



Disentangling drivers of power line use by vultures: Potential to reduce electrocutions

Marina García-Alfonso^{a,*}, Thijs van Overveld^a, Laura Gangoso^{b,c}, David Serrano^a, José A. Donazar^a

^a Department of Conservation Biology, Estación Biológica de Doñana (CSIC), C/Américo Vespucio 26, 41092 Sevilla, Spain

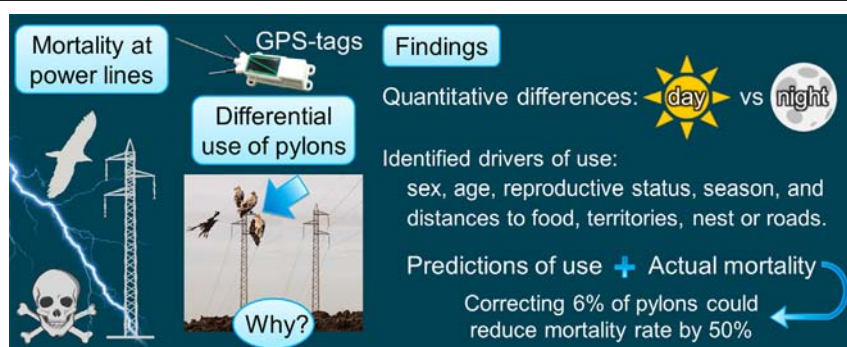
^b Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, the Netherlands

^c Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Complutense University of Madrid, C/José Antonio Novais 2, 28040 Madrid, Spain

HIGHLIGHTS

- Mortality associated with power lines is a major threat for many avian species.
- Understanding power line use for roosting and perching is key to minimise the problem.
- We used GPS-technology to determine the main drivers of power line use by vultures.
- Power line use varied strongly according to environmental and individual factors.
- Model validation shows that correcting 6% of pylons may reduce mortality rate by 50%.

GRAPHICAL ABSTRACT



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ABSTRACT

Accidents on power lines are the leading cause of mortality for many raptor species. In order to prioritise corrective measures, much effort has been focused on identifying the factors associated with collision and electrocution risk. However, most studies lack of precise data about the use of pylons and its underlying driving factors, often relying on biased information based on recorded fatalities.

Here, we used multiple years of high-resolution data from 49-GPS tagged Canarian Egyptian Vultures (*Neophron percnopterus majorensis*) to overcome these typical biases. Birds of our target population use electric pylons extensively for perching (diurnal) and roosting (nocturnal), so accidents with these infrastructures are nowadays the main cause of mortality. Predictive models of pylon intensity of use were fitted for diurnal and nocturnal behaviour, accounting for power line, environmental, and individual vulture's features. Using these measures as a proxy for mortality risk, our model predictions were validated with out-of-sample data of actual mortality recorded during 17 years. Vultures used more pylons during daytime, but those chosen at night were used more intensively. In both time periods, the intensity of use of pylons was determined by similar drivers: vultures avoided pylons close to roads and territories of conspecifics, preferentially used pylons located in areas with higher abundance of food resources, and spread their use during the breeding season. Individuals used pylons unevenly according to their sex, age, and territorial status, indicating that site-specific mitigation measures may affect different fractions of the population. Our modelling procedures predicted actual mortality reasonably well, showing that prioritising mitigation measures on relatively few pylons (6%) could drastically reduce accidents (50%). Our findings demonstrate that combining knowledge on fine-scale individual behaviour and pylon type and distribution is key to target cost-effective conservation actions aimed at effectively reducing avian mortality on power lines.

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* Corresponding author.

E-mail address: margaralf@gmail.com (M. García-Alfonso).

1. Introduction

Electric transmission and distribution facilities are rapidly growing worldwide at annual rates of about 5% due to the global increase of energy demand. As such, the high-voltage transmission grid alone is currently composed of 65 million of km (ABS Energy Research, 2008; IEA, 2016; Jenkins et al., 2010; T&D Europe, 2016). It is well-known that these infrastructures have a number of environmental impacts (Bagli et al., 2011; Bevanger, 1998), with avian mortality as one of the most prominent ones (Jenkins et al., 2010; Loss et al., 2015). Power lines are responsible for killing tens of millions of birds in many regions of the world, causing the decline of local populations and aggravating the status of endangered species (APLIC, 2006; Lehman et al., 2007; Loss et al., 2014). Consequently, the identification of the most conflictive pylons and lines so as to the search for effective mitigation measures have been the focus of extensive research (APLIC, 2006; Bevanger, 1998; Ferrer and Janss, 1999; Gangoso and Palacios, 2002; Lehman et al., 2007; Tintó et al., 2010). Many of these studies focused on electrocutions of large winged species, one the most affected avian groups. Pylons of distribution power lines (<60 kV) are responsible for most of the accidents involving large body-sized birds (APLIC, 2006; Harness and Wilson, 2001; Olendorff et al., 1981), which occurs when the bird simultaneously touches two wires or a wire and the grounded metallic pylon (APLIC, 1996; Bevanger, 1998).

Attempts to identify avian electrocution risk indicate that mortality is largely determined by pylon location and design, with important contributions of other variables such as bird abundance, species-specific traits (e.g., morphology or behaviour), individual traits (e.g., age or sex), and environmental conditions (e.g., topography, prey density, land cover, or weather) (APLIC, 2006; Bevanger, 1998; Dixon et al., 2020; Dwyer et al., 2014; Mañosa, 2001; Mojica et al., 2018; Olendorff et al., 1981; Tintó et al., 2010). Traditionally, most studies are reactive, focusing on the correlates of observed mortality (Hernández-Lambrano et al., 2018) and, subsequently, proposing corrective measures on those pylons having killed birds in the past (Lehman et al., 2007). Some proactive initiatives have used fatalities to predict electrocution risk at large-scale areas (Dwyer et al., 2014; Harness et al., 2013; Hernández-Lambrano et al., 2018; Mojica et al., 2018; Tintó et al., 2010). These approaches are useful to alleviate the problem, but may also be highly sensitive to well-known biases such as carcass detectability, representativeness of surveyed sections, and observer efficiency (Shaw et al., 2015).

Predictive models can be improved when combined with high-quality maps accounting for the electric pylons density (Dwyer et al., 2020a), as well as the distribution and abundance of sensitive species (Bedrosian et al., 2020; Pérez-García et al., 2017; Smeraldo et al., 2020). This procedure, however, is contingent upon information availability. For example, the areas used by juveniles and non-breeding birds are often much less known than the spatial distribution of the breeding populations. In addition, data about use of power lines by birds may also suffer from important biases. In some cases, this use has been simply inferred from large-scale habitat use information (D'Amico et al., 2019; Pérez-García et al., 2017). More frequently, it has been deducted from visual observations of birds using these facilities, which biases detection of pylon use towards easily-detected behaviours such as communal roosting and nesting (Arkumarev et al., 2014; Crespo-Luengo et al., 2020; Moreira et al., 2018). Observations may also be influenced by the visibility of pylons from points accessible by car (Galmes et al., 2018) ("convenience sampling," Anderson, 2001). As a result, detailed data on the frequency and intensity of use of pylons by birds are almost lacking (Hernández-Matías et al., 2020; Pavón-Jordán et al., 2020). To fill these gaps, data describing how individual birds use power lines throughout the entire daily cycle are needed, since daytime and nighttime utilisation patterns may respond to different intrinsic and extrinsic constraints such as prey availability, territory attendance, social roosting, and human disturbances. Discerning

between them may be essential to obtaining more accurate predictions of power line use prioritising mitigation measures and planning future power developments (Buechley et al., 2018; Moreira et al., 2018).

