Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Windfarm collisions in medium-sized raptors: even increasing populations can suffer strong demographic impacts

O. Duriez[1], P. Pilard[2], N. Saulnier[3], P. Boudarel[4] & A. Besnard[1]

1 CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France
2 Ligue pour la Protection des Oiseaux – Mission Rapaces, Mas Thibert, France
3 Ligue pour la Protection des Oiseaux – Association Locale Hérault, Villeveyrac, France
4 DREAL Occitanie, Montpellier Cedex, France

Keywords
lesser kestrel; survival; mortality surveys; immigration rate; demographic analysis; population matrix model; windfarms; collision mortality.

Correspondence
Olivier Duriez, CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France.
Email: olivier.duriez@cefe.cnrs.fr

Editor: Karl Evans
Associate Editor: Lisanne Petracca

Received 13 December 2021; accepted 16 August 2022

doi:10.1111/acv.12818

Abstract

The impact of bird mortality by collision on windfarms has often been evaluated at the individual level, but rarely at the population level. The Lesser kestrel *Falco naumanni* is an endangered short-lived migratory raptor, susceptible to collision with wind turbines. We evaluated the impacts of windfarm turbine collisions on the demography of the largest lesser kestrel population in France. Using data from local monitoring of reproduction and windfarm mortality surveys, combined with capture-recapture ringing data at a nearby population, we quantified vital parameters of fecundity and survival in order to parameterize a matrix population model to study the viability of this population. The breeding success was high and varied in synchrony with survival probabilities. Between 2013 and 2020, 43 carcasses were found below wind turbines, and when accounting for carcass detection and persistence rates, the true mortality should approach 154 individuals in that period, i.e. 3% of the studied population was affected by collisions each year. The matrix model showed that the population growth observed was only possible if there was a constant recruitment of 26 immigrant individuals each year into the population. Without the excess mortality by the windfarm, we predict that this population would have 22% more breeding pairs than what was observed in 2020. Simulations over 30 years showed that, under the current immigration rate, the population should decline if the excess mortality exceeds 11%. If immigration ceases, the population would decline above 5% excess mortality per year. It is urgent to monitor and reduce the excess mortality by windfarm collisions that threatens this lesser kestrel population. More generally, we advocate the use of population matrix demographic models in impact assessment studies to avoid placing new windfarms close to rare species that could not sustain additional mortality by collisions.

Introduction

Wind farms have been identified as a major cause of bird mortality (Drewitt & Langston, 2006; De Lucas, Janss, & Ferrer, 2007; Arnett & May, 2016). Wind farms can affect bird species in two ways: directly via collisions with the wind turbines or indirectly via habitat loss for species that avoid wind farms (Marques *et al*., 2014; Perrow, 2017, 2019). However, very few studies have estimated the precise demographic impacts of wind farms on populations of the species concerned, even though such quantification is critical to make the issue seriously considered by politicians, stakeholders and the general public (May *et al*., 2019).

Collisions are additional mortalities induced by humans, hence considered in this paper as 'excess mortality'. Studying their impact on population dynamics is theoretically similar to studying population dynamics of species exploited by humans (e.g. management of fisheries or hunted species) (Williams, Conroy, & Nichols, 2002). Yet, to our knowledge, only a few studies have used population dynamics modelling to quantify the long-term impact of windfarm mortalities, on bat (Frick *et al*., 2017) or bird populations (Carrete *et al*., 2009; Schaub, 2012; Cook & Robinson, 2017). So far, these few studies conducted on birds concerned only long-lived species with slow pace of life (large raptors or seabirds) and thus especially sensitive to additional adult mortalities. Yet windfarm collisions could also affect shorter-lived bird species; however, their impact on population dynamics of such species has never been quantified.

In a global study aiming at assessing vulnerability to collision risk for all bird species worldwide, diurnal raptors (Accipitriformes and Falconiformes) were classified as the most vulnerable taxa to collision with wind turbines (Thaxter *et al*., 2017). The Lesser kestrel *Falco naumanni* was ranked at 40 out of 9500 species considered worldwide, with an estimated value of 0.15 collisions per turbine per year (Thaxter *et al*., 2017). The lesser kestrel collision risk has already been reported in several studies on windfarm mortality in Spain (Barrios & Rodriguez, 2007; Lekuona & Ursua, 2007; De Lucas *et al*., 2008). Although listed as Least-Concern status in Europe (BirdLife International, 2015), this migratory species is listed as 'vulnerable' in France (Moncorps & Siblet, 2016). After it being almost extirpated in the 1980s, a National Action Plan was approved for the lesser kestrel and implemented aiming at restoring population growth by reducing threats, as well as favouring the settlement of new populations (Pilard, 2011; Pilard *et al*., 2021). The largest population of lesser kestrels in France breeds in villages of the Herault department, within a 20-km radius around the Aumelas plateau, an important feeding area for falcons. The installation of a windfarm on this plateau in 2006 had the potential to negatively affect their population viability in the long term. The monitoring of mortality cases in this windfarm conducted between 2010 and 2021 confirmed this risk while finding about 60 carcasses of lesser kestrels in this area.

Here, we aimed at quantifying the long-term demographic impact of the additional mortality caused by collisions with wind turbines on this lesser kestrel population. As a first step, we estimated vital parameters (fecundity, survival rates), as well as immigration numbers, thanks to a detailed monitoring of the reproduction of the studied population and monitoring of marked individuals from a nearby population. In a second step, we estimated the mortality rates induced by the wind turbines, by using the results of the carcasses searches in the windfarm. In a third step, we ran population dynamics simulations, based on matrix population models, using the vital parameters previously estimated, to predict population trajectories over 30 years, accounting for immigration or not. The goal was to predict the maximum sustainable mortality rate that should not be exceeded in order to keep a growing population (population growth rate $\lambda > 1$).

Methods

Study site

The Aumelas plateau (Longitude: 3.64°, Latitude: 43.57°), with an area of 15 000 ha, is among the largest natural areas in the vicinity of Montpellier city (Herault, southern France) (Fig. 1). This karstic limestone plateau holds typical open shrub vegetation, with meadows of False-brome *Brachypodium retusum* and forests of Kermes oak *Quercus coccifera*, Evergreen oak *Quercus ilex* and White oak *Quercus alba*. The Aumelas plateau holds two Natura 2000 sites (Special Area of Conservation 'Montagne de la Moure et causse d'Aumelas', listed in 2006 – FR9101393; and Special Protection Area 'Garrigues de la Moure et d'Aumelas' listed in 2016 – FR9112037).

A windfarm of 31 wind turbines has been progressively built on Aumelas plateau in three phases: phase 1 with 11 wind turbines built in July 2006 (thus potentially affecting falcons in spring–summer 2007 onwards); phase 2 with 13 additional turbines built in March 2009; phase 3 with 7 additional turbines built in July 2014 (thus potentially affecting falcons in spring–summer 2015). The total power output of the windfarm is 62 MW. The wind turbines have a pole height of 56–78 m, blade length of 35–41 m, maximum height of 97–119 m, and the height between the ground and the bottom of the blade of 15–37 m.

