several of which tracked for multiple years. GPS-tracking data are increasingly used to assess the potential impact of renewable energy generation facilities on birds and represent an unprecedented opportunity to support evidence-based conservation of large- to medium-sized avian species (Buchan et al., 2023; Gauld et al., 2022; Largey et al., 2021; Oppel et al., 2021). With these data, we tested for differences in the exposure to wind turbines among the three European biogeographical populations and different

phases of the annual cycle, which take place within a latitudinal range spanning >35° latitude across Europe and Africa. We expected greater exposure to wind turbines during migration and pre-migratory phases, when kestrels move furthest distances across Europe and north Africa, than during the non-breeding phase in sub-Saharan Africa, where the development of wind farms is still in its infancy and wind turbines are nearly absent (Dunnett et al., 2020). Wind turbine exposure during the breeding season relative to other annual cycle phases is instead more difficult to predict because it is strongly dependent on the location of breeding colonies (and their associated foraging ranges) with respect to wind turbines location.

Our overarching goal is to provide operational knowledge to identify areas of potential conflict between lesser kestrel conservation and wind power generation infrastructures. Our results could be useful to prevent further conflicts between biodiversity conservation and renewable energy production.
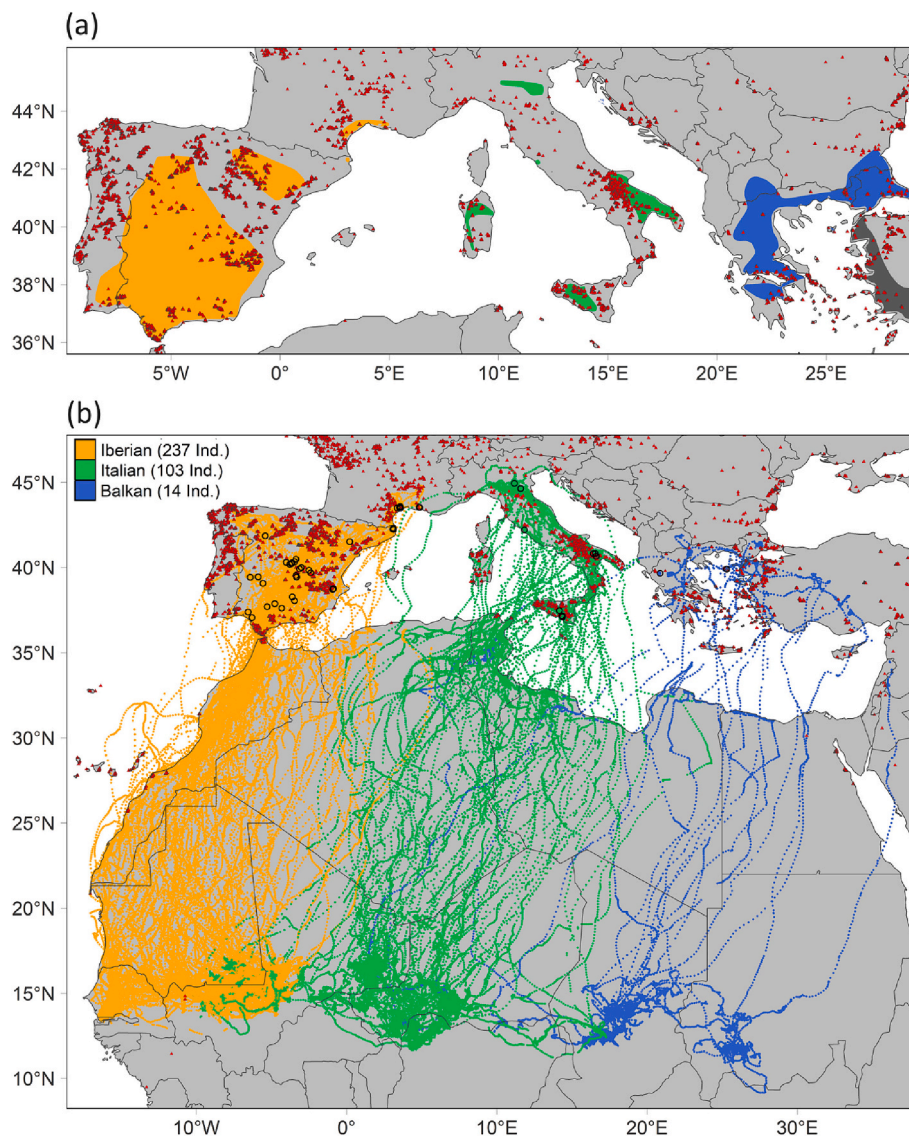

Fig. 1. a) European breeding range of the lesser kestrel (from Bazzi et al. in prep.) and b) annual movement of GPS-tracked individuals (N = 354; this study) according to the three biogeographical populations defined in Section 2 (Materials and Methods). The distribution of wind turbines (red triangles) is also shown (from Dunnett et al., 2020). In b) black circles represent colonies of origin of tracked individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Species and geographical context

The lesser kestrel is a small (approximately 150 g) diurnal, colonial and trans-Saharan migratory raptor. It is a secondary cavity nester that usually breeds below roof tiles, holes in ruins or ancient buildings and in rocky cavities (Morinay et al., 2021). It currently breeds across southern Europe (Gameiro et al., 2020; Kmetova et al., 2020), North Africa, the Middle East, and Central Asia (Ferguson-Lees and Christie, 2001). The vast majority of the European population spends the non-breeding season in the Sahel and reaches the European breeding grounds in February/March (Sarà et al., 2019). Females start laying between April and early May (usually 3–5 eggs) and chicks fledge from late June onwards.