Our main objective here was to identify those factors driving variation in the intensity of use of power lines and to investigate whether this information may be helpful in predicting vulture mortality risk. Large body-sized avian scavengers are highly susceptible to accidents in power lines, which has contributed to the precipitous global decline of this functional group of vertebrates (Koenig, 2006; McClure et al., 2018; Ogada et al., 2012; Proffitt and Bagla, 2004). It is particularly concerning in arid habitats with a scarcity of trees or other perches (Angelov et al., 2012; Benson, 1981; Donázar et al., 2002b; Lehman et al., 2007; Mainwaring, 2015; Phipps et al., 2013). Our model species is the globally endangered Egyptian Vulture. With up to 1.8 m of wing-span, it is especially susceptible to electrocution not only because it frequently lives in dry, treeless landscapes, but also because of its social habits that determine large concentrations of roosting birds on electric pylons (Arkumarev et al., 2014; van Overveld et al., 2018).

This research is based on the GPS tracking of 49 Canarian Egyptian Vultures from a long-term monitored population present in the island of Fuerteventura (and to some extent Lanzarote), Canary Islands, Spain. This methodology allows diminishing the above-mentioned biases by covering the entire infrastructures and time-activity periods. In addition, GPS tracking allows for jointly studying the use of power lines at fine spatial (individual pylons) and temporal (daily patterns of activity and behaviour) scales, as well as investigating potential differences associated with individual traits (e.g., sex, age and territorial status of birds). Despite some studies having used this technology to evaluate mortality risk associated to human infrastructures (Gustin et al., 2018; Watson et al., 2017), there is to date no published research that has assessed the use of power lines based on this extraordinary information combined with the above mentioned variables, with the exception of Dwyer et al. (2020b), who focused only on juveniles and did not address in-depth factors driving differences in power lines use.

More specifically, the aim of this study was to develop predictive models of pylon use from both, a pylon and an individual vulture approach. The focus is on factors describing the spatial and social structure of the population, the spatial distribution of feeding resources, the type of power line, and the environmental features linked to pylons' location and vultures' characteristics (see specific predictions in Table 1 and the description of the tested variables in Table 2). Then, the identified drivers of power line utilisation were applied to determine potential use of all the existing pylons on the study area. Finally, these predictions were compared with out-of-sample data on mortality recorded during the past 17 years.

2. Materials and methods

2.1. Study area and target population

The Canarian Egyptian Vulture is a sedentary, long-lived territorial scavenger with deferred sexual maturity (6–7 years, Agudo et al., 2012). Its population, endemic to the archipelago (Donázar et al., 2002a), declined strongly during the 20th century due to the incidence of non-natural mortality, mainly accidents with power lines and indirect poisoning (Donázar et al., 2002b). Currently, it survives only in the eastern islands of the archipelago, with the bulk of the population concentrated in Fuerteventura, where it dwells in semi-arid landscapes dominated by grass and scrublands (Rodríguez Delgado et al., 2000). It breeds from February to late June in cliff holes and ledges where one or two fledglings are raised. It relies heavily on goat carcasses (Gangoso et al., 2006; Medina, 1999) obtained at farms, but also exploits natural resources as well as supplies provided at two supplementary feeding stations (SFS) created in 1998 and 2008, and a large garbage dump (Fig. 1). Both feeding stations are provided with goat and sheep

Table 1

Predictions for each variable included in the modelling procedure aimed at determining the intensity of use of electric pylons by Canarian Egyptian Vultures in Fuerteventura (Canary Islands, Spain). See Table 2 for a full description of considered variables.

Categories	Variable	Predictions		References	
		Territorial	Non-territorial		
Main food resources	Livestock	An increase of use in areas with more livestock and higher probability of abandoning livestock carcasses.		Donázar and Fernández, 1990 van Overveld et al., 2018	
	Dist HPFP	A decrease of use with distance to highly predictable feeding points because these places offer spatially predictable food resources also acting as social meeting points. Therefore, individuals concentrate their activity around these points. Since they have different characteristics, we considered them together and separately, except for the less used SFS in the north.			
	Dist mSFS				
Temporal constraints	Dist Dump	An increase of use on the breeding season due to changes in spatial patterns derived from territory attendance (territorial birds) and prospecting behaviour (non-territorial birds) which would spreads the use of pylon.		van Overveld et al., 2018	
	Breeding				
Territories spatial constraints	Territories	An increase of use in areas with more density of territories of targeted individuals because they will rest preferably near to their territories due to central-place foraging restraints.	–	Fluhr et al., 2017	
	Dist Terr	–	An increase of use with distance to the nearest occupied territory because owners defend the surroundings of their nests.		García-Heras et al., 2013
	Dist Nest	A decrease of individual use with distance to its own nest due to territoriality constrains.	–		
Pylons spatial constraints	Dist Road	An increase of use with distance to roads because of less human disturbance.		Gavashelishvili and McGrady, 2006	
	Wind	A decrease of use with wind speed due to increasing difficulties for flying and maintaining resting positions.			
Pylon characteristics	Line	Higher use on T. Line 66 since it is the oldest power line together with D. Line but having more altitude and lower in T. Line 132 due to its novelty.		Peters and Otis, 2007 Infante and Peris, 2003; Moreira et al., 2017, 2018	
	Age	A decrease of use with age because of lower needs of exploring thanks to higher experience.	An increase of use with age because of wider exploratory movements		Daunt et al., 2007; de Grissac et al., 2017
Vultures characteristics	Sex	A differential use according to sex since males and females animals usually differ in their behaviour and ecology.		Catry et al., 2006; Rubin and Bleich, 2006	
	K95 K50	A decrease of use with wider home range area (95%) or core area of use (50%) due to an expected increase in the number of used pylons.			

carcasses by local farmers, but the one located in the centre of the island is also supplied with slaughterhouse remains (ca. 200 kg per week) (van Overveld et al., 2018). This is the oldest feeding station and most used by the vultures, so it was considered as the main SFS (mSFS). Particularly during the non-breeding season, vultures gather in large numbers at this feeding station (up to 150 different individuals during a day), congregate at communal roosts on power lines but in lower numbers (up to 35 simultaneous individuals in a pylon), and conform small aggregations at the garbage dump (up to 15 simultaneous individuals) and large livestock farms (up to 10 simultaneous individuals) based on field observations (see also Donázar et al., 2002b; van Overveld et al., 2018, 2020b for details).

This population has been intensively monitored since 1998. Intensive ringing schemes (metallic and plastic rings readable with spotting scopes) have determined that about 90% of the population was individually identifiable in 2018 (Badia-Boher et al., 2019). Field work is done each year during the breeding season when territories are regularly visited to identify territorial birds and to record breeding parameters. Birds are considered territorial when they actively defend a breeding area independently of the occurrence and success of their breeding attempts.

2.2. Data collection

2.2.1. GPS data

From June 2013 to September 2017, 49 Canarian Egyptian Vultures were trapped with cannon-nets, involving 23 males and 26 females, aged from 0 (fledgling) to 14 years old (see SM1 for details). All territorial vultures belonged to different nests except by one pair (Bird ID 221 and 222). This accounted for 14.3% of the total population size estimated in 2018 (authors, own data). Birds were fitted with the following GPS-devices: 27 UvA-BiTS (Bouten et al., 2013)

and 21 E-obs (GmbH, Munich, Germany) that were attached to 30 (including reusing) and 21 individuals, respectively. Both kinds of devices have multiple on-board sensors providing the geographical coordinates, altitude, and speed of each individual according to a defined time interval (see below). Devices were attached as backpacks using 0.84 and 1.12 cm wide Teflon harnesses. Total system weight was between 31 g (UvABiTS) and 54 g (E-obs), accounting for the 1.4–2.4% of the mean total body mass so that negative effects can be discarded (see Sergio et al., 2015).