Model species and population monitoring

The lesser kestrel is a relatively short-lived species of raptor, weighting between 140 and 160 g, mainly feeding on insects (orthopterans) (Cramp & Simmons, 1982). It is able to breed in its second calendar year. Breeding pairs arrive on breeding grounds in March and start breeding in April. Clutches (1–6 eggs) are laid in May and chicks fledge in July. From September, all individuals migrate to Africa, south of the Sahara Desert (Pilard, Bourgeois, & Sylla, 2017).

The French breeding population is located at the northern tip of the species' distribution range which extends through the Mediterranean area, from Iberia to the Middle East, out to southern Asia (Cramp & Simmons, 1982). While it was a widespread breeder in southern France until the 1950s, the French population declined down to a few pairs in the Crau steppic plain in the 1980s. Active protection and a reintroduction operation (2006–2010) in the Aude department allowed a recovery of the breeding populations into two nodes: the Crau and Aude plains (230 and 81 pairs, respectively, in 2020). A third node was created by natural recolonization in the Herault department since the 1990s (population size of 254 pairs in 2020), which is affected by the Aumelas windfarm. A distance of *c*. 100 km separates the Crau and the Herault populations (Fig. 1). In Crau, colonies are settled in stone piles and nest-boxes under barn roofs, while they are settled under house roofs in 13 villages in Herault and 6 villages in Aude.

Herault population monitoring

Monitoring kestrels in villages of Herault was performed at a distance (<50 m, using binoculars and telescopes), combining fixed observation points and adapted transects, aiming at locating each nesting site and quantifying the total number of fledglings. This monitoring was performed weekly between March and June and twice weekly in July (fledging period), for each colony. During these counts, the observers recorded the identity of the individuals marked in other areas in France or Spain (Supporting Information Appendix S1).

Because nests were very difficult to reach underneath the roofs of houses, only a few birds have been ringed in the Herault population (N = 107 from 2009 to 2020, only chicks

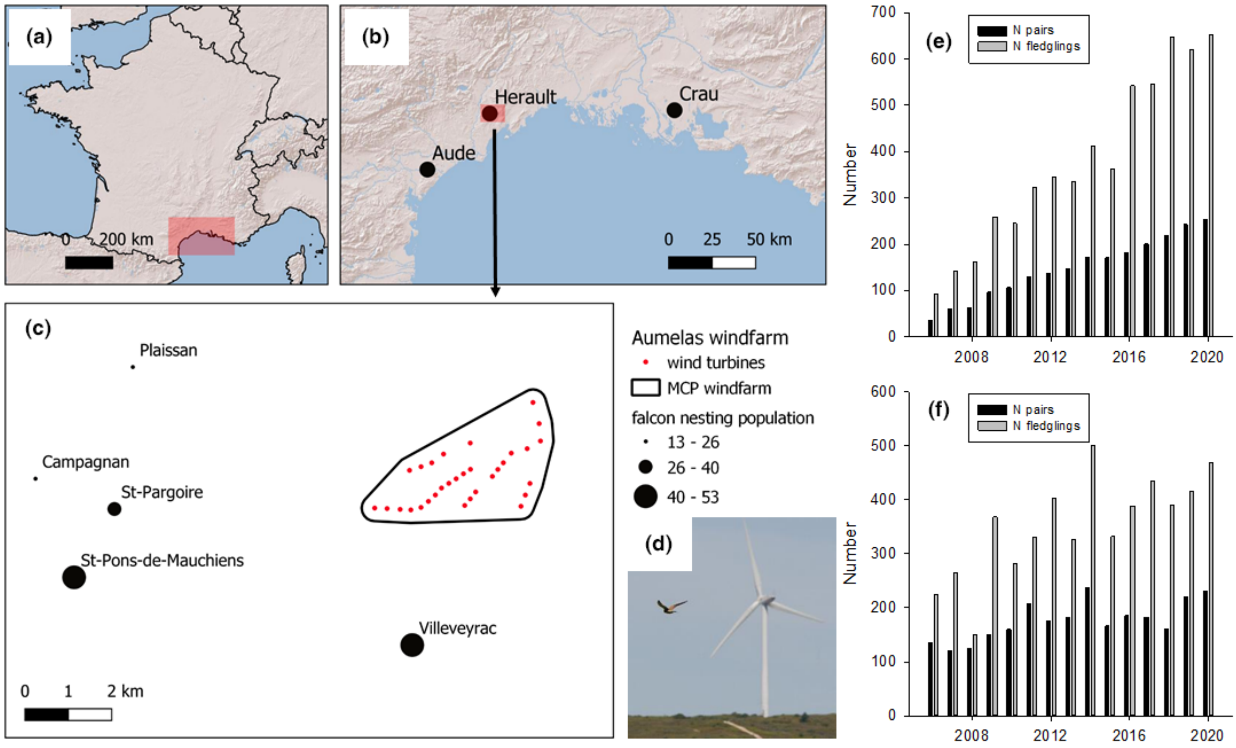

Figure 1 Maps of the study sites. The maps (a) and (b) show the locations of the three breeding populations of Lesser kestrels *Falco naumanni* in France (see text). The map (c) shows the locations of main breeding colonies in villages (black dots, with size varying according to the number of breeding pairs in 2020) and the Aumelas windfarm (red dots). The photo (d) shows a falcon close to Villeveyrac with Aumelas wind turbine in the background. The panels on the right show the annual numbers of breeding pairs and fledglings in the Herault population (e) and the Crau population (f).

fallen from nests and rehabilitated) and this sample size was too limited to allow robust survival analysis for this population.

The monitoring of dead falcon victims of collision at the Aumelas wind farm was performed twice weekly (from March to mid-November) between 2010 and 2020, and is explained in detail in Supporting Information Appendix S2. Briefly, the mortality monitoring was completed with specific protocols to estimate carcass persistence and detection rates performed yearly between 2013 and 2020. Once these sources of biases had been estimated, we estimated the number of casualties over the study period using Huso's (2011) formula that most efficiently accounts for biases in carcass detectability and persistence (see Supporting Information Appendix S3 for details).

Crau plain population monitoring

In Crau, where nests are easily accessible, a total of 4794 fledglings have been marked since 1994, using metal and colour rings (between 19 and 96 chicks each year before 2000, then on average 212 ± 57 chicks after 2000). Each week from April to July, observation sessions at all colonies allowed resightings of 224 ± 113 marked individuals on average each year, totalling 79 261 resightings between 1994 and 2020 (Pilard, Bourgeois, & Sylla, 2017). These data allowed estimating local survival rates as well as breeding proportion depending on the age of the individuals (see "Results" section).

Survival analyses

We estimated annual variations in survival rates in the Crau population because it was the only population with a sufficient sample size of marked birds. Previous studies showed that annual variations in survival rates in the Crau population were mainly driven by climatic conditions encountered in the west African wintering grounds (annual pluviometry in the Sahelian zone that drives orthopteran densities), with marginal contribution of events on breeding sites (Mihoub *et al.*, 2010). Since birds from Herault and Crau share the same wintering grounds (Pilard, unpublished telemetry results), we therefore assumed that the general patterns of variation in survival rates in Herault should be correlated with those in Crau.