According to its migration flyways and migratory connectivity analyses (Sarà et al., 2019), we assigned European lesser kestrels to three distinct biogeographical populations, largely coinciding with the three main peninsulas: 1) Iberian (i.e., Portugal, Spain, and southern France), 2) Italian (Italy), and 3) Balkan (Greece) (Fig. 1). These regions host 99.8 % of the whole EU population (BirdLife International, 2017).

2.2. Wind turbine data

Wind turbine data were obtained from Dunnett et al. (2020), the first global, open-access, harmonised spatial dataset of wind power generation infrastructures based on OpenStreetMap data. This dataset provides the location of each turbine within a wind farm around the globe for the year 2020 (Fig. 1). Given that OpenStreetMap data is derived from a citizen science project, socioeconomic factors could affect the reliability and accuracy of the data in different regions of the world. To this end, Dunnett et al. (2020) performed a technical validation suggesting that although country governance and land area contribute to explain variability in OSM observations, the observed pattern is largely reflective of the true distribution of wind power generation infrastructure.

This dataset is increasingly being used for the large-scale assessment of the impact of wind power generation infrastructures on biodiversity (Buchan et al., 2022; Dunnett et al., 2022a), including GPS tracking studies of birds (Buchan et al., 2023; Oppel et al., 2021).

2.3. Colony size data

Data on colony location and size (number of pairs) were obtained from the literature (Bustamante et al., 2020; Gustin et al., 2018; Morganti et al., 2017) and unpublished reports of national and regional counts (Table S1). For each colony, we considered all the data available for the period 2016–2021, using mean values for multi-year counts. For some large urban colonies, the number of breeding pairs referred to single clusters (e.g. colony sectors or single buildings with nestboxes; Morinay et al., 2023) within the colony. In those cases, we attributed individual clusters to the same colony when they occurred within a given urban area (defined according to the CORINE Landcover 2018) in the same municipality. We then summed the number of pairs of each cluster to obtain colony size and used the centroid of the clusters as the colony location. Breeding sites with only a single breeding pair (N = 624, corresponding to 2.3 % of all breeding pairs) were discarded from the analysis because they are generally occupied discontinuously (our pers. obs.).

2.4. GPS tracking dataset

The GPS tracking dataset generated for this study was derived from several projects carried out in Spain, France, Italy, and Greece between 2014 and 2021 and focused on breeding adults. Lesser kestrels were mostly captured by hand at nest boxes/cavities and equipped with GPS tags, usually a few days before egg hatching or during the nestling-rearing phase. In France, lesser kestrels were captured at the foraging grounds using bal-chatri traps. In Spain, some of the adults were caught close to the colony using bal-chatri or mist-nets. Solar-driven, remote-downloading GPS-UHF tags (<5 % of body mass) were deployed with permission from national/local authorities and according to animal welfare legislation (further details in Supplementary MM1). We discarded individuals with either <100 GPS locations or <10 tracking days, which were equipped with malfunctioning devices in most cases (Assandri et al., 2022). GPS accuracy was not available for all the individuals, but when the number of satellites was provided, we considered only those GPS locations with >5 visible satellites (Gauld et al., 2022).

For each individual, tracks were visually inspected and each GPS location was assigned to one of the following 5 key phases of the annual cycle, from the breeding phase when the bird was first tagged to the end of the subsequent pre-breeding migration, namely: (1) breeding, (2) pre-migratory, (3) post-breeding migration, (4) non-breeding and (5) pre-breeding migration (details in Supplementary MM2 and Fig. S1). The final dataset includes individuals tracked for a mean (± SD) of 1.33 ± 0.57 (range: 1–4) annual cycles, and phase delimitation was repeated for each annual cycle.

Considering that the GPS sampling rate applied in different projects or different annual cycle phases was variable (mostly between 10 and 30 min), we linearly interpolated our dataset at 30 min using the function *redisltraj* in the R package *adehabitatLT* (Calenge, 2006). Temporal gaps >120 min between consecutive locations were not interpolated and thus not included in further analyses. Lesser kestrel tracking data were filtered for spatial and temporal duplicates and unreliable speed (>50 km/h during breeding and 90 km/h during the other phases) by applying the *SDLfilter* R package (Shimada et al., 2016). Lesser kestrels generally do not fly at night, except during migration across ecological barriers (Liminana et al., 2012; Lopez-Ricaurte et al., 2021). Hence, we removed all night positions except for migration phases. To this end, we identified night and day locations based on local astronomical twilights using the R package *suncalc* (Thieurmel and Elmarhraoui, 2022). In addition, only for the breeding phase, we removed locations within 100 m from the nest (or putative nest location based on visual inspection of tracks), which most likely referred to incubating/resting individuals.