All procedures were subject to ethical review and were carried out in accordance with the approved guidelines set out by the Bioethics and Animal Welfare Committee (CEEA-EBD-CSIC). Vulture trapping and marking were approved by the Canarian Government.

2.2.2. Mortality data

All of the Canarian Egyptian Vulture carcasses found since 1998 ($N = 100$) were assigned to one of six death causes through necropsy in wildlife rehabilitation centres and veterinary facilities: (1) intoxication due to indirect poisoning by toxic baits; accidents with power lines either due to (2) electrocution, (3) collision, or (4) entanglement; (5) other causes, including shooting, lead poisoning, collision with wind turbines, and apparent natural mortality (e.g., diseases or malnutrition); and (6) unknown causes (see Badia-Boher et al., 2019 for details on carcasses recovery). From 2014 onwards, accidents in power lines, and particularly electrocutions, were the main known cause of mortality (Fig. 2). A total of 27 carcasses were found associated to accidents with power lines, corresponding to 19 electrocutions, 4 entanglements, and 4 collisions. These quantities could be higher considering other carcasses that were found close to power lines: in 16 cases, the cause of the death was not determined because the rapid decomposition of the remains precluded an accurate necropsy, whereas only 4 cases corresponded to other mortality causes not associated to power lines.

2.3. Characteristics of pylons

There are three power lines that belong to two electric companies operating in Fuerteventura. These two electric companies provided coordinates of all the pylons (Fig. 1). Two different transmission lines are property of Red Eléctrica de España (REE). The oldest line has a power of 66 kV (hereafter “T. Line 66”). It comprises 356 pylons, whose heights vary between 15 and 40 m (mean \pm SD = 22.2 ± 4.8 m) and are separated from each other by a mean \pm SD distance of 240 ± 69 m. The most modern line (see below) has a power of 132 kV (hereafter “T. Line 132”) and comprises 192 pylons, whose heights vary between 28 and 49.2 m (mean \pm SD = 36.8 ± 5.4 m), and are separated by a mean \pm SD distance of 319 ± 83 m. Finally, the distribution line grid (hereafter “D. Line”) is property of ENDESA ENEL. It has 2110 pylons, whose heights are between 11 and 18 m (individual heights were not available), separated by a mean \pm SD distance of 135 ± 68 m. T. Line 66 and D. Line were already operating at the beginning of this study. However, the T. Line 132 was built during 2016 and hence, for analytical procedures, it was only considered from the 1st of January 2017 onwards.

2.4. Use of pylons by GPS-tracked vultures

Data were recorded from the 1st of July 2013 to the 31st of December 2018 (SM1) and split annual data into two six-month intervals (see below). For vultures tagged before 2015 ($n = 21$), and due to initial tests of the functioning, the time interval between locations

varied from 3 s to 20 min. From 2015 onwards, all devices had diurnal settings with time intervals between 1 and 10 min. For UvABITS, nocturnal settings involved a time interval of 1 h from 21:00 (UTC) to 5:00 (UTC) whereas E-obs devices did not collect locations approximately from 30 min after sunset to 30 min before sunrise, the schedule depending on the daylight duration and the charge of batteries of each specific device.

For the whole dataset, we first determined when a vulture was potentially perched on a specific pylon. Those GPS fixes associated with a pylon (<25 m, see SM2 for methodological issues) and with instantaneous speed lower than 2 m/s (García-Alfonso et al., 2018; Klaassen et al., 2017) were classified as “perched/roosted locations”. Then, nocturnal and diurnal locations were considered separately, distinguishing hereafter roosting (nocturnal) and perching (diurnal) behaviour. Nocturnal use of pylon was determined by using locations collected while the sun was 6° under the horizon, which minimised the loss of data while avoiding diurnal resting behaviour. To avoid imprecisions derived from movements between pylons during the night, nocturnal locations were clustered and a mean position was calculated based on locations of the cluster where individuals spent most of the time (details in SM3). Diurnal use was calculated using locations collected between sunrise and sunset always accounting by the circannual variation in these hourly limits (see the amount of retained locations in SM4). Diurnal information was resampled (time interval of 30 min with tolerance of 5 min, see details in SM5) to diminish temporal autocorrelation derived from short intervals between locations. When the first pylon used during a day matched the pylon used for roosting the previous night, that diurnal use was discarded to avoid duplications of a same use. The same criterion was applied when the last pylon used during a day matched the pylon used for roosting the next night.

Table 2

Description of explanatory variables considered for modelling the use of electric pylons by Canarian Egyptian Vultures on Fuerteventura.

Variable	Description
Fixed factors	
Dist HPFP	For each pylon, distance to the nearest highly predictable feeding place (dump or supplementary feeding stations).
Dist mSFS	For each pylon, distance to the main supplementary feeding station.
Dist Dump	For each pylon, distance to the garbage dump.
Dist Road	For each pylon, distance to the nearest road.
Dist Urb	For each pylon, distance to the nearest urban area.
Line	For each pylon, the kind of power line to which it belongs, i.e., T. Line 66, T. Line 132, or D. Line (see Section 2.3).
Wind	For each pylon, mean wind speed (m/s) at 40 m of altitude according to ITC (2021).
Dist Terr ^b	For each pylon, and semester, distance to the nearest territory occupied during the year.
Dist Nest ^c	For each pylon, territorial vulture, and semester, distance to its nest during the year.
Territories ^{a,d}	For each pylon and semester, density of territories of GPS-tracked vultures included in analyses of the corresponding semester.
Livestock ^d	For each pylon and semester, density of goats and sheep on the basis of livestock censuses multiplied by the probability of abandoning carcasses based on the predictive model performed (SM9).
Breeding	For each semester, breeding season (1) or not (0).
Sex ^c	For each individual, male or female.
Age ^c	For each individual and semester, age calculated as the year of the semester minus the year of birth.
K95 ^c	For each individual and semester, the home range area (95%) or core area of use (50%) in km ² , calculated using kernel density estimation with a smoothing parameter of 1500 m.
K50 ^c	
Random factors	
Semester ID	Period comprising the former or later six months of each year from 2 nd semester of 2013 to 2 nd semester of 2018.
Pylon ID	Pylon identity.
Bird ID ^c	Individual vulture identity.

^a Used only in PYLONS models for territorial individuals.

^b Used only in PYLONS models for non-territorial individuals.

^c Used only in VULTURES models.

^d See SM10 for details on how densities were calculated.

2.5. Analytical and statistical procedures

Since vulture foraging behaviour depends to a large extent on territorial status and breeding season (van Overveld et al., 2018), annual data were split into two six-month intervals (*Semester ID*), so that the first semester of each year (January–June) was considered as the breeding season (*breeding* = 1) and the second (July–December) as the non-breeding season (*breeding* = 0).

Two response variables were considered in the modelling procedure:

- (1) **PYLON**. It describes the intensity of use of each pylon on the basis of an index that jointly accounts for the number of individuals and the number of different days with use, i.e., “Number of days/individuals” ($N \text{ days/indv}$). To calculate this index, firstly, the number of days that each individual was recorded at least once at each pylon was quantified. Then, the values obtained for all individuals for each pylon were summed to obtain the final index value.
- (2) **VULTURE**. It describes the number of different days ($N \text{ days}$) that each individual used each pylon. Analyses were focused on those pylons used at least once during the study period not to increase unnecessarily model uncertainty.

