



Tracking data highlight the importance of human-induced mortality for large migratory birds at a flyway scale

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ARTICLE INFO

Keywords:

Tracking technologies
Mortality
Bird conservation
Energy infrastructure
Renewable energy
Illegal killing
Poisoning

ABSTRACT

Human-induced direct mortality affects huge numbers of birds each year, threatening hundreds of species worldwide. Tracking technologies can be an important tool to investigate temporal and spatial patterns of bird mortality as well as their drivers. We compiled 1704 mortality records from tracking studies across the African-Eurasian flyway for 45 species, including raptors, storks, and cranes, covering the period from 2003 to 2021. Our results show a higher frequency of human-induced causes of mortality than natural causes across taxonomic groups, geographical areas, and age classes. Moreover, we found that the frequency of human-induced mortality remained stable over the study period. From the human-induced mortality events with a known cause ($n = 637$), three main causes were identified: electrocution (40.5 %), illegal killing (21.7 %), and poisoning (16.3 %). Additionally, combined energy infrastructure-related mortality (i.e., electrocution, power line collision, and wind-farm collision) represented 49 % of all human-induced mortality events. Using a random forest model, the main predictors of human-induced mortality were found to be taxonomic group, geographic location (latitude and longitude), and human footprint index value at the location of mortality. Despite conservation efforts, human drivers of bird mortality in the African-Eurasian flyway do not appear to have declined over the last 15 years for the studied group of species. Results suggest that stronger conservation actions to address these threats across the flyway can reduce their impacts on species. In particular, projected future development of energy infrastructure is a representative example where application of planning, operation, and mitigation measures can enhance bird conservation.

1. Introduction

Across the world, anthropogenic stressors are contributing to the decline of bird populations of many species, resulting in the deterioration of their conservation status (BirdLife International, 2022; Lees et al., 2022; Rosenberg et al., 2019; Şekercioğlu et al., 2004). Some stressors directly kill individuals (e.g., road collision, illegal shooting, or trapping) while others have indirect impacts (e.g., habitat loss and degradation). Annually, millions of birds die from direct anthropogenic stressors (hereafter referred as human-induced mortality), affecting hundreds of bird species worldwide (Calvert et al., 2013; Loss et al., 2015). For some species groups like predatory raptors (Madden et al., 2019), vultures (Ogada et al., 2016b), and bustards (Collar et al., 2017), human-induced mortality can be particularly important, with impacts on their conservation status (Chevallier et al., 2015; Di Vittorio et al., 2018; López-López et al., 2011). Despite its importance, relatively little is known about how human-induced mortality varies geographically and temporally, and the anthropogenic, ecological, and abiotic factors influencing this variation (Loss et al., 2015). For many species with declining populations, reducing direct mortality can help arrest those declines (Etheridge et al., 1997; Oppel et al., 2023; Whitfield et al., 2004). Thus, a better understanding of human-induced mortality is crucial for the effective conservation of birds (Longcore and Smith, 2013).

Tracking technologies have been increasingly used during the last 30 years to gain insights into avian ecology and biology (Kays et al., 2020; Nathan et al., 2022; Wilmers et al., 2015). During the last decade, there has been an increasing interest in understanding bird mortality, with important examples of studies for a variety of species like white stork (*Ciconia ciconia*) (Cheng et al., 2019; Rotics et al., 2021; Rotics et al., 2017; Rotics et al., 2016), black stork (*Ciconia nigra*) (Cano et al., 2013), Egyptian vulture (*Neophron percnopterus*) (Buechley et al., 2021; Oppel et al., 2015), black kite (*Milvus migrans*) (Sergio et al., 2019; Sergio et al., 2018; Sergio et al., 2014), little bustard (*Tetrax tetrax*) (Marcelino et al., 2018), osprey (*Pandion haliaetus*), European honey buzzard (*Pernis ptilorvus*) and harriers (*Circus spp*) (Klaassen et al., 2014; Strandberg et al., 2010). While a wealth of conservation-relevant data pertinent to understanding bird mortality are generated during tracking projects, these data are often not analysed or published by researchers whose focus is typically on other research questions. The high spatial and temporal

accuracy of tracking technologies allow to reduce the biases in detection and reporting of bird mortalities, providing a great opportunity to investigate general trends in avian migrants' mortality in a multi-species framework.

