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ORIGINAL RESEARCH

# Bat mortality in wind farms of southern Europe: temporal patterns and implications in the current context of climate change

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## Abstract

The expansion of renewable energy production, especially wind power, is one of the cornerstones of our strategy for mitigating climate change. However, there is growing concern about the impacts of this energy source on biodiversity. In particular, very little is known about the impact on groups of fauna such as bats, which are especially sensitive to environmental changes. We investigated the temporal patterns of bat fatalities in wind farms in the province of Cádiz, in the south of the Iberian Peninsula. An eleven-year data set (2009–2019) from a surveillance program of bird and bat mortality in wind farms was analysed. A total of 2,858 fatalities concerning 10 bat genera were reported, although more than 90% of the affected animals were individuals of the genera *Pipistrellus*, *Eptesicus* and *Nyctalus*. Bat mortality occurred mainly during the summer and autumn, especially in August. However, species such as the genus *Pipistrellus*, present collisions throughout the year, including all winter months in the case of the genus *Pipistrellus.* The probability of mortality was positively correlated with the maximum daily temperature. According to the model prediction, the probability of fatality begins to increase slightly from 20 °C and then rises sharply when the temperature exceeds 30 °C, that can be interpreted as a consequence of increasing bat activity at local scale. According to the regional projections of global climate models, an increase in maximum temperatures and the arrival of milder winters may lead to an increase in the annual mortality of bats in wind farms in the coming decades.

**Keywords** Chiroptera · Fatalities · Global warming · Maximum temperature · Wind power

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## Introduction

The current magnitude of species loss has drawn attention at a global level, driving attempts to rapidly assess and conserve biodiversity (Dawson et al. 2011; McCallum 2015). Some drivers related to global change, such as changes in land use or climate change, may accentuate this loss of biodiversity in groups of fauna that are particularly sensitive to environmental conditions, such as bats (Jones and Rebelo 2013; Mehl et al. 2016). The expected increase in temperatures, due to global warming, can induce changes in the distribution and behavior of bat species (Barros et al. 2021; Festa et al. 2022) making them more vulnerable to certain emerging threats. In this sense, many studies have reported locally decreasing bat populations worldwide, with anthropogenic influences often cited as a likely cause (e.g. Rodhouse et al. 2019; Rydell et al. 2020). In this sense, a deep understanding of the behavioural responses of bats to environmental changes, their status, and current threats to them, are highly necessary to reveal their vital role in the functioning of many ecosystems (Tuneu-Corral et al. 2020; Smeraldo et al. 2021).

The effect of emerging threats makes the Chiroptera one of the most threatened taxa of fauna on the planet (Arnett and Baerwald 2013; Dietz and Kiefer 2018). Recent research revealed that many bat species could be severely affected in the years to come, with some extinctions predicted to occur by the end of the century (Rebelo et al. 2010). In recent decades, bats have faced a new threat that, paradoxically, is promoted to mitigate the effects of climate change: the development of wind power (Arnett et al. 2015; Hein and Schirmacher 2016). This development is predicted to increase in scale, with the Recovery and Resilience Facility of the European Commission recognizing renewable energy as one of its main priorities (European Commission 2021). In this sense, the promotion of new facilities and the repowering of old wind farms are both part of the strategy to achieve the EU's renewable energy target of 40% by 2030 (European Commission 2021). In parallel to the development of wind power, growing concerns have been raised about the impacts associated with this infrastructure, particularly on flying animals. Currently, there is an important body of knowledge demonstrating the remarkable impact of wind farms on bird mortality, as well as the patterns and mechanisms that determine the relative dangerousness of the different turbines which cause this mortality (e.g. Devereux et al. 2008; Ferrer et al. 2012; Gradolewski et al. 2021). However, the impact on the mortality of other flying organisms, such as Chiroptera, has received less attention, even though there are signs that it is even more significant than the impact on birds (e.g. Thaxter et al. 2017; Cabrera-Cruz et al. 2020). An adequate understanding of interactions between bats and turbines, including the timing and predictability of fatalities, is fundamental for developing solutions to mitigate bat fatalities (Arnett et al. 2008).

Like other small endothermic animals, bats have a limited ability to properly thermoregulate at low temperatures and therefore rely on heterothermy to respond to energetically stressful conditions (Speakman and Racey 2011; Bergeson et al. 2021). In addition, their search for food in winter is usually unproductive since many of their food sources (insects) are not seasonally available (Matheson et al. 2010). Furthermore, bats cannot store food for long periods, nor can they transport the large amounts of fat needed to maintain their metabolic output in low-temperature areas (Turbill and Geiser 2008). For these reasons, the activity of many bats during the winter season is less pronounced; it is even assumed that a large number of bat species hibernate or enter torpor during winter (Turbill and Geiser 2008;

Speakman and Racey 2011). Under these circumstances, it is expected that the impact of wind farms on bat populations will be restricted to the less cold months in temperate areas. However, there are indications that in some of these areas bats may remain active during winter, depending on climatic and meteorological conditions (Geluso 2007; Barros et al. 2021), which may lead to the fatalities extending throughout the year, with the consequent impact at the level of their populations.