Survival analyses were performed on the whole capture-recapture dataset from the Crau population from 1994 to 2020 (i.e. 27 annual capture occasions). We used a multistate model with three states (non-breeder, breeder and dead) and coded into three events (1: resighted as non-breeder; 2: resighted as breeder; 0: not resighted) with the first occasion being the marking of the individual as fledgling. The transitions from one state to another were split into two steps. First, we modelled the survival probability [i.e. the probability to move from live state (breeder or non-breeder) to dead state]. Then we modelled the probability to breed (i.e. the transition from breeder and non-breeder states to the breeder state). As Mihoub *et al*. (2010) did not detect large differences in survival probabilities between males and females, we did not account for sex differences in our models. Details of the model selection procedure are explained in Supporting Information Appendix S4.

We performed goodness-of-fit (GOF) tests for multi-state Joly-Move model (JMV) with program U-CARE (Choquet *et al*., 2009). We detected both transience and trap-dependence (see "Results" in Supporting Information Appendix S4) that indicated some heterogeneity in capture or survival rates. Transience was explicitly dealt with by the age structure we fitted in the models. Positive trap dependence was treated with an over-dispersion coefficient *c-hat*, estimated as the sum of values of χ^2 tests for each component of the GOF test, divided by the sum of degrees of freedom for each component of the test. Model selection was performed on the basis of Akaike Information Criterion (corrected for small sample size) and is derivative with *c-hat* (QAICc). A model was considered as significantly better to describe the data if the difference in the AICc values (ΔQAICc) was larger than 2. All the survival models were fitted using the program E-SURGE (Choquet, Rouan, & Pradel, 2008).

Fecundity analyses

The breeding proportion was defined as the proportion of individuals of each age class undertaking reproduction each year. This parameter could only be estimated in the Crau population, thanks to the large number of ringed individuals and intense monitoring to identify the parents in each nest (Mihoub, 2012). We estimated the proportion of breeders in Crau with the multi-state CMR model (presented above), which allowed estimating each year the probability of breeding. We assumed that these proportions were similar in Herault.

To estimate fecundity in Herault, we used the annual productivity, estimated as the number of fledglings divided by the number of pairs in Herault. However, the monitoring data from Herault did not allow distinguishing productivity from nests where the female was subadult or adult. Therefore, we used a subset of data from nest-boxes in Crau, where we could measure an average female productivity of 1.26 ± 0.77, that could be further differentiated between nests of subadult (productivity of 0.83 ± 0.73, i.e. 34% below the average; n = 174 clutches) and adult females (productivity of 1.40 ± 0.74, i.e. 11% above the average; n = 532 clutches) ($t_{704} = -8.85$, $P < 0.001$). We thus applied the same ratio to differentiate age-related female productivity in Herault.

Population dynamics analyses

Matrix population models

We used a female-only pre-breeding life cycle based on two age classes and three stages (Fig. 2). Individuals older than 1 all had the same survival rates S_1 for adults (following the results of the survival analysis: individuals in their first year in the matrix population model corresponded to the survival value of second calendar year birds in the survival analysis). The juvenile survival S_0 corresponded to the value of first year birds in the survival analysis. The fecundity was estimated by multiplying breeding frequency C and productivity B (number of female fledglings produced per female): the values of these parameters were lower for subadults compared to adults (Table 1).

Similarly to the Crau population which was known to host immigrants every year (Mihoub, 2009), the Herault population also grew at a pace that seemed incompatible with sole

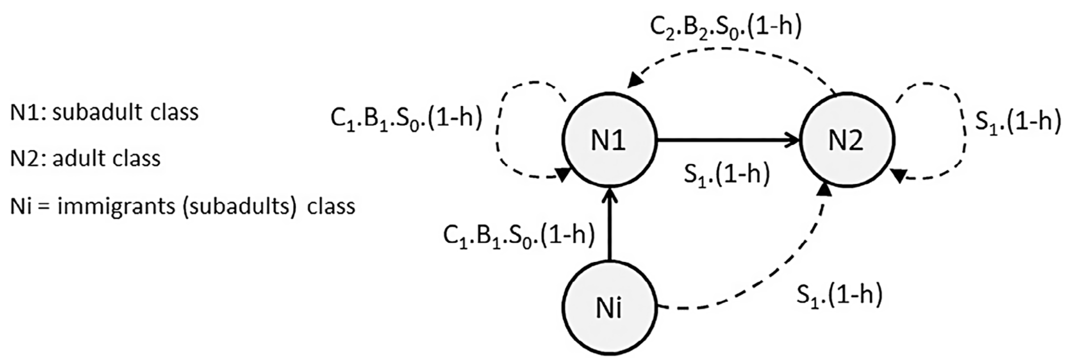

Figure 2 The life cycle of Lesser kestrel *Falco naumanni* used to build the matrix population model, based on three stages (N1 as subadult females, N2 as adult females, Ni as subadult immigrant females), including the following parameters: S_0 as survival probability in the first year (juvenile); S_1 as survival probability in second year (subadult) and older (adult), h as mortality rate induced by collisions with wind turbines (this number changed over the years, see Table 1); C_1 and C_2 as proportions of subadult and adult breeders, respectively, and B_1 and B_2 as productivity of subadult and adult breeders, respectively, expressed as the number of females produced by a female. The values of each parameter are given in Table 1.

Table 1 Parameter values used in the matrix population model, based on the life cycle shown in Fig. 1

Parameter	Population	Age	Years	Mean estimates ± SE
Productivity	Herault		2006–2020	
B_1		Subadult		0.838 ± 0.078
B_2		Adult		1.409 ± 0.131
Breeding frequency	Crau		2006–2020	
C_1		Subadult		0.349 ± 0.040
C_2		Adult		0.824 ± 0.025
Survival	Crau		2006–2020	
S_0		Juvenile		0.474 ± 0.0305
S_1		Subadult and adult		0.674 ± 0.026
Annual immigration	Herault			
Ni		Subadult		26
Mortality rate	Herault			
h_1	11 turbines		2007–2008	0.011
h_2	24 turbines		2009–2014	0.023
h_3	31 turbines		2015–2020	0.030

The population indicates the origin of the dataset used to estimate each value in the model. The productivity was approximated from the number of juvenile females fledged per breeding female. The mortality rate referred only to collisions with wind turbines.

internal recruitment. Moreover, occasional resightings of marked individuals prove that the Herault population hosted immigrants from other neighbouring source populations (notably Crau, Aude and Spanish populations) (see Supporting Information Appendix S1). We thus built matrix models explicitly including immigration. Results from Mihoub (2009) suggested that a constant number of immigrants (i.e. independent of the number of individuals already present in the Crau population) was a more credible scenario than the hypothesis of a constant rate of immigrants (i.e. proportional to the number of individuals already present in the Crau population). We therefore built our model according to this first hypothesis of constant number of immigrants per year in the Herault population. To do so, we added a third stage in the Leslie matrix, called ‘immigrant’ Ni, that allowed adding to the population a fixed number of individuals each year (see Doxa *et al.*, 2013). The immigrants were considered as subadults (in their second year) settling into the population just before breeding, hence contributing immediately to the breeding population in their year of arrival, with the same breeding parameters as the local subadults, and with a survival rate identical to the local individuals until the next breeding season.