Our final dataset consisted of 1,302,755 GPS locations from 354 individuals (200 from Spain, 37 from France, 103 from Italy, and 14 from Greece) breeding in 51 colonies (29 in Spain, 8 in France, 12 in Italy, and 2 in Greece) that were tracked over a median of 70 days (min-max: 10–1117) (Fig. 1b; Appendix S1 and S2).

2.5. Statistical analyses

2.5.1. Colony-level exposure to wind turbines

Throughout the breeding season, lesser kestrels behave as central place foragers, traveling from the colony to foraging patches surrounding it, generally within a 5–10 km buffer (Assandri et al., 2023; Cecere et al., 2020; Ramellini et al., 2022). Previous studies have shown that this foraging range increases with colony size (Cecere et al., 2018). Based on data collected for a different study, we estimated the radius of the foraging buffer (in m) for a colony of a given size based on the following equation: radius of the foraging buffer (m) $= 1659.5 \times \log_{10}(\text{colony size}) + 4348.2$. This equation was derived from the analysis of 3920 maximum daily distances from the nest site of 157 nestling-rearing adult lesser kestrels breeding in 22 colonies across Europe (authors unpubl. data), under the assumption that the maximum daily distance in a sample of nestling-rearing individuals can be equated to the radius of the foraging buffer. The predicted radius was in line with the observed variation in the extent of the foraging range according to colony size in this species (e.g. Cecere et al., 2018; Assandri et al., 2023). We then counted the number of turbines within the foraging buffers centred on the coordinates of each colony as a metric of colony-level exposure to wind turbines.

To assess whether the N2k extent around colonies mitigated wind turbine exposure, we determined the proportion of foraging buffer covered by N2k sites per colony (percentage N2k hereafter) using the N2k cartography updated to 2020 (https://sdi.eea.europa.eu/data/b1777027-6c85-4d19-bdf2-5840184d6e13?path%253D%25252FNatura2000_end2020_shp).

We modelled separately data from the Iberian and Italian populations because exploratory analyses showed that the distribution of the number of turbines within the foraging buffer varied considerably among populations. Balkan data could not be modelled as only two colonies (out of 114) had wind turbines within the foraging buffer. Data from the Iberian population were modelled using a negative binomial generalized linear model (GLM), including the number of wind turbines within the foraging buffer as a dependent variable, and the percentage N2k as a predictor. Data from the Italian population were modelled with a similar negative binomial GLM, but adding a zero-inflation component (i.e. ZINB GLM) because of an excess of zeroes in the data. The percentage N2k was included as a predictor also in the binomial component of the ZINB GLM. In both models we included colony size (number of breeding pairs) in the 'weight' argument, hence giving more importance to larger colonies; in practice, such weighting returned the estimated exposure to wind turbines per breeding pair.

GLMs were fitted with the *glmmTMB* package (Brooks et al., 2017) and model fits were checked with the R package *DHARMa* (Hartig, 2021). Significance was assessed by likelihood ratio χ^2 tests performed with the package *car* (Fox and Weisberg, 2011) followed by Tukey *post hoc* tests performed with the *emmeans* package (Lenth, 2020).

2.5.2. Variation in exposure to wind turbines among annual cycle phases

To assess variation in the exposure to wind turbines among different annual cycle phases, we used an individual-level approach. We first measured the distance between two consecutive GPS locations of individual tracks and applied a circular buffer equal to this distance at each location. This represents the potential area of movement which a kestrel leaving location *A* could have encountered before reaching the subsequent location *B*. We then assessed if at least one wind turbine occurred within each of these buffers. When this happened, we considered the individual at such location as exposed to wind turbines. We then quantified how many locations were exposed to wind turbines for each individual during each annual cycle phase.

Assessing exposure to wind turbines in flying animals implies considering the vertical dimension (Gauld et al., 2022; Morant et al., 2024). If the flight altitude of a bird is well above (or well below) the rotor swept zone, a given location with a wind turbine within the buffer should not be regarded as exposed to that turbine (Gauld et al., 2022; Morant et al., 2024). Lesser kestrels generally fly at relatively low altitude above ground level, except possibly during their autumn migration cruising flights (Sarà et al., 2021). Using GPS-derived flight altitudes obtained from some of our tracking devices, we observed that approximately 90 % of all locations were within 250 m above ground level (a.g.l.) (i.e. within a rotor swept zone of 210 m a.g.l. as in Gauld et al., 2022 and considering a 40 m GPS altitudinal error; details in Supplementary MM3), with no major differences between annual cycle phases (Fig. S2, Table S2 and S3). The GPS altitudinal error does not allow an evaluation of whether the species consistently flies below the risk threshold (i.e. 15 m; Gauld et al., 2022). Nevertheless, flight altitude data (see Supplementary MM3), together with authors' personal observations, indicate that the species mostly flies above 15 m a.g.l. during commuting and traveling flights. Hence, for simplicity, all locations were considered as potentially exposed to wind turbines based on flight altitude, which may have led to negligible overestimation of exposure during all annual cycle phases.