In this study, we aimed to characterize the temporal patterns of bats' mortality in the province of Cadiz (Spain), one of the pioneering areas of southern Europe in the development of wind energy. This area, with almost a thousand turbines, is one of the sites where the greatest impact on flying fauna has been reported (Ferrer et al. 2012; Sánchez-Navarro et al. 2020). Using the mortality data available for the period 2009–2019, we analysed the distribution of fatalities throughout the year and the environmental factors that may be related to this distribution. These results have been discussed in the context of global warming in southern Europe, where warmer summers and milder winters are expected in the coming decades.

## Methods

### Study area

The province of Cádiz is located on the southern tip of the Iberian Peninsula, and includes the European portion of the Strait of Gibraltar (Fig. 1). The climate is typically Mediterra-

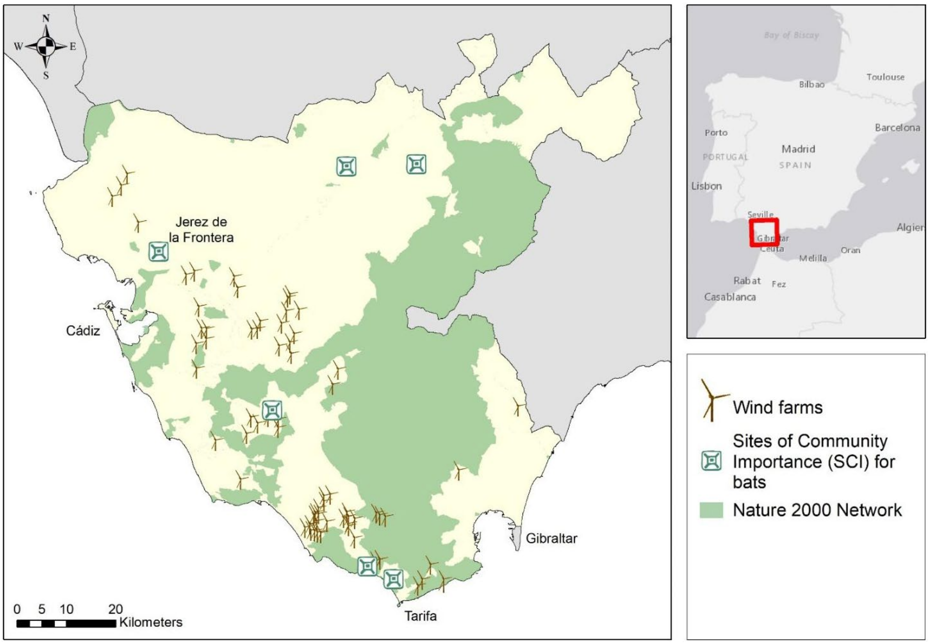



**Fig. 1** General map of the study area showing Natura 2000 network areas and Sites of Community Importance (SCI) declared due to the presence of cave-dwelling bats and wind farms

nean with Atlantic influences, characterized by mild winters and hot, dry summers and low rainfall. Its proximity to the Strait of Gibraltar (between Europe and Africa, and between the Atlantic Ocean and the Mediterranean Sea), gives rise to particular climatic conditions, with particularly milder summers and the prevalence of intense wind. These characteristics led to the great development of inland wind energy projects in the province from the 1990s onwards (Espejo 2004). After a period of thirty years of construction, installation and repowering of different wind farms, the area reached 904 turbines belonging to 59 fully operational wind farms by 2019. Some wind farms are located in protected natural areas of the Natura 2000 Network or on their limits, and parts of these areas are protected due to the presence of cave-dwelling bats (Fig. 1).

## Monitoring database

Information about bat collisions was obtained from the database of the *Monitoring Program of the Mortality of Birds and Bats in Windfarms of the Province of Cadiz*, which is promoted by the Council for the Environment of the Regional Government, Junta de Andalucía (hereafter CMA). This program involves daily monitoring of dead birds and bats in the wind farms of the province of Cadiz. The information is collected by independent environmental consultancy companies, in collaboration with the wind farm promoters and supervised by CMA. The database includes bat fatalities from 2005 but it was not until 2009 that the Delegation of the Environmental Authority in Cádiz developed a Program of Windfarms Monitoring with standardized data collection (CMA 2009). As the carcasses of bats remain for a short period before being removed, it must be assumed that any carcasses found died one, two or three nights before being detected. Injured or dead bats were identified by wind company technicians.

## Statistical analyses

Fatalities were grouped according to the main taxa (genus level) because the identification of bats at the species level is difficult. Thus, the main taxonomic groups were: (1) Genus *Pipistrellus*: including *P. kulhii, P. pipistrellus* and *P. pygmaeus*: bats of a small size with a very wide distribution and fissuric habits, although they also take advantage of hollows in trees; they are very abundant in the study area (Ibáñez 1998). (2) Genus *Eptesicus*: only *E. isabellinus* occurs in Andalucía (Pérez and Ibañez 1994); these are bats of great size, with fissuric habits, which are widely distributed and very abundant in Andalusia (Pérez and Ibañez 1994; Ibáñez 1998). (3) Genus *Nyctalus*: in Andalucía the species *N. lasiopterus* and *N. leisleri* are present (Franco and Rodriguez 2001); these are large forest bats, able to travel long distances to seek shelter and food, although the population of Cadiz province is not considered to be migratory (Ibáñez et al. 2009). *Nyctalus leislery* is listed in the National Catalogue of Threatened Species as of Special Interest and *Nyctalus lasiopterus* as Vulnerable (Agirre-Mendi 2007; Juste 2007); both *Nyctalus* species are listed as Vulnerable in the Red Book of Endangered Vertebrates of Andalusia (Franco and Rodriguez 2001) and *N. lasiopterus* is listed as Vulnerable globally by the International Union for Conservation of Nature's Red List (Alcaldé et al. 2016). According to existing information, all these bat species in the south of the Peninsula Iberica are non-migratory, although they can undertake long regional movements to seek shelter and food (Ibáñez et al. 2009; Juste et al. 2009).