We included in the model an additional mortality probability due to collisions with wind turbines (identical to a ‘harvest’ rate in the framework of an exploited population and called h thereafter). We derived this h rate from the number of mortalities estimated from carcass monitoring (see Supporting Information Appendix S2). Since windfarm mortalities occurred mainly during the breeding period, we applied h both on survival and reproduction, considering that the clutch of an individual that has died cannot survive and therefore is lost in terms of fecundity. We also considered that mortality rate was fully additive as it occurred during the breeding season and that selective mortality was unlikely. The final life cycle and the resulting matrix population model, based on three stages and two age classes, are detailed in Fig. 2.

Population trajectory simulations

In a first retrospective approach, we explored the potential of our model to describe the population growth of the Herault population. This step aimed at calibrating the model to ensure the quality of model predictions and to estimate the annual number of immigrants. We modelled the population growth from 2006 to 2020 by using 15 annual matrices. Each annual matrix was filled with survival and breeding proportions estimated in Crau, and productivity estimated in Herault in that year. For each year, we only knew the number of breeding pairs in Herault, combining adults and subadults in unknown proportions. To obtain the number of individuals in each age class, including breeders and non-breeders, we then used the stable age-structure predicted by the matrix population model (i.e. stable structure at equilibrium and independent of initial population size) upon which we added the frequency of breeders in each age class (estimated from the Crau population survival analysis).

The number of wind turbines in Aumelas increased progressively over the years (in three phases, see above) but the mortality rate could only be estimated properly during the last phase (2013–2020). Therefore, we defined the mortality rate induced by collisions (h) as proportional to the number of wind turbines in operation each year. We thus considered that h was maximal for the last phase of construction (31 turbines in 2015–2020: h_3), then reduced proportionally in the second phase (24 turbines in 2009–2014: $h_2 = h_3 \times 24/31$) and further reduced in the first phase (11 turbines in 2007–2008: $h_1 = h_3 \times 11/31$) (Supporting Information Appendix S2).

We then used this projection to estimate the most probable number of immigrants Ni each year. To do that we added a number of immigrants in the model until the simulated population size fitted the observed population size in Herault. The fit between the simulated and the observed population size was performed by an iterative process, searching for the number of immigrants that resulted in a simulated population growth rate similar to the observed mean population growth rate over the entire study period (leading to a perfect match between the observed and the predicted population size in 2020). We also simulated the population trajectory without windfarm mortality or without immigration to estimate what should have been the population size without this additional source of mortality induced by collisions.

In a second prospective approach, we simulated how population size and population growth rate would be affected when varying the collision rate and the number of immigrants. We performed 1000 projections of population size over 30 years, starting from population size recorded in 2020 in Herault (392 females corresponding to 254 breeding pairs, see "Results" section). The population growth rate λ was estimated on the local population (2 stages), by calculating the mean of inter-annual growth rates for each simulation. We studied the changes in λ according to different scenarios of collisions (varying from 0 to 25% of the population dying from collisions) and immigration [comparing the current situation with 26 immigrants per year (see "Results" section), to a situation without any immigrants]. In this analysis we took into account uncertainty around demographic parameter estimates by sampling parameter values in a normal distribution with mean of estimates and their associated standard error for each year and each simulation.

For both steps, the number of initial individuals in each age class was obtained from the stable stage structure predicted by the determinist matrix population model as for mortality rate estimation. All population trajectory simulations were performed with R program (R Development Core Team, 2010), notably using packages 'popbio' (https://cran.r-project.org/web/packages/popbio/popbio.pdf).

Results

Survival

The model selection and goodness-of-fit tests are detailed in Table 2 and Supporting Information Appendix S4. The results of the fully age-dependent model on survival probability showed that survival was low in juveniles (first year), then increased and remained globally stable for subadults and adults (Supporting Information Appendix S4 – Figure B). For the following models, we therefore pooled ages into two classes: juvenile (hereafter *Juv*, aged 1) and adults (hereafter *Ad*, aged 2–14).

The best model included resighting probabilities that depend on breeding status without time effect. Resighting probabilities for non-breeders and breeders were estimated respectively at 0.66 ± 0.02 and 0.99 ± 0.005. The model that best described survival and breeding probabilities included time and age variations in addition (model M#9, Table 2), where survival and breeding probabilities varied in a parallel manner between the two age classes (Fig. 3). The mean survival probabilities (±SE) between 2006 and 2020 for juveniles and adults were, respectively, 0.47 ± 0.03 and 0.67 ± 0.03.

Fecundity

In Crau, the mean breeding probabilities (±SE) between 2006 and 2020 were estimated by the joint survival analysis for subadults and adults at 0.35 ± 0.04 and 0.82 ± 0.03, respectively (model M#9, Table 2; Fig. 3).

In Herault, the annual female productivity between 2006 and 2020 varied between 1.06 and 1.49, with a mean value of 1.269 ± 0.118 females fledgling produced per female, showing no particular trend over time ($R^2 = 0.016$, $F_{1,16} = 0.263$,

Table 2 Model selection for survival analysis (with overdispersion coefficient of 1.7)

Model number	Model name	np	Deviance	QAICc	Delta QAICc
9	Phi(a+t) B(a+t) E (b)	56	22732.338	13484.523	0.000
3	Phi(a.t) B(a.t) E (b)	104	22566.835	13484.530	0.007
6	Phi(a.t) B(a + t) E (b)	80	22655.368	13487.825	3.302
8	Phi(a(1).t+a(2)) B(a+t) E (b)	56	22742.513	13490.508	5.985
11	Phi(a+t) B(a(1).t+a(2)) E (b)	56	22777.639	13511.170	26.648
5	Phi(a.t) B(a(1).t+a(2)) E (b)	80	22708.479	13519.066	34.543
2	Phi(a.t) B(a.t) E (b.t)	150	22485.947	13531.029	46.506
7	Phi(a) B(a+t) E (b)	31	22940.892	13556.816	72.293
10	Phi(a+t) B(a) E (b)	31	23011.854	13598.558	114.035
4	Phi(a.t) B(a) E (b)	55	22935.044	13601.742	117.219
12	Phi(a) B(a) E (b)	6	23233.096	13678.534	194.011
1	Phi(a26) B(a26) E (b)	41	23181.380	13718.407	233.884

For survival (Phi) and Breeding (B) estimates, we used Cormack-Jolly-Seber model framework and considered either all age classes (a26) or 2 age classes (model a, subdivided into Juveniles (a(1)) and adults (a(2)); see Supporting Information Appendix S4). For resighting estimates (p), we separated breeders and non-breeders (E(b)). For all models, we compared the additive or multiplicative effect of time (+t or .t, respectively) on the survival, breeding and resighting parameters. The metrics used for model selection were the number of estimable parameters (np), deviance, Akaike Information Criterion corrected for small samples and overdispersion (QAICc), and variation in QAICc relative to model with smallest QAICc value, listed on top (ΔQAICc).