We estimated the average number of locations exposed to wind turbines in different annual cycle phases and geographical populations by fitting a generalized Poisson GLMM (the best option to deal with the under-dispersion of the data) with the overall count of locations exposed

to wind turbines as a response variable. This approach allowed us to account for different annual cycle phase durations (see Supplementary MM2). As predictors, we included geographical population, phase (4-level-factor: pre-breeding migration, breeding, pre-migratory movement, and post-breeding migration), and their interaction, plus individual and colony identity as random intercept effects. The non-breeding phase was excluded from the analysis as wind turbine exposure for the Italian and Balkan individuals was zero.

Significance was assessed by Wald χ^2 tests (Fox and Weisberg, 2011) followed by pairwise Tukey *post hoc* tests performed with the *emmeans* R package (Lenth, 2020). All statistical analyses were performed within the R (ver. 4.2.1) computing environment (R Core Team, 2022).

3. Results

3.1. Colony-level exposure to wind turbines

Our final dataset included colony size data from 1837 colonies across five countries, collected during 2016–2021, hosting a total of 26,324 pairs: 1513 colonies from the Iberian population (10,895 pairs; Spain, Portugal and France), 210 from the Italian population (9136 pairs), and 114 from the Balkan one (6293 pairs). Areas showing a higher exposure to wind turbines were located in south-eastern Italy, especially the Appulo-Lucanian region (Fig. 2). Other high-exposure regions were scattered in Southern Andalusia, Castilla, and Navarra (Spain), Southern France, and Sicily (Fig. 2).

Overall, 26.2 % of the European population breeds in colonies with at least one turbine within the foraging buffer, with large differences among geographical populations, being negligible for the Balkan population (<1 %), low for the Iberian (10 %), and considerably high for the Italian one (62.8 %) (Table 1). At the country level, the highest values were observed in Italy, whereas none of the Portuguese colonies had any turbine within the foraging buffer. Almost 40 % of the French lesser kestrel pairs have at least one turbine within the foraging buffer, a considerably larger value than Spain (about 9 %). Contrary to expectations, wind turbine exposure in Italian lesser kestrels (both the number of turbines within the foraging buffer and probability to have at least one turbine within the buffer) increased with the increase of N2k area within the foraging buffer (Fig. 3; Table S4). This was not the case for the Iberian population, for which the percentage N2k did not significantly covary with the number of wind turbines within the foraging buffer (Fig. 3, Table S4).

3.2. Variation in exposure to wind turbines among annual cycle phases

The geographical areas in which GPS-tagged lesser kestrels were most exposed to wind turbines were Spain (particularly the strait of Gibraltar, the regions of Andalusia, Castilla La-Mancha, and Aragón), south-eastern France, most of the Italian peninsula (particularly southern Italy and Sicily), and the eastern Aegean (Fig. 4). However, exposure varied considerably according to the annual cycle phase. Specifically, during breeding, higher exposure areas were detected in south-eastern France and southern Italy (Fig. S3), whereas during the pre-migratory phase, areas with higher exposure included central-western Iberia and western Sicily (Fig. S4). During both migrations, the Strait of Gibraltar represented a critical spot for the Iberian population, along with the southern portion of the Iberian Peninsula (Fig. S5 and S6). For the Italian population, southern Italy, Sicily, and Malta were the areas with the highest exposure during migration (Fig. S5 and S6). In addition to these areas, during pre-breeding migration, further critical areas for the Iberian population included the Moroccan and the Western Sahara coast in front of the Canary Islands, and Cape Bon and Cape Tarf/Cape Blanc in Tunisia, along with the central-eastern Aegean (Fig. S5). Unless for a few individuals that overwintered in Andalusia and one small area in Mali (Fig. S7), no turbine exposure was detected during the non-breeding phase due to the lack of wind farms in the non-breeding grounds of
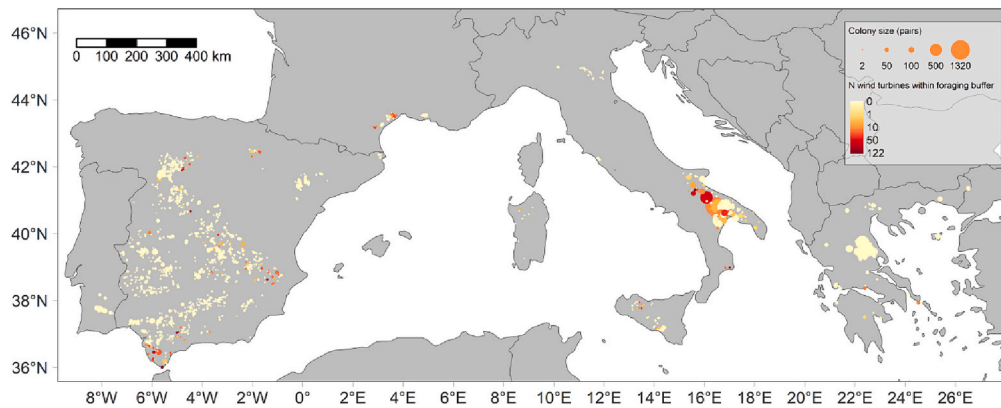
Fig. 2. Lesser kestrel colony exposure to wind turbines. Dot size represents the size of the colony (number of breeding pairs), while dot colour shows the number of wind turbines within the colony foraging buffer. Darker colours imply a higher exposure to wind turbines. N = 1837 colonies; 26,324 breeding pairs.