For the groups mentioned above, we analysed the following parameters related to the temporality of the collisions: (1) the percentage of years in which the mortality of individuals belonging to each group was registered; (2) the total number of fatalities; (3) the average day of the first fatality; (4) the average of the yearly median, that is, the date on which 50% of the cumulative annual fatalities is reached each year for the main bat groups; (5) the average day when the last fatality occurs; and (6) the average length of the period of fatalities (that is, the number of days between the first and last fatalities, per year). For other bat groups, we only considered the earliest and latest fatalities that occurred during the entire study period.

The Kruskal-Wallis test was used to compare the temporal characteristics of different groups of species. When statistically significant differences were detected, post-hoc comparisons were made using the Wilcoxon matched-pairs signed-ranks test (Wilcoxon 1945) and applying the Benjamini-Hochberg correction (Benjamini and Hochberg 1995). All the analyses were performed using open-source R software (R Core Team 2022).

## Modelling procedure

For the modelling procedure we considered two different scenarios. First, we considered the fatalities identified across the entire study period, and second we considered only the fatalities that occurred during winter, which was defined as the period from November to February, when the average daily maximum temperature was below 20 °C.

We investigated the influence of meteorological factors that have been mentioned in the literature as potential predictors of bat fatalities in our study area (Erickson and West 2002; Frick et al. 2012; Smith and McWilliams 2016; Barros et al. 2017) (see Table S1). The daily occurrence of bat mortality at each windfarm (presence / absence data) was considered to be the dependent variable. Meteorological variables were obtained from the Spanish Meteorological Agency (www.aemet.es). Information from two strategically located meteorological stations in the province (Jerez de la Frontera and Tarifa; Fig. 1) was used, and each wind farm was assigned to the closest station. Since bats are generally most active at twilight and in the first hours of night (Rydell 1992; Agosta et al. 2005), some parameters were tested both throughout the day and during this period of maximum activity (see Table S1).

Generalized Linear Mixed Models (GzLMM) (Barré et al. 2018) were used for modelling purposes, by applying the 'glmer' function from the 'lmer4' R package (Bates et al. 2015). The factor year was settled as a random effect to control any possible pseudo-replication (Barré et al. 2018). A binomial error distribution and logit link function were used (Zuur et al. 2009). The Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) plot was taken as a measure of the overall fit of the models (Fielding and Bell 1997). AUC values range from 0 to 1, where the maximum score of 1 represents perfect discrimination and a medium score of 0.5 represents random predictive discrimination (Phillips et al. 2006).

Prior to model building, weather variables were standardised: the scales were converted to z-scores in order to avoid convergence problems and to allow the comparison of the different outputs (Thippa Reddy et al. 2020). We then tested for collinearity among continuous independent variables, using an estimate of the pairwise Spearman-rank correlation coefficient. When a pair of environmental variables was highly correlated ($|rs|>0.70$) the variable with the greatest explanatory capacity according to its AIC in the univariate model was included to be tested it into the final model (Table S2, supplementary material). This was determined by comparing the Akaike information criteria values of GzLM univariate models (fitted with a binomial error distribution and logit link function) (Zuur et al. 2009). The selected variables were then incorporated into the models following a stepwise forward procedure, according to their explanatory capacity, and ranked by their AIC (Akaike 1973; Burnham and Anderson 2002). Once the best model was chosen, the variables were transformed back to their real values by descaling the z-score values. The best model was used to predict the mortality probability per turbine.

## Results

Over 11 years covered by the time-series dataset, 2,858 bat fatalities were reported. Not all specimens could be identified at species level, but the majority (95.3%) were identified at genus level. Only three of these genera exceeded 1% of fatalities: *Pipistrellus* spp. (69.9%), *Eptesicus* spp. (19.2%) and *Nyctalus* spp. (4.0%; Table 1).

Bat fatalities occurred throughout the year, although most of the mortality was concentrated between July and October (Fig. 2a). The length of the period for which the fatalities were detected differed significantly between the three main affected taxa, although the peak mortality (expressed as the cumulative median days of fatalities) was very similar among them (see Table 1). The genus *Pipistrellus* presented the longest period of mortality (268 ± 49.2 average days), recording fatalities throughout the year with a marked peak in August and September. The genus *Eptesicus* presented a period of mortality of intermediate duration (151 ± 33.1 days on average), between February and November, with a peak also occurring in the months of August and September. The genus *Nyctalus* had the shortest period of mortality (96 ± 37.8 average days), which was concentrated in summer (i.e. between June and October) with a marked peak in August. Only 57 fatalities (2%) were registered between November and February, with 90% of bats identified during this period corresponding to the *Pipistrellus* genus, whereas no fatalities were recorded in this winter periods for bats belonging to the genera *Nyctalus* and *Eptesicus*. (Table 1; Fig. 2b).