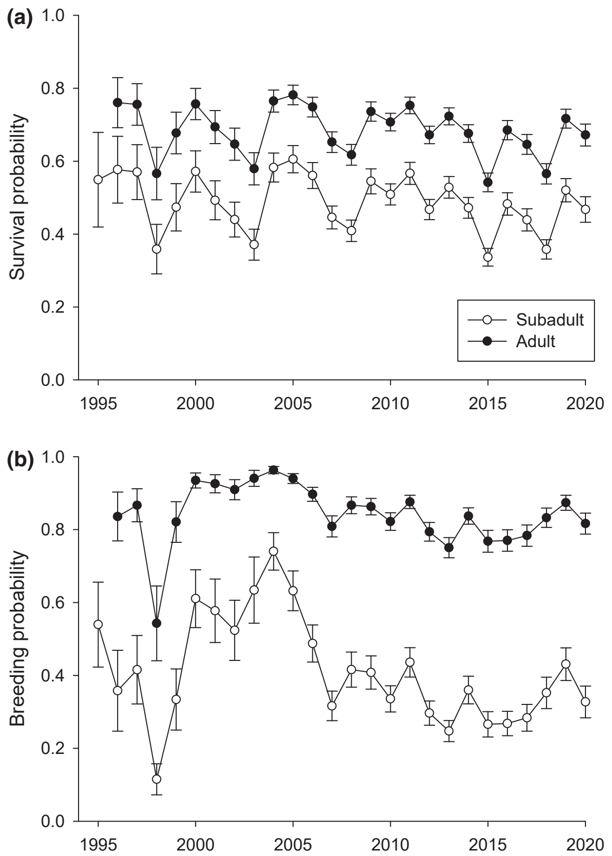

Figure 3 Annual survival (a) and breeding (b) probabilities (±SE) from the Crau population of Lesser kestrel *Falco naumanni*, for the two age classes (subadults (in white), and adults (in black) with an additive effect on time (from model M#9 in Table 2).

P = 0.615; Supporting Information Appendix S5). We further differentiated productivity by age class, using the ratio found in Crau (subadult female 34% below average productivity = 0.838 ± 0.078 and adult 11% above average = 1.409 ± 0.131; Table 1).

Retrospective population matrix demographic models

The matrix model predicted a stable-age structure with 36.5% of one-year old (subadult) females and 63.5% of adult females. With 254 breeding pairs in 2020, when accounting for the proportion of breeders in each age class, the total number of adult and subadult females should be around 392 individuals in Herault.

From the observed population size in Herault, the inter-annual population growth rate λ was 1.166 between 2006 and 2020 (Fig. 4). To obtain such population growth rate with additional mortality due to the windfarm, the model predicted that 26 immigrants per year were necessary, whereas a lack of immigrants would have produced a stable and low population size (Fig. 4). From the 43 falcon carcasses found below wind turbines between 2013 and 2020, combined with the carcass detection and persistence experiments, we estimated that 154 falcons should have been killed during this period (Supporting Information Appendix S2). The additional mortality rate (h) due to collisions was estimated at 3% of females every year (Supporting Information Appendix S2). When modelling the population trajectory without windfarm mortality, the population size should have reached a peak of 308 breeding pairs in 2020, i.e. 22% higher than the 252 pairs predicted by the model with windfarm mortality (Fig. 4).

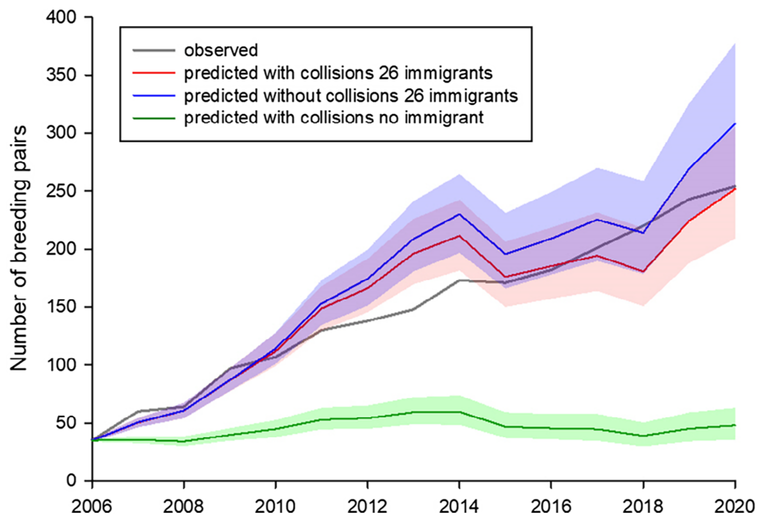

Figure 4 Number of breeding pairs of Lesser kestrel *Falco naumanni* between 2006 and 2020 in the Herault population observed (grey line) and predicted by the matrix population model. The red line represents the predicted breeding population with an additional mortality due to collisions with wind turbines (observed mortality of 1.1% for the period 2007–2008; 2.3% for the period 2009–2014; 3% for the period 2015–2020); the blue line represents the predicted breeding population without additional mortality. The green line shows the predicted breeding population with collisions and without immigration. The shaded areas represent 95% confidence intervals.

Prospective population matrix demographic models

If the current situation prevails in the next 30 years, with 26 immigrants per year, the population would continue to grow up to 869 breeding pairs in 2050 [95% confidence intervals: 331–2657] (Fig. 5a). Without additional mortality due to collisions, the population would reach 1742 breeding pairs [95% confidence intervals: 590–5722] in 2050 (Fig. 5a). The relative impact of collisions was progressively increasing over the years, reaching 21% difference (with the projected population without collisions) after 10 years and 50% after 30 years (Fig. 5b). The population growth rate λ would decline with increasing mortality rates (Fig. 6). With the current number of immigrants, the population would decline ($\lambda < 1$) if mortality rate would exceed 11%. Without immigration, λ would decrease linearly with the mortality rate induced by collisions (Fig. 6). Hence each percent of increase in mortality rate would result in a 1% decrease in λ, and the population in the absence of immigration would decline if the mortality rate would exceed 5%, i.e. 1.6 times the current mortality rate.

Discussion

This study is among the first to quantify the potential long-term demographic impact of collisions to anthropogenic structures like windfarms in a relatively short-lived bird species. To our knowledge, this has been attempted only in long-lived species such as bats, seabirds and raptors (Carrete *et al.*, 2009; Schaub, 2012; Cook & Robinson, 2017; Frick *et al.*, 2017). In the Golden eagle *Aquila chrysaetos*, population growth rates are particularly sensitive to adult mortality rates and only a 4% reduction in adult survival is enough to trigger population decline, which cannot be offset by increased productivity (Tack *et al.*, 2017). Despite lesser kestrels being shorter-lived birds with higher fecundity, we found that additional mortalities induced by collisions with turbines may also have a strong impact on their population dynamics. We found that the current population growth rate was correlated with the mortality rate induced by collisions.

When lesser kestrels settled in Herault in the 1990s, the population experienced very high population growth rates ($\lambda > 1.5$; Fig. 1), becoming the second largest population in France (in 2008) and the largest one from 2017 onwards.