Table 1
Population-level exposure of breeding lesser kestrels to wind turbines expressed as the percentage of the breeding population (percentage of breeding pairs) with at least one wind turbine within the estimated foraging buffer. Data are presented separately for biogeographical population and country and sorted by decreasing values of exposure. Total population size (breeding pairs) is also provided.

	% population	Population size
Biogeographical population		
Italian	62.8	9136
Iberian	10.1	10,895
Balkan	0.9	6293
Country		
Italy	62.8	9136
France	39.5	552
Spain	9.2	9589
Greece	0.9	6293
Portugal	0.0	754

the European lesser kestrel population.

Exposure to wind turbines did not significantly vary among populations ($\chi^2 = 3.2$, d.f. = 2, $p = 0.20$) but significantly varied among annual cycle phases ($\chi^2 = 28.9$, d.f. = 3, $p < 0.001$). The interaction between annual cycle phases and population was also significant ($\chi^2 = 80.9$, d.f. = 6, p < 0.001) (Fig. 5). The highest level of exposure occurred generally during pre-breeding migration (and during migration periods in general) and the lowest during breeding (Fig. 5). The Italian population had similar values of exposure during all annual cycle phases, whereas both the Iberian and Balkan populations had significantly lowest levels of exposure during breeding compared to at least one of the pre-migratory/migratory phases (Fig. 5).

4. Discussion

Strategies and policies aimed at mitigating the impact of climate change, such as the development of green energy infrastructure, may potentially clash with biodiversity conservation targets (Jackson, 2011; Kati et al., 2021; Neri et al., 2019; Santangeli et al., 2016). We provide an assessment of the exposure to onshore wind farms in European lesser kestrels using both colony- and individual-level approaches. This was achieved by gathering information from two large datasets compiled *ad hoc* for this study: colony size (>1800 colonies) and one of the largest GPS-tracking datasets ever generated for an avian species (>350 individuals).

The first remarkable outcome of our study was that 26 % of the European lesser kestrel breeding population had at least one wind turbine within the foraging buffer. This represents a pressing conservation issue, considering that turbines can have a detectable impact on lesser kestrel mortality due to collisions. In Southern France, 60 lesser kestrel carcasses were reported over 11 years at a single wind farm consisting of 31 turbines located within 10 km of five colony sites. Correcting for carcass persistence and detection biases would make these figures three times higher (Duriez et al., 2023). Demographic modelling suggested that such a mortality rate, induced by a single wind farm, has led to a reduction of the local population size by 22 % in 15 years.

Furthermore, we showed that the three European lesser kestrel populations considerably differed in their exposure to onshore wind turbines. Italian breeding pairs had on average many more wind turbines within their foraging range than Iberian ones, which in turn have slightly more turbines than Balkan ones.

At the population level, almost two-thirds of the Italian breeding population (63 %) had at least one wind turbine within the foraging areas surrounding colony sites. This figure was considerably lower for Iberian (10 %) and even more so for Balkan colonies, where it dwindled to <1 %. This finding suggests that each country should prioritize different measures to mitigate (or not increase) the risk of collision with wind turbines. Italian, and to a lesser extent French authorities, should for instance focus more on mitigation of the potentially detrimental effect of existing wind farms by e.g. installing Automatic Detection Systems to curtail turbines when a given threshold of bird activity is detected around wind farms (Happ et al., 2021), as well as prioritize decommissioning wind turbines at the end of their operational life (Topham et al., 2019) in areas surrounding larger colonies, whereas Portuguese, Spanish, and Greek authorities should rather focus on identifying those areas where wind farms development allows to keep the risk of collision low (as is currently the case) and include sustainable spatial planning criteria in the development of new wind farms (Kati et al., 2021).