The taxa with lower levels of mortality included *Miniopterus schreibersii*, *Tadarida teniotis*, and those of the genus *Myotis* (Table 1). The mortality of *Myotis* spp. peaked between July and August, whereas *Miniopterus schreibersii* had two peaks of fatalities, the first in late summer (August-September), and the second in November. *Tadarida teniotis* reached maximum fatalities in October (Fig. 2). The other taxa were recorded only occasionally and at a very low frequency (0.35% of total fatalities) (Table 1).

### Factors influencing annual and winter mortality

After the collinearity analysis, the following parameters were retained to be tested against daily occurrence of bat mortality: average humidity, accumulated precipitation, precipitation, maximum temperature and wind speed and direction (Table S2, supplementary material).

Maximum temperature was the first explanatory variable to be incorporated into the model, and had a positive effect. This factor accounted for a 12.3% of deviance and the AUC value (0.833) and had good predictive performance (Table 2). The probability of daily bat mortality began to increase as temperatures exceeded 20 ºC, and increased more mark-

**Table 1** Number of fatalities and parameters related to the temporality of the collisions. For the three main groups (*Pipistrellus* spp., *Eptesicus* spp. and *Nyctalus* spp.), averages and standard (SD) deviations are shown, and *p* values refer to the post-hoc Wilcoxon matched-pairs signed-ranks test (Wilcoxon 1945). For the other groups, the earliest and the latest fatality dates during the entire study period are shown

| Taxon | # Years with fatalities | # fatalities | First fatality | | | Median | | | Last day | | | Period length | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Date | SD (days) | *p* | Date | SD (days) | *p* | Date | SD (days) | *p* | No. of days | SD (days) | *p* |
| *Pipistrellus* spp. | 11 | 1999 | 27-feb | 36,4 | 1–2** | 25-aug | 7,2 | 1–2 n.s. | 23-nov | 20,7 | 1–2*** | 268,5 | 49,2 | 1–2*** |
| *Eptesicus* spp. | 11 | 548 | 13-may | 35,2 | 2–3* | 25-aug | 6,6 | 2–3 n.s. | 11-oct | 13,9 | 2–3*** | 151,5 | 33,1 | 2–3*** |
| *Nyctalus* spp. | 11 | 114 | 19-jun | 32,3 | 1–3*** | 3-aug | 32 | 1–3 n.s. | 23-sep | 17,2 | 1–3* | 95,9 | 38,7 | 1–3** |
| *Myotis* spp. | 8 | 22 | 15-apr | | | | | | 29-sep | | | | | |
| *Miniopterus schreibersii* | 6 | 17 | 12-jul | | | | | | 26-nov | | | | | |
| *Tadarida teniotis* | 8 | 14 | 23-apr | | | | | | 11-nov | | | | | |
| *Hypsugo savii* | 4 | 6 | 13-jul | | | | | | 01-sep | | | | | |
| *Rhinolophus* spp. | 1 | 2 | 14-sep | | | | | | 23-sep | | | | | |
| *Barbastella barbastellus* | 1 | 1 | 21-may | | | | | | | | | | | |
| *Plecotus* spp. | 1 | 1 | 12-aug | | | | | | | | | | | |
| Unidentified | 6 | 134 | | | | | | | | | | | | |

Legend: (1) *Pipistrellus* spp.; (2) *Eptesicus* spp.; (3) *Nyctalus* spp.; n.s.: non-significant; *p < 0,05; **p < 0,01; ***p < 0,001; spp.: species edly above 30–35 ºC (Fig. 3). The incorporation of additional predictors did not contribute substantially to improving the explanatory capacity of the model (Delta AIC < 1%; Table 2).

When modelling winter data (November-February), the best model also incorporated maximum temperature as the only significant factor (Table 3). The AUC value (0.747) indicates a relatively good predictive performance. The probability of daily bat mortality also increased as temperatures rose above 20 ºC in the winter (Fig. 4).

## Discussion

There is now increasing evidence that wind farms may be an important cause of bat mortality (e.g. Kruszynski et al. 2022). In this study, we analysed an extensive database containing more than ten years of information on bat mortality at different wind farms, all of them located in the extreme south-west of Europe.

We found that a wide range of bat taxa died at these wind farms. Nonetheless, the vast majority of fatalities were concentrated among bats of the genus *Pipistrellus* (~70%), followed by those of the genera *Eptesicus* and *Nyctalus*. These results are in line with studies conducted in northern and central Europe (Rydell et al. 2010). These groups of fissuric and forest bats are aerial hunters with long and narrow wings (Norberg and Rayner 1987), are morphologically adapted for life in the open air (Rydell et al. 2010), and fly at the same height as turbine rotors (Endl et al. 2005; Brinkmann et al. 2006; Seiche 2008). These species are considered common or very common in our study area, with the exception of *Nyctalus lasiopterus* (Ibáñez 1998). In contrast, other genera such as *Myotis*, *Plecotus* and *Barbastella* exhibited lower mortality rates. These bats are relatively broad-winged and manoeuvrable species that usually feed near surfaces or within vegetation and avoid open and exposed situations (Norberg and Rayner 1987). Therefore, they normally tend to fly below rotor height (Endl et al. 2005; Seiche 2008; Collins and Jones 2009), and are thus less susceptible to being killed by wind turbines. This would explain why, in our study area, few collisions were recorded between bats of the genus *Myotis* and wind turbines, despite this genus being relatively common (Ibáñez 1998).