Human socio-economic features, as well as ecological and biological factors, may influence the magnitude of different causes of mortality to bird populations (Buchan et al., 2022) and these can vary geographically throughout their ranges (Oppel et al., 2021; Santangeli et al., 2019). Studies at large spatial and temporal scales are particularly important to analyse this variability and assess how particular causes of mortality impact species (Kirby et al., 2008; Vickery et al., 2014). However, many studies are conducted at national or regional scales or relate to only a single population or species. Multi-species approaches can be helpful in providing information about shared causes of mortality that can be pooled among taxonomic groups and different geographic areas to generate a more complete picture. In this way, tracked individuals can act as sentinels, providing data which, when pooled across many species, contribute to our understanding of spatial patterns and temporal trends.

To assess the relative importance and prevalence of different causes of mortality in the African-Eurasian flyway, we gathered information from multiple researchers/studies on 45 migratory bird species. Specifically, our main objectives were to: i) investigate multi-species tracking data to gain insights into causes of bird mortality, ii) investigate temporal trends in human-induced and natural causes of bird mortality, iii) identify the main causes of human-induced mortality and iv) investigate factors influencing human-induced causes.

2. Material and methods

2.1. Data collation

The study area focused on the African-Eurasian flyway. This flyway has been intensively studied compared with other parts of the world in terms of the number of tracking studies (Guilherme et al., 2023; Kays et al., 2020), making it an ideal focal flyway for this work.

Our analysis was restricted to large bodied terrestrial birds: storks (Family Ciconiidae), cranes (Family Gruidae), and raptors sensu lato (Family Accipitridae, Falconidae and Pandionidae) identified as meeting the Convention on Migratory Species (CMS) definition of 'migratory' (Article I of the CMS convention text <https://www.cms.int/en/convent>

ion-text, and UNEP/CMS 2020) and distributed within the African-Eurasian flyway (see full list of species in Supplementary material – Table S1). The reason for restricting the study to these taxonomic groups was that until recently only larger-bodied bird species could be tagged with the heavier transmitter types that generate accurate positional information (Bridge et al., 2011) that could be retrieved from dead animals. We focused exclusively on data from PTT, GPS, and GPS-GSM since these have the necessary spatial and temporal accuracy for identifying mortality events correctly and transmit the geographical information remotely. Moreover, the selected taxonomic groups comprise many species that have been studied for sufficiently long in the study area that there were enough tagged individuals to permit robust analyses.

To identify potential data holders working on the focal species, we conducted a literature review (scientific and grey) and web search (completed in February 2021). For the literature review we employed Google scholar, using the formula = TITLE-ABS-KEY (“common name” OR “scientific name”) AND (“ptt” OR “satellite” OR “gps” OR “tracking”). The web search was done using Google, with a particular focus on tracking databases (e.g., Movebank, Satellitetracking.eu, Birdtelemetry.cz, Birdmap.5dvision.ee). BirdLife International partners (national NGOs) assisted in identifying and contacting potential collaborators. In total, 207 potential collaborators were contacted and requested to contribute data related to mortality events in a standardized data template. This comprised a summary information section and a mortality information section (Supplementary material – Table S2). In the summary section we requested data from each species on i) number of individuals tagged, ii) number of mortality events identified, iii) number of technical failures, and iv) number of unknown causes of tag malfunctioning or transmission failure. Technical failures included events where researchers could confirm the tags fell from the individual or stopped transmitting before the estimated life expectancy of the device. Unknown causes included all those events in which the fate of the bird and/or the tag could not be determined. We estimated the minimum proportion of mortality events from a cohort of tagged birds by excluding unknown causes, and the maximum potential proportion of mortality events by assuming all unknown causes related to mortality of the tagged bird.

In the mortality section, we requested general information about the mortality events for each species. Since mortality events derived from tracking data can be identified using different methods with different likelihoods of a correct assessment, we asked researchers to classify the reported events according to three categories (modified from Klaassen et al., 2014):

- *Possible death of bird.* Loss of signal occurred abruptly and despite preceding good transmission and/or battery performance, or transmitter was continuously transmitting from the same position without indicating movement (activity counter stopped). No further investigation was made using any remote or on the ground method (or if used it did not provide any useful insights into the event); cause of death would be ‘unknown’ for events in this category most of the time.
- *Very probable death of bird.* Tracking data indicated mortality, and this was categorized as very probable using remote methods (see details below) that helped in the identification of the event (e.g., Sergio et al., 2018). These methods include any type of analysis performed remotely and/or assisted by other devices tagged to the birds (e.g., use of GIS software, statistical analysis of tracking data, accelerometer data, insights from weather conditions, remote sensing, temperature sensors). Since the likelihood of a correct identification varies with the precise method employed, slight differences may be found between methods.
- *Confirmed death of bird.* Tracking data indicated mortality, and this was confirmed by additional in-situ observations (e.g., field observation by researcher or local contacts). Events classified in this

category had the highest probability of correctly identifying a mortality event.