Dunnett et al. (2022a) predicted limited overlap of the area of expansion of renewable energy infrastructures and protected areas; however, this result was debated (Dunnett et al., 2022b; Niebuhr et al., 2022; Pérez-García et al., 2022), as it is likely not enough to buffer the decline of species of conservation interest, such as migratory taxa negatively affected by wind turbines, which also exploit non-protected areas. The N2k network covers 18 % of European land territory and is likely the most extended network of (at least partly) protected areas worldwide (Orlikowska et al., 2016). The network aims to ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the Habitats and the Birds Directives, the latter of which includes the lesser kestrel among species of European conservation interest. The effectiveness of the N2k network in protecting European biodiversity is debated, as scientific assessments provided mixed evidence (Donald et al., 2007; Santana et al., 2014). However, the distributions of a large proportion of threatened species of mammals,
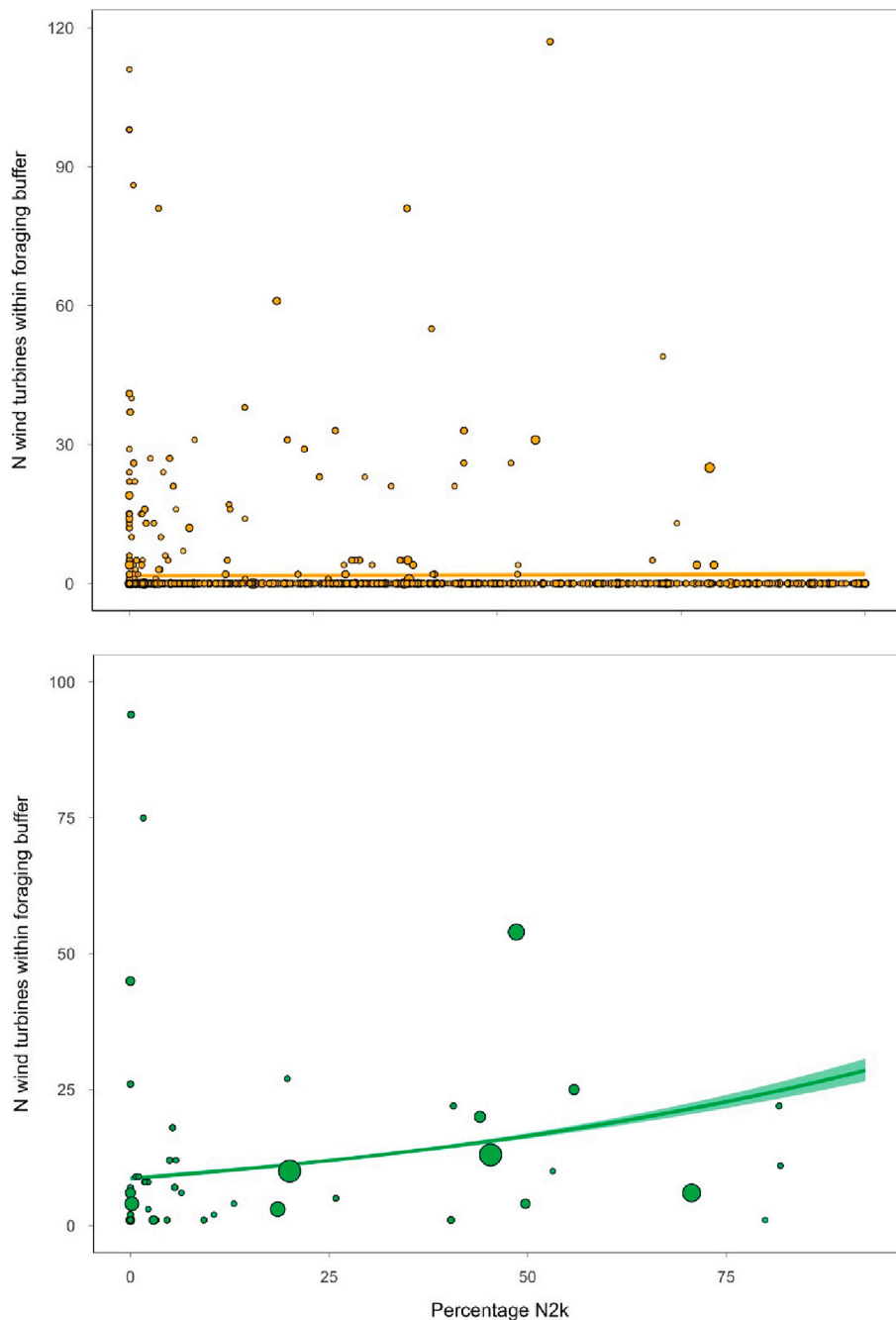
Fig. 3. Model-predicted (with 95 % confidence bands) exposure of lesser kestrel breeding pairs to wind turbines (number of turbines within the foraging buffer) according to the percentage Natura 2000 area within the foraging buffer. Predictions were derived from a negative binomial GLM (upper panel, Iberian population) or the count part of a ZINB GLM (lower panel, Italian population) (model details in Table S4). Dots represent colonies and dot size is proportional to the (square root-transformed for ease of representation) number of breeding pairs at colonies (colonies with no wind turbines within the foraging buffer are omitted for the Italian population). The effect of percentage N2k on the number of wind turbines within the foraging buffer is statistically significant (p < 0.05) for the Italian population only (see Table S4).

birds, and reptiles were largely encompassed by the N2k network (Trochet and Schmeller, 2013), with positive effects also on species not listed in the annexes of the EU Directives (Princé et al., 2021). Moreover, the establishment of the N2k network seems to have attenuated - although not reversed - the declines of farmland bird populations and other common species (Gamero et al., 2017). Differently from our predictions, our results suggest that environmental regulations governing N2k, which vary broadly among countries due to different national legal frameworks (Kati et al., 2015), did not prevent building wind power generation infrastructure around lesser kestrel breeding colonies.