Bat mortality occurred throughout the year in our study area. The vast majority of bat collisions with wind turbines in the province of Cádiz during our study period occurred during and autumn, and especially during August. For *Eptesicus* and *Nyctalus*, fatalities were concentrated from May to October, a similar temporal pattern to that found in other areas (Arnett et al. 2008; Cryan and Barclay 2009; Rydell et al. 2010). Greater bat mortality in these seasons may be due to higher foraging activity in the windfarm areas linked to greater food (mainly insects) availability, the necessity to satisfy the increasing energy demands for preparation of hibernation or torpor, as well as to the presence of juveniles, which temporarily raises population density (Cryan 2003; Dietz and Kiefer 2018; Choi et al. 2020).

In our study area, fatalities also occurred during all winter months in the case of bats belonging to the genus *Pipistrellus*, although this winter mortality accounted for a very low percentage of the overall recorded fatalities throughout the year. Studies reporting mortality in winter, when most bats show little or no activity, are very rare (Stawski et al. 2014; Weaver et al. 2020). The majority of studies have focused their efforts on warmer months, when mortality peaks are reported (Arnett et al. 2008; Rydell et al. 2010; Squires et al. 2021). However, some species of bats may be also active during the winter months, as has

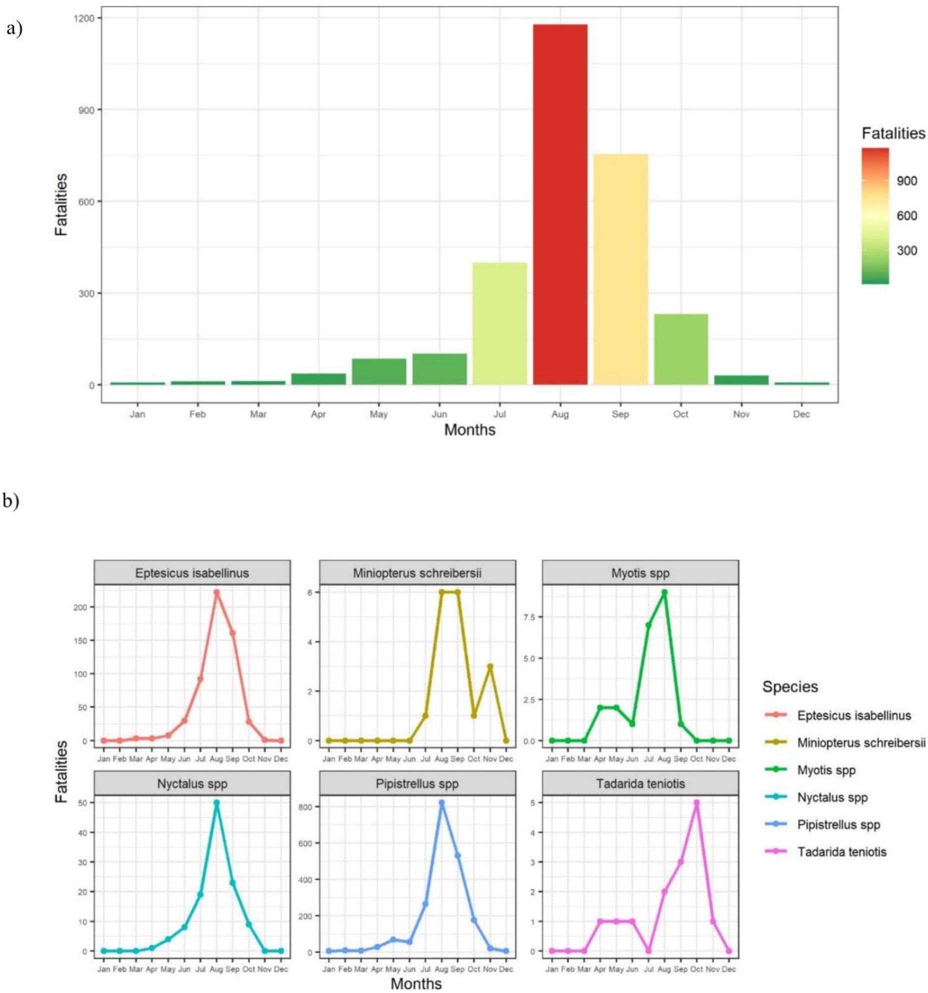



**Fig. 2** Temporal distribution of bat fatalities at wind farms in the province of Cádiz. **a** Absolute frequency of mortality per month, accumulated by year; **b** fatalities per month for the main taxonomic groups

been shown for the free-tailed bat Tadarida teniotis and Pipistrellus spp. in northern Portugal (Barros et al. 2017, 2021). In fact, some bat species have been recorded as active in southern Canada and in the Coastal Plain and Piedmont of North Carolina even at temperatures below 0 °C (Lausen and Barclay 2006; Grider et al. 2016).