Lastly, information was requested about causes of death. The data form included five natural and eight human-induced categories covering the most common causes reported. The natural category included: i) drowning, ii) predation, iii) starvation/exhaustion, iv) disease, and v) other. The human-induced category included: i) illegal killing (i.e., intentional direct killing, considered illegal in some countries of our study), ii) electrocution, iii) power line collision, iv) wind-farm collision, v) road collision (i.e., hit by vehicle), vi) other collision (e.g., building), vii) poisoning, and viii) other. Within the poisoning category we did not distinguish between different types of poisoning (e.g., intentional, accidental, environmental) because of the difficulty in determining the nature of these events. No information was collected on the certainty of the method used to identify the cause of mortality.

2.2. Data analyses

To investigate the relative importance of human-induced, natural, and unknown causes of mortality, we calculated the proportion of each of these three categories in relation to total deaths across different taxonomic groups, geographic areas, and age classes. Moreover, to investigate whether the proportion of human-induced mortality changed over time, we fitted generalized linear models (GLM) with a logit-link function and a binomial error distribution using the R package “stats” (R Core Team, 2023). The response variable was the percentage of human-induced mortality in relation to the total known causes of mortality (i.e., natural mortality + human-induced mortality) pooling all species together, and the year in which the mortality occurred was used as a continuous explanatory variable. To explore the effect of the unknown causes of mortality in the compiled dataset, three different models were developed. The first model included only mortality events with known causes of mortality excluding those with unknown causes of mortality ($n = 1026$); the second model included mortality events with unknown causes assigned to the category ‘human-induced mortality’ ($n = 1697$). The third model included mortality events with unknown causes assigned to the category ‘natural mortality’ ($n = 1697$). In this way, we could explore the minimum and maximum proportions between human-induced and natural mortalities. A total of seven mortality events did not include a death date and were excluded from this part of the analysis. To ensure model suitability, we tested uniformity of residuals using the function provided in the R package “DHARMA” (Hartig, 2017).

Different factors may influence the probability of a bird dying from a natural or a human-induced cause. These can be socio-economic factors that affect the prevalence of certain threats like illegal killing (Brochet et al., 2016), the degree of landscape modification (Arrondo et al., 2020), or simply intrinsic biological and ecological traits of the species (De Pascalis et al., 2020). Moreover, these threats can also show geographical gradients that may influence their importance on bird mortality (Buchan et al., 2022; Opperl et al., 2021), and ultimately inform conservation efforts across regions. To analyse this probability and the influence of different socio-economic, ecological, geographical, and biological factors, we fitted random forest (RF) models for classification of the mortality events with an identified cause. To simplify the response variable, we pooled the different mortality causes into two categories: natural and human-induced mortality ($n = 1030$).

RF is a machine learning algorithm and a powerful statistical classifier that is widely used for statistical analysis of ecological data; the approach creates an ensemble of classification trees and then combines the predictions from all trees (Breiman, 2001; Cutler et al., 2007; Liaw and Wiener, 2002). Moreover, RF can deal with continuous and categorical data as predictor variables in the models. In our analysis, a total of 500 trees were constructed using bootstrap samples from the dataset without replacement (Strobl et al., 2007). To assess the accuracy of the

model, c.63 % of the original data are used to construct the trees, the rest of the observations ('out-of-the-bag' sample) were used to assess the classification success of the tree structure. The relative importance of each predictor variable was evaluated as the mean decrease in accuracy of the model if that predictor was randomly permuted (Cutler et al., 2007), and its statistical significance was tested using the permutation algorithm implemented in the library `rfPermute` using 1000 runs (Archer, 2015).