Four different datasets were analysed for each response variable, separating *diurnal* (*D*) or *nocturnal* (*N*) locations, and information from *territorial* (*T*) or *non-territorial* (*NT*) individuals, because territoriality strongly affects individual behaviour (van Overveld et al., 2018). In datasets dealing with nocturnal locations and for each semester, only vultures with a reliable roosting place defined for at least half of the nights of each month were considered ($N = 282$ semesters from 46 individuals, resulting amount of locations in SM6). In the case of diurnal behaviour, locations were resampled to improve the balance of time interval between consecutive locations, using a range of 25–35 min. Then, for each semester, those vultures with at least 70% of

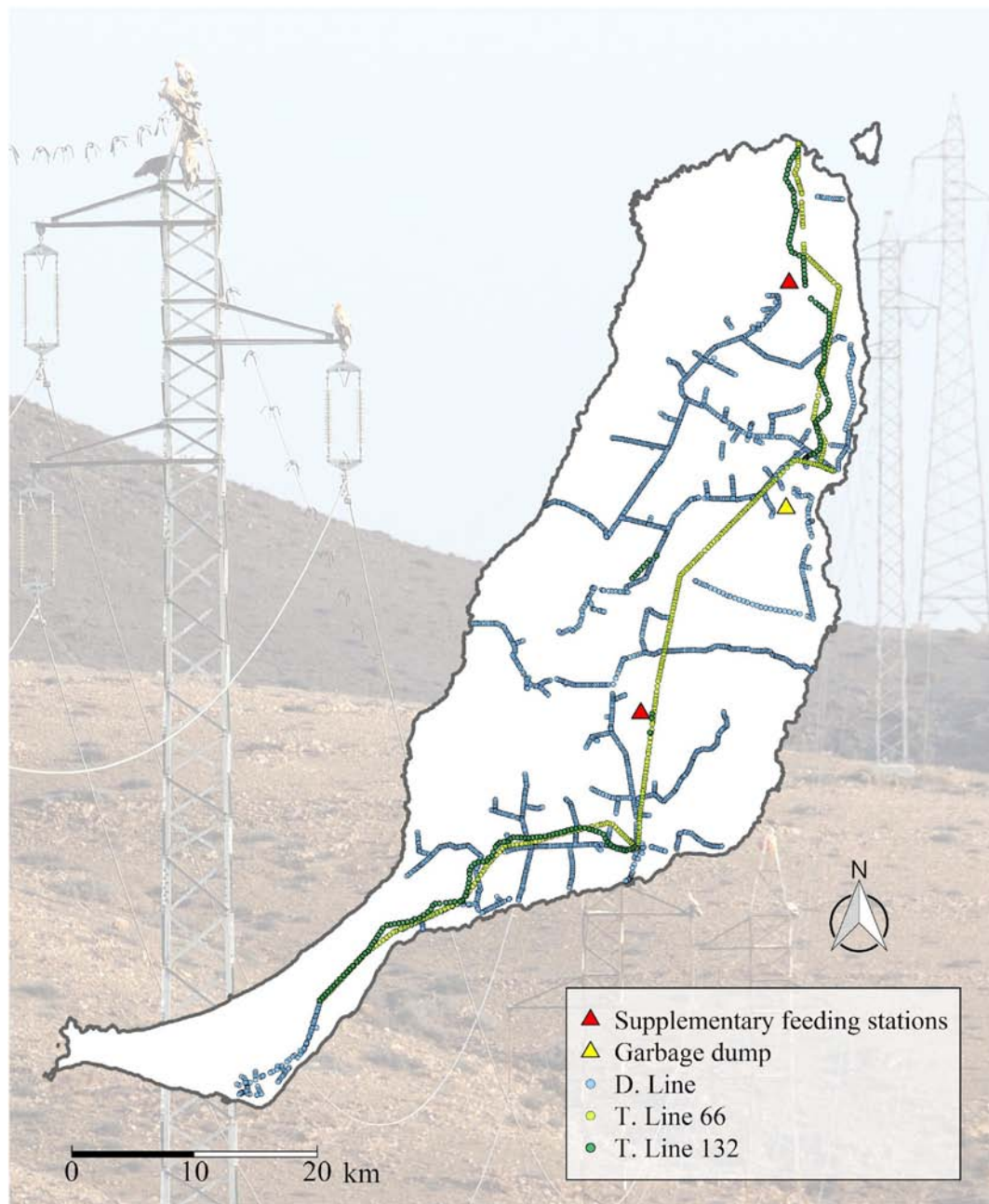


Fig. 1. Map showing the two transmission lines, the distribution power line, the garbage dump, and the two supplementary feeding stations available for Canarian Egyptian Vultures in Fuerteventura. Fuerteventura is the most south-easterly island of the Canary Islands (Spain) located in the north-east Atlantic Ocean (27.62° to 29.42° N and 13.33° to 18.17° W).

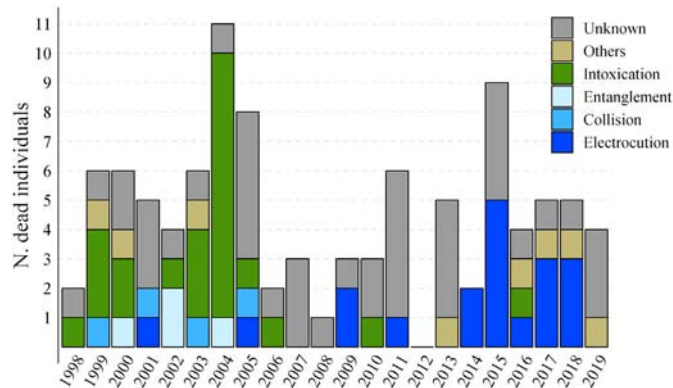


Fig. 2. Causes of detected mortality of Canarian Egyptian Vultures during the whole population monitoring period.

resulting time intervals adjusted to the resampling range were retained. Finally, only vultures with available information for at least half of the days of each month for each semester were considered ($N = 275$ semesters from 46 individuals, details in SM5 and resulting amount of locations in SM7).

A total of 15 fixed explanatory variables were considered, which are described in Table 2. Of these, all continuous variables were standardised to mean 0 and variance 1 by subtracting the means and dividing by the standard deviations. Pairs of variables with a Spearman's correlation coefficient higher than $|0.5|$ were never included in the same model to avoid collinearity problems (Graham, 2003), and additionally, multicollinearity was checked using the Variance inflation factor (VIF) before modelling procedure, which showed low values for all the explanatory variables (SM8). The variable *Dist Urb* was discarded because it was highly correlated with *Dist Road* and both variables could ultimately indicate a very similar environmental effect (human

disturbance). For the *VULTURE* approach, the variables *Dist mSFS* and *Dist Nest* on the datasets of territorial individuals were correlated. Due to the biological importance of *Dist Nest*, the variable *Dist mSFS* was discarded in that dataset and the locations of highly predictable feeding points (i.e., HPFP = supplementary feeding stations and the garbage dump) were considered only with the variable *Dist HPFP*, hence discarding *Dist Dump*. The two variables measuring the density of both territories (*Territories*) and availability of food (*Livestock*) were calculated using kernel density estimation per semester. This was done because the livestock census changed over time, because the nest occupied within a territory could vary each year, and because the number of tracked territorial individuals included in the analyses varied each semester (see details in SM9 and SM10).