## Global warming is expected to increase bat mortality at windfarms

Our results indicate that maximum daily temperature is the variable that best explains the probability of bat mortality at wind farms in our study area. According to the model prediction, the probability of fatality throughout the year started to increase slightly as temperatures rose beyond 20 °C, but increased sharply when the temperature exceeded 30 °C. These

**Table 2** Best explanatory models for the probability of bat mortality at wind farms throughout the year

| | | Estimate | Std. Error | Z – value | Pr(>\|z\|) | Random effects (YEAR) | | AIC | ΔAIC | deviance | df.resid | AUC index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Variance | Std. Dev | | | | | |
| Step | Null model | -4.714 | 0.115 | -41.05 | <0.001 | 0.14 | 0.37 | 22,500 | | 22495.5 | | |
| **1** | **Intercept** | **-4.291** | **0.12** | **-35.6** | **<0.001** | **0.15** | **0.39** | **19,738** | **2762** | **19731.9** | **214,410** | **0.833** |
| | **T_max** | **0.171** | **0.003** | **50.7** | **<0.001** | | | | | | | |
| 2 | Intercept | -3.629 | 0.138 | -26.24 | <0.001 | 0.18 | 0.42 | 19,553 | 184.5 | 19545.4 | 214,409 | 0.835 |
| | T_max | 0.228 | 0.005 | 40.12 | <0.001 | | | | | | | |
| | Ave_hum | 0.035 | 0.003 | 13.2 | <0.001 | | | | | | | |
| 3 | Intercept | -4.116 | 0.144 | -28.609 | <0.001 | 0.17 | 0.41 | 19,441 | 112.6 | 19424.8 | 214,405 | 0.84 |
| | T_max | 0.219 | 0.006 | 37.906 | <0.001 | | | | | | | |
| | Ave_hum | 0.034 | 0.003 | 12.281 | <0.001 | | | | | | | |
| | Direct_wind_north | 0.538 | 0.111 | 4.851 | <0.001 | | | | | | | |
| | Direct_wind_south | 0.498 | 0.081 | 6.176 | <0.001 | | | | | | | |
| | Direct_wind_variable | -14.917 | 28.622 | -0.521 | 0.602 | | | | | | | |
| | Direct_wind_west | 0.66 | 0.063 | 10.406 | <0.001 | | | | | | | |

Only models with most significant variables, ordered by Akaike Information Criterion (AIC) value, have been included in the table. The best model has been bolded

T_max: maximum daily temperature; Ave_hum: average daily humidity; Direct_wind, wind direction; df.resid: residual degrees of freedom; AUC index: area under the curve index ranges of temperature are relatively common in the south of Spain from spring to autumn (Fig. 5). On the other hand, the mortality response during the winter showed a similar pattern, with a slight increase as temperatures exceeded 20 °C. In our study area, winter maximum temperatures are typically lower than 20 °C. However, they can exceed this threshold on some days, particularly during November and December (Fig. 5).

With regard to absolute mortality, daily collision figures were very low in winter. Nevertheless, given the high number of turbines in the area (there are more than 900 turbines operating in the province), even these low mortality rates can produce considerable casualties among bat species which are active during winter.

The positive correlation between temperature and mortality can be interpreted as a consequence of bat activity at local level, particularly in winter. Several studies have shown positive correlations between the abundance and level of activity of bats and temperature (Wolbert et al. 2014; Jorge et al. 2021), but studies showing relationships between temperature and bat mortality are uncommon (Amorim et al. 2012). The increase of temperature in spring triggers an increase in the biomass and availability of insects that are a food resource for many species of bats (O'Donnell 2000; Meyer et al. 2016). Moreover, previous studies highlight the important influence of temperature on the time at which bats emerge from torpor (Erickson and West 2002; Frick et al. 2012; Lemen et al. 2016; Barros et al. 2017).

In this sense, whereas bats are expected to be particularly sensitive to climate change (Voigt and Kingston 2015), the concrete evidence for the responses of this group to the expected changes is not yet clear (Festa et al. 2022). In Spain, the regionalized projections of global climate models (Amblar Francés et al. 2017) foresee an increase of 1.5 °C in maximum winter temperatures by 2050 for the south of Spain, and an increase of 1.8 °C in maximum annual temperatures. While previous studies have focused on geographical distribution changes as the main response of bats to climate change (e.g. Rebelo et al. 2010; Smeraldo et al. 2021; Thapa et al. 2021), the present study highlights an association between the potential increase in bat mortality at windfarms in temperate areas and the expected increase in temperature.

## Potential biases

Positive identification at the specific level is not always easy within the bat group. Some examples in our study area include the difficulty of distinguishing between the complex species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus, Eptesicus serotinus* and *Eptesicus isabellinus*, or *Myotis nattereri* (e.g. Hulva et al. 2004; Ibáñez et al. 2006). This implies significant difficulties when determining the impact on a particular species. This is the case for endangered species, such as *Nyctalus lasiopterus*, classified as Vulnerable at global level (Alcaldé et al. 2016). In our study, 6.3% of registered fatalities could not be identified at the species level, while the majority of the carcasses were only identified at the genus level (92.4%).