Rather, the species' foraging grounds, including vast, open extents of pseudo-steppic cereal farmland (Morganti et al., 2021), were apparently highly favourable sites for the deployment of wind turbines (e.g. in south-eastern Italy). Yet, it should also be mentioned that at least in Italy the construction of any further wind farm within N2k sites has been banned since 2007 (Decreto Ministeriale 17 ottobre 2007 on minimal conservation measures to be adopted within Italian N2k sites).

The analysis of tracking data showed clear evidence of differential exposure to wind turbines according to geographical populations, annual cycle phases and geographical areas. When evaluating these
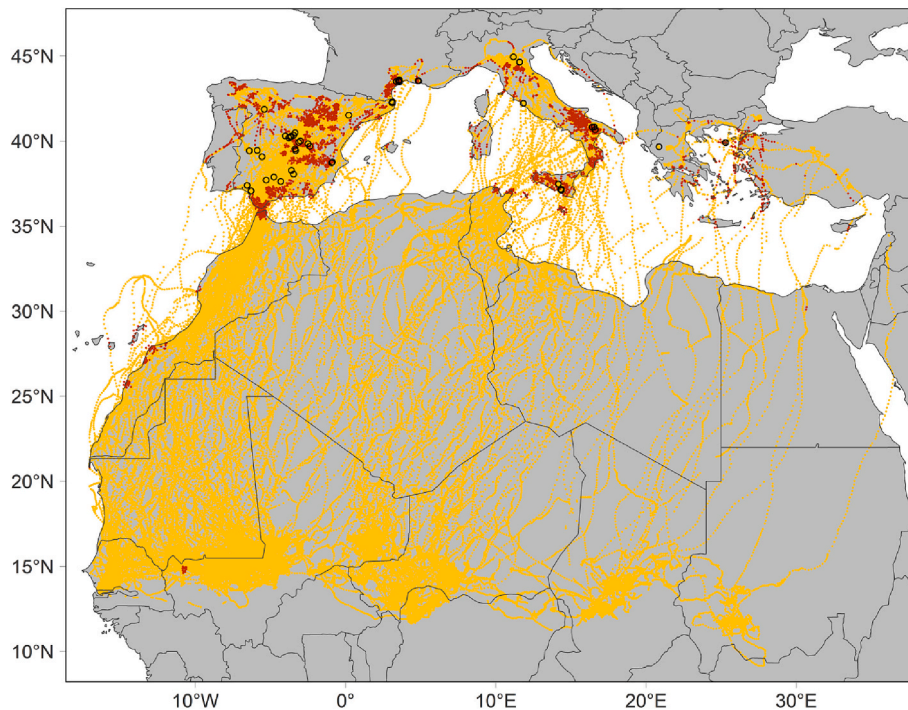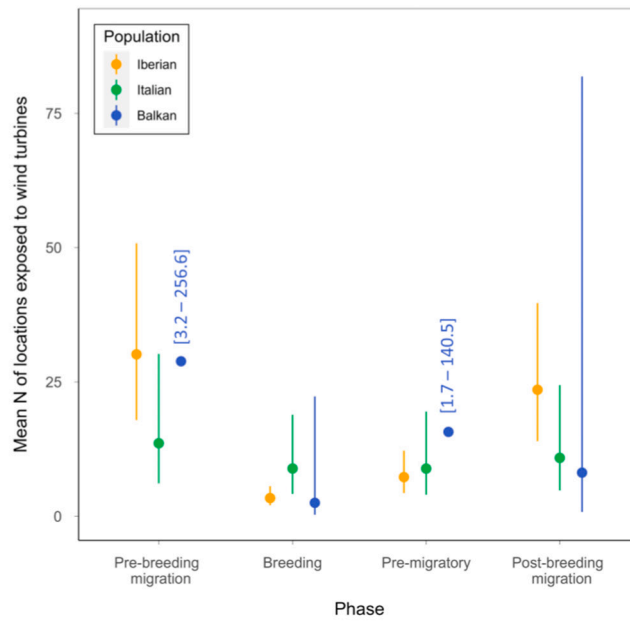
Fig. 4. Map showing movements of lesser kestrels between southern Europe and sub-Saharan Africa through their annual cycle based on GPS tracking. Red dots represent the locations exposed to at least one wind turbine according to the methodology detailed in Section 2.5.1. Yellow dots represent locations not exposed to any turbine. Black circles represent the colonies of origin of the tracked individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