Response variables were modelled as proportion data with a binomial denominator by means of Generalised Linear Mixed Models (GLMMs, binomial error distribution and logit link function). Hence, the total number of days or days/indv with available information for each semester was included as binomial denominator. *Bird ID*, *Pylon ID*, and *Semester ID* were included as crossed random factors (Table 2) based on improvements in values of the Akaike's Information Criterion corrected for small sample size (AICc) (Sugiura, 1978) after testing different combinations of these variables (see SM11). Models were fitted with all possible combinations of explanatory variables up to a maximum of 6 variables to avoid over-parameterisation. See SM12 for the total amount of fitted models and the size of each database. For the same reason, models were fitted including one interaction at most, considering all two-way interactions between the variable *Breeding* and the remaining explanatory variables when modelling *PYLON*, and between the variables *Breeding*, *Sex*, or *Age* and the remaining explanatory variables when modelling *VULTURE*. Model selection was done on the basis of AICc. Models including uninformative parameters were discarded, i.e., variables not explaining sufficient deviance to provide a net reduction in AICc (Arnold, 2010; Burnham and Anderson, 2002). Overdispersion was checked (Crawley, 2002) and the marginal and conditional R^2 (Johnson, 2014; Nakagawa et al., 2017; Nakagawa and Schielzeth, 2013) were determined in the selected models (hereafter R^2_m and R^2_c).

Absence of spatial autocorrelation was shown by an examination of the model residuals based on Moran's index between the 15 closest neighbouring pylons (SM13) and spline correlograms based on this index (Bjørnstad and Falck, 2001). R statistical software version 3.6.0 (R Core Team, 2019) was used for analyses with the *maptools* package (Bivand and Lewin-Koh, 2019) for calculating sunrise and sunset, *stats* for confidence intervals, *lme4* (Bates et al., 2015) for the GLMM analysis, *AICcmodavg* (Mazerolle, 2016) for model ranking, *MuMIn* (Barton, 2019) for calculating marginal and conditional R^2 (Barbosa et al., 2016), *usdm* (Naimi et al., 2014) for calculating VIF, and *RVAideMemoire* (Hervé, 2018) for calculating overdispersion in GLMMs.

Finally, the identified drivers of power lines utilisation by vultures were used to predict potential use of all the existing pylons on the study area. Then, pylons were sorted in a decreasing order of predicted intensity of use (*PYLON*) separately for territorial or non-territorial vultures and diurnal or nocturnal behaviour. Lastly, those predictions were compared with out-of-sample data on mortality recorded during the past 17 years. The locations of the pylons responsible for 18 electrocution fatalities were precisely known. Specifically, the number of these accidents that would have been avoided according to different amounts of pylons corrected was calculated following that priority order.

3. Results

The number of pylons used by the GPS-tagged birds differed between day and night (1118 vs. 532) with more pylons used during the day, while the intensity of use (*PYLON*) was higher during the night (Fig. 3). Considering the values found in each semester and only those pylons with at least one detected use, the correlation between the diurnal and nocturnal intensity of use (*PYLON*) during the breeding season

ranged from 0.18 to 0.50 with a mean of 0.34 ± 0.04 SD, and 0.36 ± 0.12 SD for territorial and non-territorial individuals, respectively. During the non-breeding season, this correlation ranged from 0.28 to 0.62 with a mean of 0.51 ± 0.07 SD, and 0.58 ± 0.07 SD, respectively. In addition, the three power lines (T. Line 132, T. Line 66 and D. Line) were used in different proportion, with 130, 289 and 699 pylons used (i.e. 68, 81 and 33% of each line) during the day and 88, 254 and 190 (i.e. 46, 71 and 9% of each line) during the night, respectively. Moreover, during the breeding season, the number of pylons used increased mainly in the case of non-territorial birds as compared to territorial ones, and the intensity of use decreased for territorial individuals, but increased for non-territorial ones, which overall showed higher intensity of use (Fig. 3).

Overall, GPS-tagged birds visited 42%–20% (day–night) of the 2658 electric pylons existing on Fuerteventura, with a maximum of 38–36 (day–night) different vultures detected in a single pylon throughout the study period (Fig. 4). Along the study period, a mean of 116 ± 78 SD pylons was visited by vultures during daytime and 63 ± 40 SD pylons during night (range 336–16 and 178–6, respectively) (Fig. 4).

Modelling of intensity of pylon use by non-territorial individuals (*PYLON NT*) showed only one top-ranked model for both diurnal and nocturnal datasets, showing an $R^2_m - R^2_c$ of 26.4–71.4 and 30.4–84.0, respectively, and the rest of models having $\Delta AICc > 25$ and 27, (SM14). Both models indicated that intensity of use was higher for those pylons that had higher density of available livestock in close proximity, and were farther from roads and vultures' territories (Table 3). Moreover, the use of power lines was unequal: T. Line 66 > T. Line 132 > D. Line. Additionally, the interaction between breeding season and distance to the main supplementary feeding station (mSFS) indicated that pylons located closer to this place were more used regardless of the season, while the pylons farther from this point were more used during the breeding as compared to the non-breeding season (Table 3). Results when modelling *VULTURES NT* showed only one top-ranked model as the most plausible for both diurnal and nocturnal locations, showing an $R^2_m - R^2_c$ of 20.7–46.5 and 28.6–56.1, respectively, and with the remaining models having $\Delta AICc > 58$ and 32 (SM14). The models showed similar results to *PYLON NT* in terms of selected variables and effects (Table 3).

Focusing on the intensity of use by territorial individuals (*PYLON T*), the modelling procedure identified again only one top-positioned model in each case (diurnal and nocturnal use), showing an $R^2_m - R^2_c$ of 20.6–78.3 and 17.4–91.8, and the rest of models having $\Delta AICc > 37$ and 36 (SM15). These two models revealed that the intensity of use was higher for those pylons with greater density of available livestock and territories occupied by GPS-tagged individuals in their surroundings (Table 3). Again, T. Line 66 and D. Line were the most and the least used power lines, respectively. Attending to diurnal use, the interaction between *Breeding* and *Dist Road* indicated that pylons located closer to roads were less used regardless of the season, while those farther from roads were more used during the breeding season (Table 3). For nocturnal use, the interaction between *Breeding* and *Dist mSFS* showed the same trend (Table 3) than for non-territorial individuals. The approach for *VULTURE T* showed slightly different results (Table 3), but there was also only one top-positioned model in both cases, showing an $R^2_m - R^2_c$ of 69.0–86.3 for diurnal and 58.6–85.5 for nocturnal use, and the rest of models having $\Delta AICc > 14$ and 13, respectively (SM15). Both models showed the same effect of livestock and type of power line as in the *PYLON* approach. In these cases, there was an attractive effect of highly predictable feeding points (HPFP), indicating a similar effect than that previously observed with the variable *Dist mSFS*. The proximity to roads had again some kind of negative effect on the use of pylons, but on nocturnal use such effect was less pronounced for males than for females. Additionally, results showed that for each individual, the distance between pylons and its nest has a strong negative effect on its use. This effect, in the case of diurnal use, was more pronounced in older than in younger territorial vultures (Table 3).