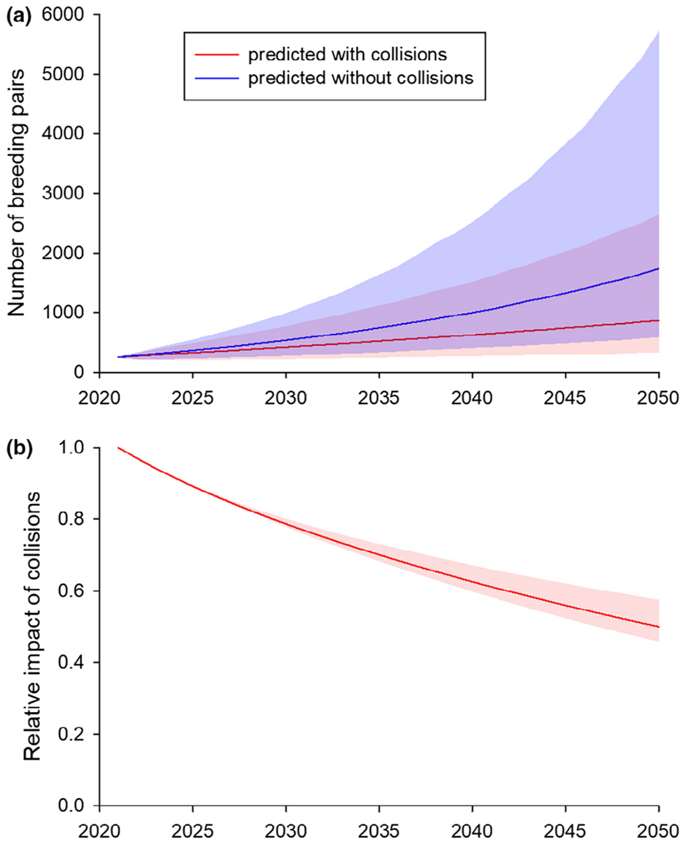

Figure 5 Projection of Lesser kestrel *Falco naumanni* population sizes in the Herault population, as simulated by the matrix population model until 2050 (a). The red line represents mean values with collisions with wind turbines and the blue line without collisions. The shaded areas represent 95% confidence intervals. For both cases, the immigration rate was kept at the same values as in 2020 (26 immigrants per year). The panel (b) shows the relative impact of collisions, as estimated by the difference in population size between projections with collisions and without collisions.

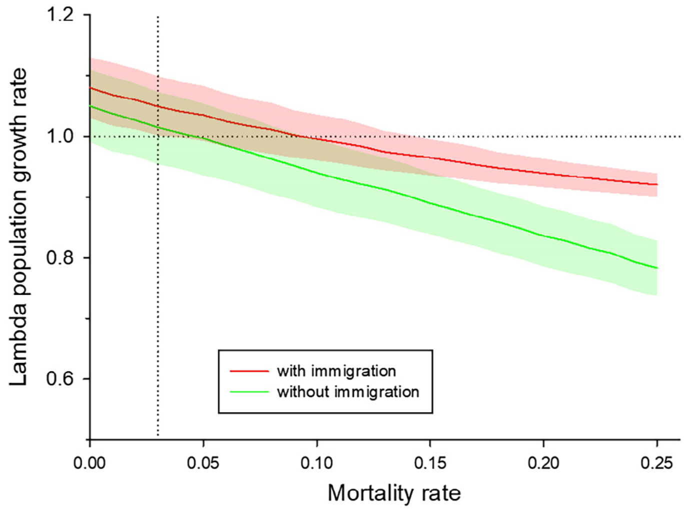

Figure 6 Variation of projected interannual population growth rate λ (with 95% confidence intervals represented by the shaded area) of the population of Lesser kestrel *Falco naumanni*, according to the mortality rate induced by collisions with wind turbines. The red line represents the case with 26 immigrants per year, while the green line represents the situation without immigration. The horizontal dotted line indicates the mortality threshold beyond which the population declines ($\lambda < 1$) and the vertical dotted line indicates the current collision rate (3%) in the Herault population.

This fast population growth was mostly due to abundant immigration (26 individuals per year) from neighbouring populations (probably from Spain, Aude and Crau, as revealed by the resightings of a few individuals every year). We showed in the retrospective analysis that the population would have grown only very slowly in the last 15 years without immigration, remaining as <50 pairs in 2020. Another reason was probably the high quality of natural shrub habitats at the Aumelas plateau. With 254 pairs in 2020, this population was still increasing numerically, but at a much lower pace ($\lambda < 1.1$) after 2015. We showed that the mortality induced by just a 31-turbine windfarm, estimated at 3% annually, eventually contributed to the decrease in population growth rate in the late years (as the predicted population size in the absence of collisions would be 308 pairs instead of 254 observed in 2020). Thus the mortality rate induced by this single windfarm on this lesser kestrel population is not anecdotal, and its impact on the local population is strong, reducing the population size by 22% in 15 years of operation.

The current plans for extending this windfarm would further impact and weaken this falcon population. At a wider scale, as it is scheduled that the number of windfarms will double in France in the next 10 years, the cumulated impact of new windfarms built within the breeding home range, around the postnuptial stopover sites or along the migratory routes, should further increase the overall mortality rate of this population (Katzner *et al.*, 2017; Vasilakis, Whitfield, & Kati, 2017). With the current immigration rate, we found that if the mortality rate exceeds 11%, the population would start declining.

However, this population growth rate was tightly linked to two parameters, immigration and adult survival, that may decrease for several reasons. First, if immigration stops, we showed that a 1% increase in mortality rate would immediately result in 1% decrease in population growth rate, as expected given that mortality rate is embedded in all transitions in the matrix population model (Caswell, 2001). Without immigration, a small increase from 3 to 5% in collision mortality rate in the Herault population would lead to a population decline. This reduction in immigration is far from unlikely, since the Spanish populations of lesser kestrels where most migrants probably originate (besides Crau) are currently declining since 2015, for unknown reasons so far (Bustamante, Molina, & Del Moral, 2020). Second, adult survival rates may be reduced for reasons other than windfarm mortality. Mihoub *et al.* (2010) showed that adult survival was correlated with conditions encountered at wintering grounds in Sahel, especially drought, as also evidenced in other long-distance migrants (Schaub, Kania, & Koppen, 2005; Wilson & Cresswell, 2006; Zwarts *et al.*, 2009). If climate change triggers reduced rainfall in Sahel in the next decades, as predicted by the IPCC scenario (Dai, 2013), yielding lower abundance of orthopterans, this would result in lower survival rates in lesser kestrels. In such a case, the impact of collision excess mortality on breeding grounds would become even stronger.

Given the likely decrease in immigration rate and reduced adult survival due to changing wintering conditions, on one hand, and the planned increase in windfarm numbers in the coming years, on the other hand, the impacts of collisions on French lesser kestrel populations are predicted to increase. Therefore, the primary effort by stakeholders should be to reduce local mortality. The detection-reaction devices, which have been installed on all turbines in the Aumelas windfarm since 2017 in order to scare falcons or shut down turbines, are obviously not fully efficient in reducing mortality in this species. In the short term, the only truly efficient reduction measures would be daylight turbine shutdown during the period when falcons are present (from April to September), or when their probability of presence at the windfarm is enhanced by wind conditions (Bartholus, unpublished results). The second effort should be to record these impacts on a larger scale, by increasing the quality and quantity of mortality monitoring in all windfarms concerned by the presence of lesser kestrels. In southern France, the mortality monitoring at the Aumelas windfarm is among the most intensive. Yet since 2010 in southern France at least six other carcasses of lesser kestrels have been found in other windfarms, within areas used by Herault kestrels as post-nuptial stopovers or along migratory routes. Thus the true mortality rate for the Herault population may already exceed the 3% estimated here, as estimated locally only at Aumelas windfarm.