Mortality estimates in this research (as in most studies) were based on systematic searches for bat corpses around the turbines, but the actual mortality rate can be severely underestimated if the probability of detecting the corpses is low (Korner-nievergelt et al. 2011). In our dataset, the probability of carcass detection was not reported; this data is essential to estimate actual bat mortality at the regional level. Therefore, the apparent mortality reported in this study may underestimate the actual figures, and it is thus desirable that the carcasse detection rate should be assessed and reported in this type of surveillance program. Acous-

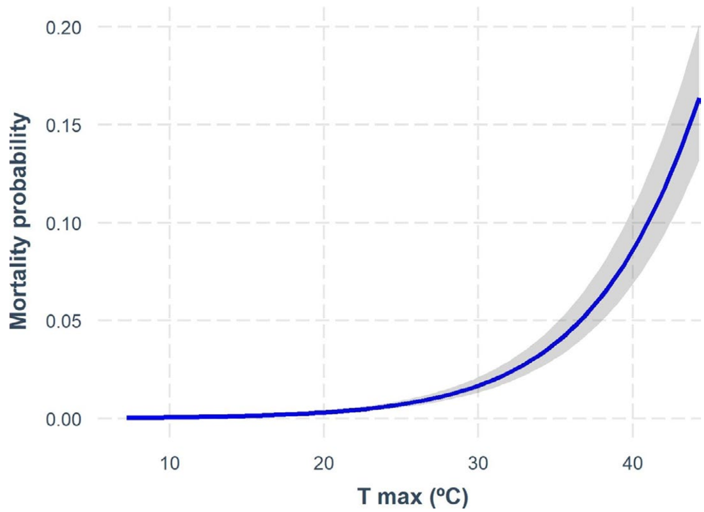



**Fig. 3** Averaged model response curve showing the relationship between bat mortality probability in wind farms and the main fixed factor in the best-fitting generalized linear mixed model (maximum temperature). The area shaded in grey represents the 0.95 confidence interval

**Table 3** Best explanatory models for the probability of bat mortality in wind farms in winter (November to February)

| | Estimate | Std. Error | Z –value | Pr(>\|z\|) | Random effects (YEAR) | | AIC | ΔAIC | deviance | df.resid | AUC index |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Variance | Std. Dev | | | | | |
| Null model | -7.343 | 0.231 | -31.82 | < 0.001 | 0.31 | 0.55 | 838.5 | | 834.5 | | |
| **Intercept** | **-10.748** | **0.83** | **-12.954** | **< 0.001** | **0.29** | **0.54** | **823.2** | **15.34** | **817.2** | **70,385** | **0.747** |
| **T_max** | **0.19** | **0.042** | **4.4241** | **< 0.001** | | | | | | | |
| Intercept | -6.126 | 0.614 | -9.976 | < 0.001 | 0.3 | 0.55 | 820.0 | 3.17 | 812 | 70,351 | 0.761 |
| T_max | 0.165 | 0.043 | 3.84 | < 0.001 | | | | | | | |
| Wind speed | -0.04 | 0.019 | -2.148 | 0.032 | | | | | | | |

Only models with significant variables, ordered by Akaike Information Criterion (AIC) value, have been included in the table. The best model has been bolded

T_max: maximum daily temperature; df.resid: residual degrees of freedom; AUC index: area under the curve index

tic surveys in the masts or nacelles of turbines may provide alternative or complementary information on bat activities in their surrounding areas (Roemer et al. 2017). However, the existence of a direct relationship between abundance and activity rates and mortality remains controversial (Amorim et al. 2012; Richardson et al. 2021).

On the other hand, although the climate variables considered get a relatively good predictive performance, our model reached a limited explanatory capacity, and many other factors can be influencing the temporal pattern of mortality in windfarms. Among these factors, seasonal increases in flight activity associated with mating (Cryan and Barclay 2009), presence of bodies of water (Rainho and Palmeirim 2011; Santos et al. 2013) or the landcover (Barré et al. 2018). More research would be necessary to account for additional factors that determine hazard for bats in wind farms.

## Implications for bat conservation in the context of global warming

Global warming is now a reality, and a fast transition to renewable energy sources is one of the main strategies used to mitigate its effects. However, there is increasing evidence that wind power is having a significant impact on biodiversity, with flying fauna being particularly affected (e.g. Devereux et al. 2008; Ferrer et al. 2012; Gradolewski et al. 2021). Bat populations are particularly vulnerable to this impact, due to their poor conservation status and their low reproductive rate, which makes them highly vulnerable to additional causes of mortality (Barclay and Harder 2003; Voigt and Kingston 2015). Recent research has revealed the impact of wind power as a possible cause of the extinction of certain bat species (Frick et al. 2017). Therefore, it is urgently important to disentangle the mechanisms underlying bat mortality at wind farms and to develop tools to reduce the negative effects of wind turbines.