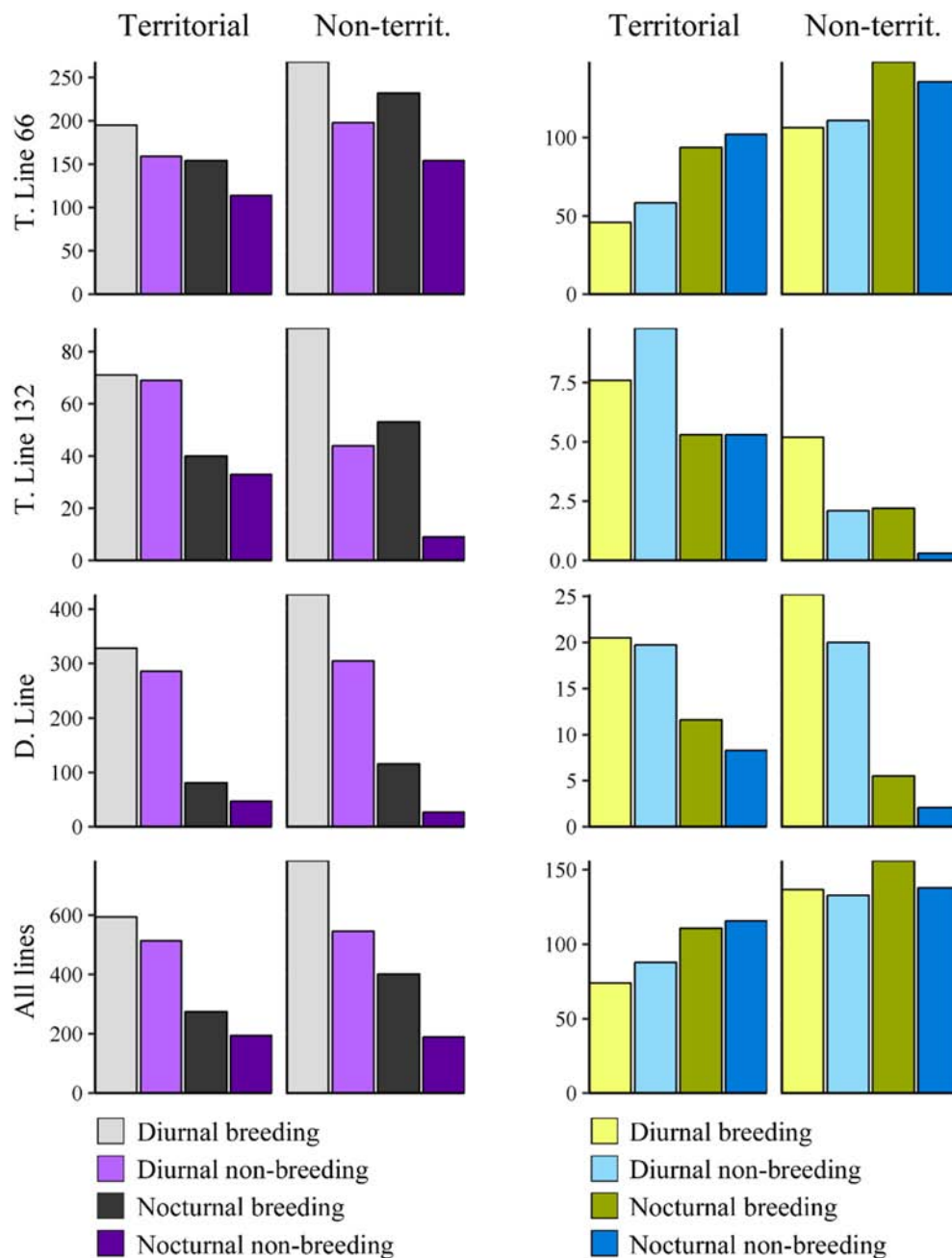


Fig. 3. Number of electric pylons used (left panel) by Canarian Egyptian vultures on Fuerteventura and intensity of use as number of days/indvs using electric pylons divided by the number of available semesters (right panel). Values are shown together and separately for each *Line*: transmission line of 66 kV or 132 kV, and distribution line; nocturnal and diurnal behaviour; breeding or non-breeding season; and territorial or non-territorial vultures.

Establishing a mitigation priority order according to the intensity of use (*PYLON*) predicted by the top-ranked models showed that effective correction of about 6% of pylons could have avoided about 50% of the observed electrocutions. These values were slightly different depending on the four different models applied: diurnal or nocturnal behaviour considering territorial or non-territorial individual birds. However, further increases in the number of corrected pylons only led to low increases in avoided fatalities (Fig. 5).

4. Discussion

Mortality associated with accidents in human infrastructures is a major concern in biodiversity conservation, especially under the unprecedented growing energetic demands and parallel declines in many

populations of large-sized birds. Approaches to solve this human-wildlife conflict have focused largely on the mitigation of mortality of birds in power lines. Research has been, however, based on potentially-biased methodologies, such as recorded fatalities, field observations of mostly roosting but also perching behaviour or partial considerations on pylon design and location. In this study, we took a step forward by incorporating modelling of intensity of use of electric pylons based on accurate field data from GPS-tracked individual birds. Our results revealed that patterns of pylon use by Egyptian Vultures can be complex and depend on individual- and environmental-based drivers. This knowledge will help to better understand differences in mortality risk between pylons, strongly improving effectiveness of mitigation strategies.

An important result was the verification of differences in diurnal and nocturnal use of pylons by birds, which, to our knowledge, has not been

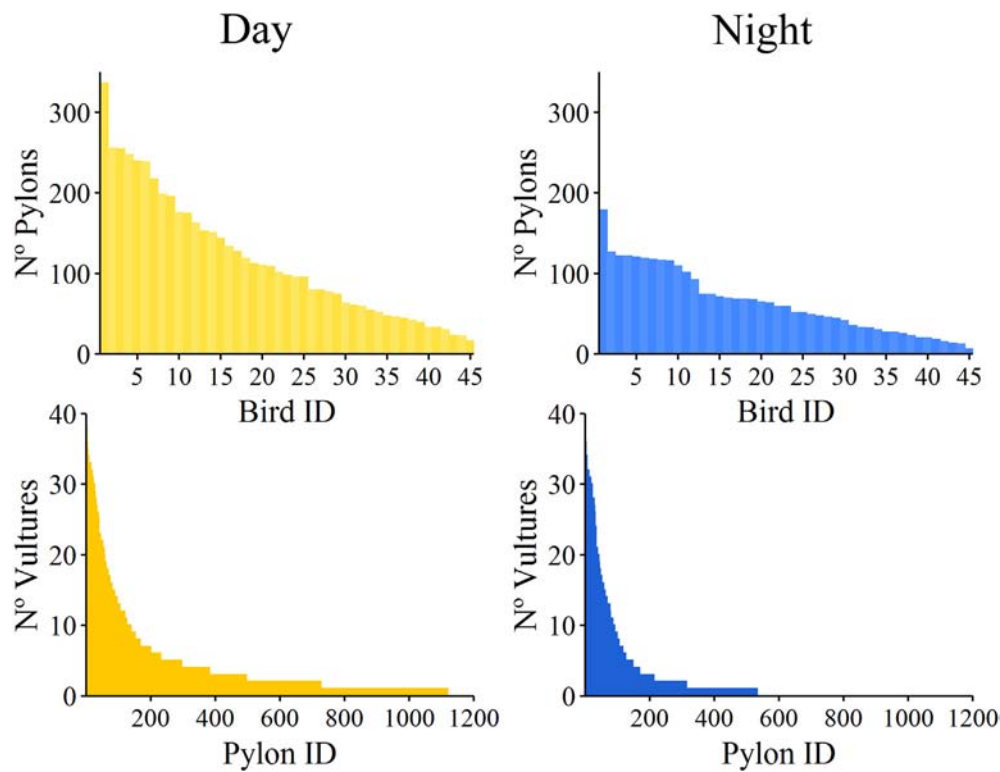


Fig. 4. Frequency distribution of (top) the number of pylons that were used by each tagged vulture (*Bird ID*) during the whole study period and (top panel) the number of vultures that used each pylon (*Pylon ID*) during the whole study period (bottom panel), showing diurnal and nocturnal behaviour (respectively, left panel and yellow colour, right panel and blue colour). From a total of 2658 of available electric pylons, only 1177 were used by GPS-tagged vultures, so only 1200 pylons were included in the figure to avoid using larger axis with data of 0 value.