We highlight the importance of assessing the demographic impact of additional mortality induced by anthropogenic infrastructures on wild populations, using population dynamics modelling approaches. However, the use of such approach is often limited by the data available. A sensitivity analysis (see Supporting Information Appendix S6) is helpful to estimate the contribution of each demographical parameter, and consequently, the lack of precision that is tolerable for input vital rates. In our case, we relied on a locally intensive monitoring of breeding pairs, to get precise estimates for fecundity. However, for survival parameters, we had to rely on survival estimates from a neighbouring population in Crau, though these parameters are the main drivers of population dynamics (Supporting Information Appendix S6). Because annual survival rates are mostly driven by conditions in the wintering grounds in West Africa (Mihoub *et al.*, 2010; Morganti, Preatoni, & Sarà, 2017), which are shared by both Crau and Herault populations as well as most Spanish populations (Sarà *et al.*, 2019; Lopez-Ricaurte *et al.*, 2021), we are confident that the variations in annual survival should follow a similar pattern over time in Crau and Herault, although the exact values may differ slightly. However, this survival rate estimated in Crau population could also be viewed as an advantage, given that mortality by wind turbines in Crau is unlikely, it could capture the natural variations in survival without the additional mortalities that we may have occurred in Herault if the survival analysis had been performed there. In the future, it would be interesting to develop an Integrated Population Model that would allow to perform the retrospective and prospective analysis in a joint framework. It might improve the estimates of the immigration rate and its potential contribution as a compensatory mechanism of local additional mortalities [see however Riecke *et al.* (2019) and Paquet *et al.* (2021)].

According to the mitigation hierarchy (Avoid-Reduce-Offset), stakeholders should first plan wind energy development in areas outside home ranges, postnuptial stopover sites and along migratory routes of threatened species (Arnett & May, 2016). This spatial planning should ideally be accompanied by a demographic assessment at a regional scale, in order to evaluate the cumulative impacts of regional windfarms on the long-term viability of local and migratory animal populations (Arnett & May, 2016). At the local scale, before implanting a windfarm, environmental impact assessment (EIA) studies should also conduct population dynamics analyses to quantify if an additional (harvest) mortality is likely to have a demographic impact. Such modelling approach is highly dependent on long-term demographic monitoring data on the target populations in the surroundings of the windfarm; and unfortunately such data are generally lacking. Yet, lists of species especially vulnerable to collisions based on empirical evidence are nowadays available (Beston *et al.*, 2016; Thaxter *et al.*, 2017). International databases of the demographic traits of many bird species have also been published (Lebreton *et al.*, 2012; Salguero-Gómez *et al.*, 2016). This information may be combined to develop population dynamics models with average survival and fecundity values as input parameters and using local population size estimates as starting values for simulations. Such tools are nowadays under development as web applications to allow an easier use by EIA staff (https://shiny.cefe.cnrs.fr/en_eolpop/, released early 2022). This would give much more credit to recommendations from ornithological experts when discussing wind energy development planning with stakeholders, in order to avoid building new windfarms that would affect threatened species that are vulnerable to collisions (May *et al.*, 2019).

Acknowledgements

We thank all the staff from LPO involved in the fieldwork and mortality monitoring surveys, in particular Mathias Bouzin, Jean-François Blanc, Mathieu Garcia and Aurélie Béa, who conducted most of mortality analyses.

Authors' contributions

OD, PB, PP and NS conceived the ideas and designed methodology; PP and NS collected the data; OD and AB analysed the data; OD and AB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

Arnett, E.B. & May, R.F. (2016). Mitigating wind energy impacts on wildlife: Approaches for multiple taxa. *Hum. Wildl. Interact.* **10**, 28.

Barrios, L. & Rodriguez, A. (2007). Spatiotemporal patterns of bird mortality at two wind farms of southern Spain. In *Birds and wind farms; risk assessment and mitigation*: 229–239. De Lucas, M., Janss, G.F.E. & Ferrer, M. (Eds). Madrid: Quercus.

Beston, J.A., Diffendorfer, J.E., Loss, S.R. & Johnson, D.H. (2016). Prioritizing avian species for their risk of population-level consequences from wind energy development. *PLoS One* **11**, e0150813.

BirdLife International. (2015). *European red list of birds*. Luxembourg: Office for Official Publications of the European Communities.

Bustamante, J., Molina, B. & Del Moral, J.C. (2020). *El cernícalo primilla en España, población reproductora en 2016–18 y método de censo*. Madrid: SEO/Birdlife.

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M. & Donázar, J.A. (2009). Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biol. Conserv.* **142**, 2954–2961.

Caswell, H. (2001). *Matrix population models*, 2nd edn. Sunderland: Sinauer Associates Inc.

Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.-M. & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* **32**, 1071–1074.

Choquet, R., Rouan, L. & Pradel, R. (2008). Program E–SURGE: A software application for fitting multievent models. *Environ. Ecol. Stat.* **16**, 847–868.

Cook, A.S.C.P. & Robinson, R.A. (2017). Towards a framework for quantifying the population-level consequences of anthropogenic pressures on the environment: The case of seabirds and windfarms. *J. Environ. Manage.* **190**, 113–121.

Cramp, S. & Simmons, K.E.L. (1982). *Handbook of the birds of Europe, the Middle East and North Africa*. Oxford: Oxford University Press.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nat. Clim. Change* **3**, 52–58.

De Lucas, M., Janss, G.F.E. & Ferrer, M. (2007). *Birds and wind farms; risk assessment and mitigation*. Madrid: Quercus.

De Lucas, M., Janss, G.F.E., Whitfield, D.P. & Ferrer, M. (2008). Collision fatality of raptors in wind farms does not depend on raptor abundance. *J. Appl. Ecol.* **45**, 1695–1703.

Doxa, A., Besnard, A., Béchet, A., Pin, C., Lebreton, J. & Sadoul, N. (2013). Inferring dispersal dynamics from local population demographic modelling: The case of the slender-billed gull in F rance. *Anim. Conserv.* **16**, 684–693.

Drewitt, A.L. & Langston, R.H.W. (2006). Assessing the impacts of wind farms on birds. *Ibis* **148**, 29–42.

Frick, W.F., Baerwald, E.F., Pollock, J.F., Barclay, R.M.R., Szymanski, J.A., Weller, T.J., Russell, A.L., Loeb, S.C., Medellin, R.A. & McGuire, L.P. (2017). Fatalities at wind turbines may threaten population viability of a migratory bat. *Biol. Conserv.* **209**, 172–177.

Huso, M.M.P. (2011). An estimator of wildlife fatality from observed carcasses. *Environmentrics* **22**, 318–329.

Katzner, T.E., Nelson, D.M., Braham, M.A., Doyle, J.M., Fernandez, N.B., Duerr, A.E., Bloom, P.H., Fitzpatrick, M.C., Miller, T.A., Culver, R.C.E., Braswell, L. & DeWoody, J.A. (2017). Golden eagle fatalities and the continental-scale consequences of local wind-energy generation. *Conserv. Biol.* **31**, 406–415.