findings, we need to take into account that there are at least two factors suggesting that exposure estimates from our tracking data might be conservative. First, we analysed breeding adult only; adults are more experienced than juveniles (Sergio et al., 2019, 2022) that are known to be more threatened by wind turbines (de Lucas et al., 2012), although not in all species (Marques et al., 2014). Second, we relied on archival GPS tags, implying that we were able to get data only from birds that survived from one year to the following one and that successfully returned to the colony, thus excluding all birds that died (for instance due to collision) during any of the phases of the annual cycle. However, regarding difference among geographical populations, estimates for the breeding phase corroborated colony-level analyses, showing higher levels of exposure in Italian individuals vs. Iberian and Balkan ones. Overall, exposure during the breeding phase was lower than during other phases, except for the Italian population that showed relatively high values of exposure across all phases. According to our predictions, the more mobile phases of the annual cycle, i.e. migrations and pre-migratory phase, were those with the highest exposure levels. This was particularly true for pre-breeding migration. Areas more exposed in this phase include well-known migratory bottlenecks such as the Strait of Gibraltar (Martín et al., 2018). Additionally, previously undocumented areas such as Cape Bon in Tunisia came into focus, underscoring the significance of GPS telemetry in evaluating potential conflicts between renewable energy infrastructure and biodiversity conservation. Tunisia is an interesting example of a potentially harsher future conflict area between renewable energy production and biodiversity, as a national target was set to increase the quota of electricity supply from renewable energy to 100 % by 2050 (Timmerberg et al., 2019). Furthermore, most of the Italian lesser kestrels cross the Strait of Sicily and the central Tyrrhenian Sea during migrations (Sarà et al., 2019; this study); to date, this area does not have offshore wind farms, but this figure is expected to rapidly evolve due to the forecasted deployment of large offshore wind farms (Soukissian et al., 2017), which are well known to impact migratory birds (Hüppop et al., 2006; Jacobsen et al., 2019).

Our analyses further showed that the Italian and Balkan populations were non-negligibly exposed to wind turbines during the pre-migratory phase, the least known part of the lesser kestrel annual cycle. Tracking data showed that during this phase many individuals moved considerably across many countries. Moreover, they oftern congregate at large roost sites hosting individuals from different areas (Bounas et al., 2018; De Frutos and Olea, 2008; Sarà et al., 2014). This implies that few wind farms located in areas of pre-migratory aggregation can potentially negatively affect populations from different countries. Exposure was currently close to zero during the non-breeding phase, when birds are in the sub-Saharan belt where virtually no wind farms occur. The only population which was limitedly exposed during such phase was the Iberian one because four Spanish GPS-tagged birds overwintered in Southern Spain and partially in Morocco. Both non-migrating or short-distance migrating lesser kestrels (Negro et al., 1991) and wind farms (Jung and Schindler, 2022) are expected to increase in response to climate change, potentially leading to increased exposure to wind turbines during the non-breeding phase.

Renewable energy development represents the main road identified by the Paris Agreement to mitigate the disruptive effects of climate change on ecosystem functioning globally(United Nations, 2015). However, a careful spatial planning of new renewable energy infrastructure is required to reduce the impacts on landscapes and biodiversity while maximizing its climate benefits in the immediate future (Baruch-Mordo et al., 2019; Kati et al., 2021; Kiesecker et al., 2019). Unfortunately, planning of renewable energy expansion and actions focusing on biodiversity conservation are too often developed separately (Köppel et al., 2014; Rehbein et al., 2020). We believe that outputs from our study, as well as our analytical framework, can be effectively exploited by conservation practitioners and renewable energy stakeholders, including national and local authorities as well as energy companies, to proactively address potential conflicts arising between bird of prey conservation and the anticipated expansion of wind energy infrastructure in the near future.

Fig. 5. Estimated mean (± 95 % CI) number of locations exposed to wind turbines from a generalized Poisson GLMM model for three lesser kestrel biogeographical populations and four annual cycle phases. 95 % CI for two Balkan population estimates were reported within square brackets above the point estimate for graphical reasons. Pairwise significant differences are shown in the table as resulting from Tukey *post hoc* tests. *: p < 0.05; ** p < 0.01; *** p < 0.001; NS: p ≥ 0.05.

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Methodology, Data curation. **Jocelyn Champagnon:** Resources. **Federico De Pascalis:** Writing – original draft, Resources, Methodology, Investigation, Data curation. **Javier de la Puente:** Resources, Project administration, Funding acquisition, Data Curation, Writing – review & editing. **Juan Carlos del Moral:** Resources. **Olivier Duriez:** Writing – review & editing, Resources, Funding acquisition, Data curation. **Angelos Evangelidis:** Resources. **João Gameiro:** Writing – review & editing, Resources, Data curation. **Daniel García-Silveira:** Resources. **Fernando Garcés-Toledano:** Resources, Funding acquisition. **Frédéric Jiguet:** Writing – review & editing, Resources, Funding acquisition. **Panagiotis Kordopatis:** Resources, Funding acquisition. **Lina Lopez-**

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110592.

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