taken into consideration in previous studies. Pylons were used more intensely during the night than during the day, likely associated with roosting aggregations, which occurred more frequently in the transmission line of 66 kV. However, a greater number of pylons were used as temporary resting spots during the day, and especially those of the distribution line. Moreover, the correlation between diurnal and nocturnal use of pylons was relatively low, especially during the breeding season. Thus, the estimated use based on nocturnal behaviour could be different from that

arising from diurnal behaviour. This suggests that observations of communal roosting behaviour, typically concentrated on transmission lines (pers. obs., Arkumarev et al., 2014), could be underestimating the actual amount of pylons used and associated potential risks.

Regarding differences in territorial status of birds and seasons (breeding or non-breeding seasons), non-territorial vultures used more pylons than territorial birds, and both used more pylons during the breeding season. This may also explain the above-mentioned higher differences

Table 3

Estimates resulting from the top-ranked model (lowest AICc) for *PYLON* and *VULTURE* variables separating territorial and non-territorial vultures and accounting for diurnal or nocturnal use of electric pylons. See Table 2 for a full description of explanatory variables. The reference level for factor *Breeding* is '0', for factor *Line* is 'T. Line 132', for *Sex* is 'Female.' The standard errors and 85% confidence intervals of the estimates (7.5% and 92.5% limits) are shown in SM16.

Variables	Non-territorial				Territorial			
	PYLON		VULTURE		PYLON		VULTURE	
	Day	Night	Day	Night	Day	Night	Day	Night
Intercept	−10.20	−12.54	−8.40	−9.13	−10.51	−14.45	−11.32	−11.32
Breeding	0.30	0.47	0.32	0.48	−0.16	0.33		
Dist Road	0.52	0.60	0.33	0.39	0.60	0.95	0.24	0.35
Dist mSFS	−0.76	−0.56	−0.52	−0.30	−0.69	−0.90		
Breeding:Dist mSFS	0.63	0.49	0.63	0.49		0.40		
Breeding:Dist Road					−0.10			
Dist Terr	0.15	0.11	0.14	0.11				
Territories					0.23	0.10		
Dist Nest							−3.42	−2.92
Livestock	0.56	0.71	0.41	0.69	0.51	1.05	0.21	0.35
D. Line	−2.58	−3.35	−1.11	−0.90	−3.29	−3.88	−0.98	−0.57
T. Line 66	1.24	2.82	0.62	1.38	0.23	1.51	0.33	0.75
Dist HPFP							−1.07	−1.27
Age							−1.71	
Age:Dist Nest							−1.30	
Sex								0.62
Dist Road:Sex								−0.17

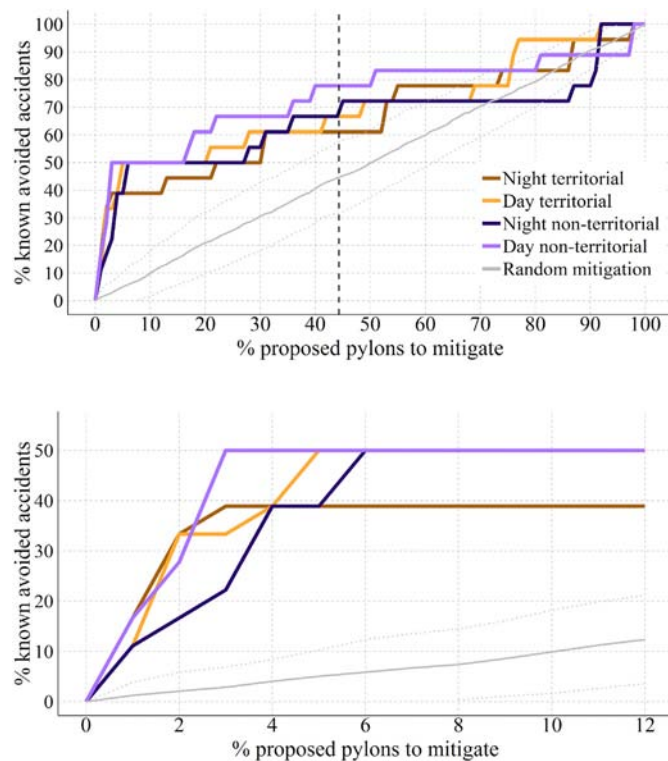


Fig. 5. Percentage of known vulture accidents (X axis) that would have been avoided on Fuerteventura prioritising mitigation measures according to developed models of power lines intensity of use (PYLON variable). These percentages depend on applying effective mitigation measures on a percentage of the total electric pylons on the island (Y axis). Predictions were done according to models of nocturnal and diurnal use, accounting for territorial or non-territorial individuals. Black dashed line indicates the maximum number of used pylons according to GPS information. Grey line indicates the results following a random selection of pylon for mitigation and grey dotted lines indicate their standard deviation ($N = 100$). Top panel: the full range of percentages. Bottom panel: a zoom of the range between 0% and 12%.

between diurnal and nocturnal use during the breeding season. During this period, and as has been observed in other long-lived avian species (Wolfson et al., 2020), non-territorial Canary Egyptian Vultures engage in wide prospective movements (Valone and Templeton, 2002) covering extensive areas that comprise almost the entire island of Fuerteventura and sometimes the neighbouring island of Lanzarote (van Overveld et al., 2018). By contrast, territorial birds typically concentrate their activities in the vicinity of nest sites and, consequently, tend to use mainly pylons close to their nesting site, which leads to the use of fewer pylons.

Focusing on territorial vultures, it is interesting to note that, during the day, older birds used pylons closer to their nesting sites compared to younger, presumably more inexperienced breeders. This difference may be associated with age-specific foraging experience and environmental knowledge (Daunt et al., 2007; de Grissac et al., 2017; Frankish et al., 2020; Riotte-Lambert and Weimerskirch, 2013; Votier et al., 2017). Increased experience could reduce the size of foraging areas exploited by older vultures. A key implication of all these findings is that depending on the spatial distribution of pylons, and the mitigation measures applied, different fractions within the adult breeding population could be differentially benefited. In particular, the correction of a reduced number of pylons used by older birds would have more effect for population viability (Badia-Boher et al., 2019; Saether and Bakke, 2000; Sanz-Aguilar et al., 2015). These measures, however, require a very good knowledge of the population structure through long-term monitoring. Additionally, it is known that in long-lived species, older, more-experienced individuals are recurrently present in the same territories instead of randomly turning over (Forero et al., 1999; Krüger and Lindström, 2001; Zabala and Zuberogoitia, 2014). Thus, once identified,

it could be a priority to concentrate conservation efforts on these spots (Sergio et al., 2004), which are usually not considered when evaluating electrocution risk (an exception in Dwyer and Mannan, 2007) due to the frequent focus on pylon rather than on birds' behaviour.