Lebreton, J.-D., Devillard, S., Popy, S., Desprez, M., Besnard, A. & Gaillard, J.-M. (2012). Towards a vertebrate demographic data bank. *J. Ornithol.* **152**, 617–624.

Lekuona, J.M. & Ursua, C. (2007). Avian mortality in wind power plants of Navarra (Northern Spain). In *Birds and wind farms; risk assessment and mitigation*: 177–192. De Lucas, M., Janss, G.F.E. & Ferrer, M. (Eds). Madrid: Quercus.

Lopez-Ricaurte, L., Vansteelant, W.M.G., Hernández-Pliego, J., García-Silveira, D., Bermejo-Bermejo, A., Casado, S., Cecere, J.G., de la Puente, J., Garcés-Toledano, F., Martínez-Dalmau, J., Ortega, A., Rodríguez-Moreno, B., Rubolini, D., Sarà, M. & Bustamante, J. (2021). Barrier crossings and winds shape daily travel schedules and speeds of a flight generalist. *Sci. Rep.* **11**, 12044.

Marques, A.T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M.J.R., Fonseca, C., Mascarenhas, M. & Bernardino, J. (2014). Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. *Biol. Conserv.* **179**, 40–52.

May, R., Masden, E.A., Bennet, F. & Perron, M. (2019). Considerations for upscaling individual effects of wind energy development towards population-level impacts on wildlife. *J. Environ. Manage.* **230**, 84–93.

Mihoub, J.B., Gimenez, O., Pilard, P. & Sarrazin, F. (2010). Challenging conservation of migratory species: Sahelian rainfalls drive first-year survival of the vulnerable lesser kestrel *Falco naumanni*. *Biol. Conserv.* **143**, 839–847.

Mihoub, J.B., Mouawad, N.G., Pilard, P., Jiguet, F., Low, M., Teplitsky, C. (2012). Impact of temperature on the breeding performance and selection patterns in lesser kestrels Falco naumanni. *J. Avian Biol.* **43**, 472–480.

Mihoub, J.B. (2009). *Réintroductions et comportements de sélection d'habitat: de la modélisation à l'application - cas du Vautour moine Aegypius monachus* et du Fancon crécerélette Falco naumanni. Paris: Université Pierre et Marie Curie, Ecologie.

Moncorps, S. & Siblet, J.-P. (2016). Oiseaux de france métropolitaine. In *La liste rouge des espèces menacées en france*: 20, Paris: UICN France, MNHN, LPO, SEOF and ONCFS.

Morganti, M., Preatoni, D. & Sarà, M. (2017). Climate determinants of breeding and wintering ranges of lesser kestrels in Italy and predicted impacts of climate change. *J. Avian Biol.* **48**, 1595–1607.

Paquet, M., Knape, J., Arlt, D., Forslund, P., Pärt, T., Flagstad, Ø., Jones, C.G., Nicoll, M.A.C., Norris, K., Pemberton, J.M., Sand, H., Svensson, L., Tatayah, V., Wabakken, P., Wikenros, C., Åkesson, M. & Low, M. (2021). Integrated population models poorly estimate the demographic contribution of immigration. *Methods Ecol. Evol.* **12**, 1899–1910.

Perrow, M.R. (2017). *Wildlife and wind farms, conflicts and solutions*. Onshore: Potential effects (Vols. 1–4), Vol. 1, Exeter, UK: Pelagic Publishing.

Perrow, M.R. (2019). *Wildlife and wind farms, conflicts and solutions*. Offshore: Potential effects (Vols. 1–4), Vol. 3, Exeter, UK: Pelagic Publishing.

Pilard, P. (2011). *Plan national d'actions pour le Faucon crécerelette 2011–2015*. Paris: Ministère de l'Ecologie, du Développement Durable, des Transports et du Logement.

Pilard, P., Bourgeois, M., Saulnier, N. & Boudarel, P. (2021). *Plan national d'actions 2021–2030 en faveur du Faucon crécerelette*. Paris: Ministère de la Transition Ecologique.

Pilard, P., Bourgeois, M. & Sylla, D. (2017). Localisation des quartiers d'hivernage et phénologie des migrations prénuptiale et postnuptiale chez la population française du Faucon crécerellette Falco naumanni à l'aide de géolocateurs. *Alauda* **85**, 1–28.

R Development Core Team. (2010). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Riecke, T.V., Williams, P.J., Behnke, T.L., Gibson, D., Leach, A.G., Sedinger, B.S., Street, P.A. & Sedinger, J.S. (2019). Integrated population models: Model assumptions and inference. *Methods Ecol. Evol.* **10**, 1072–1082.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H. & Vaupel, J.W. (2016). COMADRE: A global data base of animal demography. *J. Anim. Ecol.* **85**, 371–384.

Sarà, M., Bondì, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., Puente, J. et al. (2019). Broad-front migration leads to strong migratory connectivity in the lesser kestrel (*Falco naumanni*). *J. Biogeogr.* **46**, 2663–2677.

Schaub, M., Kania, W. & Koppen, U. (2005). Variation of primary production during winter induces synchrony in survival rates in migratory white storks Ciconia ciconia. *J. Anim. Ecol.* **74**, 656–666.

Schaub, M. (2012). Spatial distribution of wind turbines is crucial for the survival of red kite populations. *Biol. Conserv.* **155**, 111–118.

Tack, J.D., Noon, B.R., Bowen, Z.H., Strybos, L. & Fedy, B.C. (2017). No substitute for survival: Perturbation analyses using a Golden eagle population model reveal limits to managing for take. *J. Raptor Res.* **51**, 258–272.

Thaxter, C.B., Buchanan, G.M., Carr, J., Butchart, S.H.M., Newbold, T., Green, R.E., Tobias, J.A., Foden, W.B., O'Brien, S. & Pearce-Higgins, J.W. (2017). Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proc. R Soc. B Biol. Sci.* **284**, 20170829.

Vasilakis, D.P., Whitfield, D.P. & Kati, V. (2017). A balanced solution to the cumulative threat of industrialized wind farm development on cinereous vultures (*Aegypius monachus*) in South-Eastern Europe. *PLOS One* **12**, e0172685.

Williams, B.K., Conroy, M.J. & Nichols, J.D. (2002). *Analysis and management of animal populations*. San Diego: Academic Press.

Wilson, J.M. & Cresswell, W. (2006). How robust are palearctic migrants to habitat loss and degradation in the Sahel? *Ibis* **148**, 789–800.

Zwarts, L., Bijlsma, R.G., van der Kamp, J. & Wymenga, E. (2009). *Living on the edge: Wetlands and birds in a changing Sahel*. Zeist, the Netherlands: KNNV Publishing.

Supporting information

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

Appendix S1. Immigration observed with ringed birds.
Appendix S2. Estimation of mortality by collision with wind turbines.
Appendix S3. Annual mortality estimates.
Appendix S4. Survival analysis and goodness-of-fit tests.
Appendix S5. Population growth rate and productivity in Crau and Herault.
Appendix S6. Sensitivity analysis of the Leslie matrix model.