This study points out the relevance of temperature in the development of measurements aimed at reducing bat mortality, and provides a threshold for the implementation of specific mitigation measures. In fact, most of the wind farms in our study are part of a surveillance program in which wind turbines may be stopped during daylight hours to prevent bird fatalities under specific situations of risk (Sánchez-Navarro et al. 2020). However, no measure-

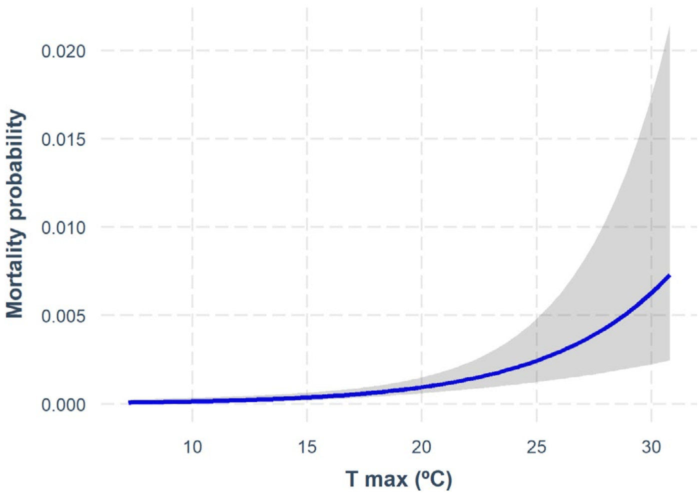
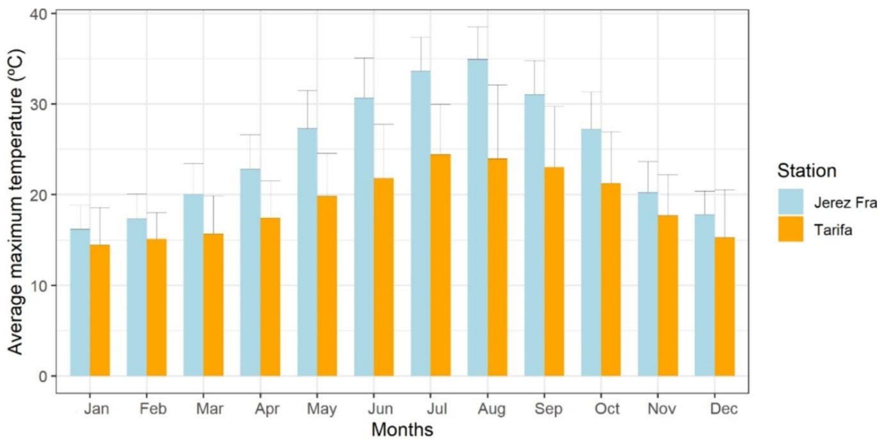



**Fig. 4** Averaged model response curve illustrating the relationship between prediction for winter bat mortality probability (November to February) in wind farms throughout the year and the main fixed factor in the best-fitting generalized linear mixed model (maximum temperature). The area shaded in grey represents the 0.95 confidence interval

ments have been implemented to specifically address the prevention of bat fatalities. The scheduling of selective shutdowns on days when the threshold temperature is exceeded, or the simple reduction of the speed of rotation of the turbine blades (Horn et al. 2008; Lintott et al. 2016), could reduce bat mortality in the study area. These measures could be concentrated in the first hours after sunset, when bat activity peaks at the edge of the forest and in open grassland (O'Donnell 2000). On the other hand, surveillance programs concentrate their attention in the period with higher risk, generally from August to October (Amorim et al. 2012), but our results indicate that winter mortality in temperate zones has an impact that should not be ignored, since it is expected to increase in the next decades. Therefore, we recommend that surveillance programs and mitigation measures should remain active

a)




b)

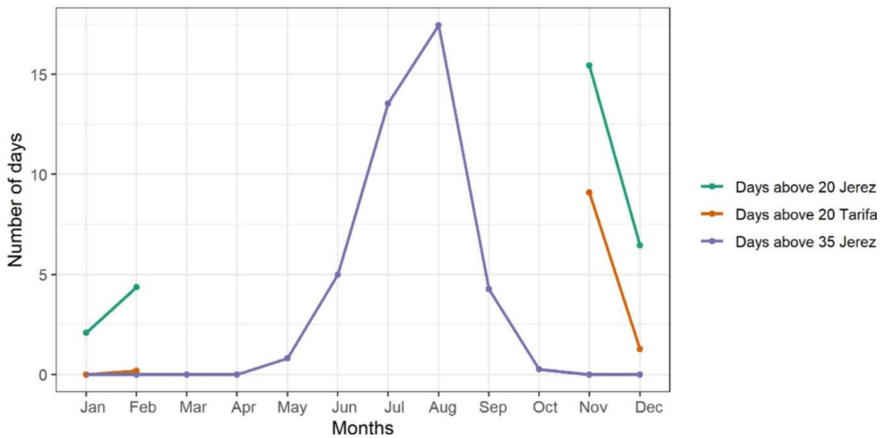



**Fig. 5** Monthly maximum temperatures (**a**, mean and standard deviation) and average number of days with temperatures above 35 ºC (throughout the year) and above 20 ºC (November to February) by months (**b**), during the study period (2009–2019). At the Tarifa weather station, no maximum temperature above 35 ºC was recorded within the study period

throughout the year. Finally, in the current scenario of climate change, the impact of global wind power on bat populations is expected to increase as global temperatures rise, and to expand to areas further north.

We conclude that both the environmental administrations and the wind power companies should adopt a new and more effective strategy for mitigating bat mortality, based on the current state of knowledge on the factors driving such mortality, and new research should be promoted to optimize mitigation measures.

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**Data Availability** The dataset generated during, and/or analysed during, the current study is available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors declare no competing interests.



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