The main drivers of use of pylons were apparently similar both for day and night and for territorial and non-territorial birds, despite the earlier discussed quantitative differences (i.e., intensity of use and pylon numbers). These drivers include the type of power line, the distribution of trophic resources, anthropic disturbances, seasonality and the spatial pattern of distribution of the vultures across the island, including the effect of territories and places of aggregation as SFS. On the other hand, the effects of age and sex were determinants only to explain the days of use by territorial individuals (VULTURE T). The older transmission line (66 kV) was the most used by Canary Egyptian Vultures, likely due to both the height of the pylons and its location with respect to food sources. Greater height implies higher security against humans and other sources of disturbance (Infante and Peris, 2003; Moreira et al., 2017). Even though the pylons of the other transmission line (132 kV) are higher, they were less used, probably because its installation is relatively recent and still incomplete, but a progressive change of use towards this new infrastructure could be expected. Regarding the distribution line, our results showed a relatively low use, indicating that the associated electrocution probability (Janss and Ferrer, 2001; Miller et al., 1975) would decrease according to its limited use because of the existence of power lines with taller pylons, which are in turn associated with higher power.

The spatial distribution and temporal predictability of resources is known to play an important role in the location of perching and roosting sites (reviewed in van Overveld et al., 2020a), which agrees with the effect of predictable feeding places and livestock farms that our analyses have shown. The higher use of electric pylons around these points suggests that risk of mortality could also increase with the presence of dangerous human infrastructures in the proximities of places that concentrate individuals.

Vultures seem to avoid human disturbance by using more those pylons located further away from roads during both day and night. This partially contrasts with the result of resource selection by Egyptian Vultures showed by Buechley et al., 2018, who found avoidance of proximity to highways during winter but a strong selection during summer, the latter being explained by the feeding resources associated with highways (roadkills, livestock carcasses, or waste). However, by using GPS-tracked birds and by taking into account the entire network of all potentially available pylons, the more detailed approach of our study revealed a different picture. Although roadkill may represent an important source of food, especially when other sources of carrion become unavailable, in our study population, however, roads seem to be not beneficial enough to act as attracting elements. In this case, we have never observed Canary Egyptian Vultures feeding on roadkills (pers. obs.); both farms and supplementary feeding stations provided more predictable and abundant feeding resources than roadkills and there is no carrion or waste specially associated with roads. It should also be considered that roads are a known source of disturbance for wildlife (de Molenaar et al., 2006; Forman and Alexander, 1998; Kaseloo and Tyson, 2004; Mumme et al., 2000; Peris and Pescador, 2004; Shannon et al., 2016; Spellerberg, 1998), even affecting patterns of territory occupancy (Oppel et al., 2017). Our findings indicated that territorial females used pylons located further from roads than territorial males. This has in fact also been observed in other vulture species, such as Griffon Vultures (*Gyps fulvus*) where males appeared to be bolder than females when facing risky situations (Gangoso et al., 2021). Similarly, other top avian scavengers have also shown differential responses between sexes to environmental risks, at small spatial scales, such as in Andean Condors (*Vultur gryphus*) (Gangoso et al., 2016). Therefore, our finding could be explained by the different perception of risk between sexes.

The effects of the proximity to the main supplementary feeding station (mSFS) and roads diminished during the breeding season, however

this was only the case for diurnal behaviours of territorial birds, which may be due to different reasons. First, as it was previously mentioned, during the breeding season, territorial birds move to their breeding territories, while non-territorial individuals perform wide-range exploratory movements. Territoriality during the breeding season poses important constraints, decreasing the use of the mSFS (van Overveld et al., 2018), while increasing the use of food sources closer to nest sites such as livestock farms (García-Alfonso et al., 2020) or probably small carcasses randomly encountered, as seems common in other scavenger species (Carrete and Donazar, 2005; Karimov and Guliyev, 2017; Margalida et al., 2012). Additionally, this constrains apparently forces birds to a higher exposition to disturbances (i.e., perching close to roads). Hence, those strong seasonal and spatial dynamics are associated with a strong shift in resource use patterns, but also, as it is showed here, with broad-scale population-level changes in patterns of power line use.

On the other hand, our results also show the importance of using an individual-based approach for fine scale assessments of the patterns of pylon use. While territorial birds typically prefer those pylons close to their nesting site, non-territorial individuals avoid using those located near occupied breeding territories. These results are in line with previous work showing Egyptian Vultures to actively be defending their nest's surroundings against intruders (Ceballos and Donazar, 1988), and to exclude conspecifics from feeding resources within their territories, such as livestock farms (García-Alfonso et al., 2020), and thus, possibly also from pylons.

Finally, by comparing model predictions with known power line fatalities, it is demonstrated that the combination of knowledge on both aspects could be key for effectively reducing avian mortality in power lines. In fact, our findings indicate that prioritising mitigation measures on a low percentage of pylons (6%) according to predictions of use by birds could avoid up to 50% of accidents. This result agrees with studies indicating that electrocution fatalities show an aggregated pattern (Benson, 1982; Mañosa, 2001; Tintó et al., 2010). These findings indicate that more accurate knowledge of bird behaviour avoiding or reducing typical biases is key when predicting mortality. Traditionally, conservation measures are adapted to populations as a whole in their distribution range. Nonetheless, as opposed to that “mean field” assumption (Turchin, 2003), there is a more complex scenario, where individuals may be unevenly affected by threats, considering fractions that compose populations, the distribution patterns of conspecifics, and seasonal events such as breeding (Donazar et al., 2009; Margalida et al., 2016; Morales et al., 2010; van Overveld et al., 2018). In addition, our findings are not the only important factors; incorporating the extensively studied role of pylon specific designs into prioritisation measures would probably improve the percentage of avoided accidents while still involving a low percentage of corrected pylons.

4.1. Perspectives

Our findings disentangle complex effects affecting the utilisation of power lines by a population of an endangered avian scavenger. Our study population is an exceptional example to address this issue in detail; Canarian Egyptian Vultures use electricity pylons intensively (alternative roosting or perching sites are scarce), associated mortality is high, and there are extensive data on the population distribution and individual behaviour. Moreover, the use modern GPS tracking technology allow collecting unprecedented accurate information at a fine resolution, which makes it possible to address complex behavioural aspects that go far beyond those obtained through direct observations. This approach in turn reduces common biases and opens new opportunities to prioritise mitigation measures of power lines supported by better scientific-based guidelines. This study indicates that common features related to the spatial distribution of food resources and anthropisation, together with species-specific population features (e.g., territorial behaviour), determined the use of pylons. All of these factors determine spatial and temporal asymmetries in the probability of accidents that

must be taken into account in conservation schemes of avian populations under similar environmental constraints.

We emphasised that in parallel to the expected growth of electric infrastructures, the distribution of both feeding sources and breeding territories should be urgently considered in order to diminish probability of accidents. Moreover, creation of new feeding points, a commonly employed conservation strategy to preserve scavenger populations worldwide, should also consider the distribution of power lines as a relevant factor of potential mortality risk. From a general point of view, we recommend close monitoring of endangered populations and the utilisation of GPS devices in order to obtain high-quality, individual-based information that allows optimising investments in the correction of dangerous power lines for birds.

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CRediT authorship contribution statement

Marina García-Alfonso: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Thijs van Overveld:** Conceptualization, Investigation, Writing – review & editing. **Laura Gangoso:** Conceptualization, Investigation, Writing – review & editing. **David Serrano:** Conceptualization, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **José A. Donazar:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148534>.

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