To build the RF model, we used a combination of categorical and continuous predictor variables that accounted for the main potential drivers of mortality. The categorical variables included in the models were: i) taxonomic group: species were pooled together in 10 taxonomic groups: buzzards (genera *Buteo*, and *Pernis*), cranes (genus *Grus*), eagles (genera *Aquila*, *Circaetus*, *Clanga*, *Haliaeetus*, and *Hieraetus*), falcons (genus *Falco*), harriers (genus *Circus*), hawks (genus *Accipiter*), kites (genus *Milvus*), ospreys (genus *Pandion*), storks (genus *Ciconia*), and vultures (genera *Aegypius*, *Gyps*, *Gypaetus*, *Necrosyrtes*, *Neophron*, *Torgos*, and *Trigonoceps*), which reflect the different ecological and biological characteristics of the species that may influence the cause of mortality, ii) age: differences in development and maturation of the different species made it difficult to impose consistent sub-categories of age or maturation on non-adult individuals. Therefore, only two generic categories that could be applied consistently were used for an individual's age: 'adult' and 'non-adult', iii) migratory status: even if all species included in our analysis are considered as migratory using the CMS definition (see methods), some populations of these species may be non-migratory or partial migratory (i.e., migratory and non-migratory individuals exist within the same population). To analyse the influence of this factor, we specifically categorized the migratory status (i.e., migratory, non-migratory, and partial migratory) at a population level for each species included through a literature review and information from the data-holders participating in the study (Supplementary material – Table S9), iv) origin: the dataset included wild individuals and individuals that had been reintroduced to the wild from captive breeding programs. The influence of this factor is context-dependent with some studies reporting an effect on bird mortality (Armstrong et al., 2017; Tavecchia et al., 2009), while others have not found any effect (Buechley et al., 2021; Efrat et al., 2022).

Four continuous predictor variables were also employed: i) latitude of mortality event, ii) longitude of mortality event, iii) year, and iv) human footprint index: created by the Wildlife Conservation Society (<https://wchumanfootprint.org/>); this index is a proxy for landscape modification and is calculated based on five categories: population density, land cover/land use, built infrastructure, accessibility, and power consumption (Sanderson et al., in press; Venter et al., 2016). Recent versions of the index cover years from 2000 to 2019 and are available at 300 m spatial resolution. This allowed us to calculate the value of the index for the same year in which the mortality event occurred and the specific geographical location. Mortality events from 2020 and 2021 were assigned to the latest information from 2019. Two different generations of maps have been produced, the so-called "first-generation" from 2000 to 2013 and the "second-generation" from 2014 to 2019. To make these two periods comparable we normalised all values from 0 to 1. To check for potential multi-collinearity between continuous predictor variables a variance inflation factor (VIF) analysis was run using the R package `HH` (Heiberger, 2018). All VIF values were lower than 2 meaning that no collinearity was detected (Supplementary material – Table S4).

Finally, partial dependence plots were constructed to represent the relationship between the predictor and the response variables based on the RF constructed. These plots evaluate the RF model based on the variation within one selected variable while all other variables remain fixed at their actual values. Thus, these plots represent averaged predictions based on a selected variable (Strobl et al., 2008).

3. Results

In total we received 1704 mortality records from July 2003 to August 2021. These records included 45 different species (Supplementary material – Table S1) tagged in 48 countries and dying in 91 countries across the study area (Fig. 1). A total of 376 events (22.07 %) were classified as "possible", 336 (19.72 %) were classified as "very probable", and 992 (58.21 %) were classified as "confirmed". From the 1704 mortality events identified, 1030 (60.45 %) had a known cause of mortality while 674 (39.55 %) had an unknown cause of mortality.

3.1. Frequency of identification of mortality events

From a total of 4097 individual birds tagged, researchers could identify 1704 mortality events (41.6 %) and 497 events of technical device failure or malfunctioning (12.13 %). There were 1124 tags that continued transmitting or that completed their expected life cycle (27.43 %). However, researchers could not determine the fate of the devices/birds in 769 events (18.77 %).

Mortality proportion (i.e., number of dead birds/numbers of total birds tagged) calculated at species and project level was 0.40 (range 0–1) on average. The technical failure proportion (i.e., number of technical failures/total birds tagged) was 0.12 (range 0–1) on average (Supplementary material – Table S3). These different proportions across species and projects were statistically significant ($\chi^2 = 2561.8$, $df = 411$, $p < 0.01$). These numbers must be interpreted cautiously since tag's manufacturer, project duration, number of tagged birds and scale and type of effort made to identify mortality varied widely between projects.

3.2. Human-induced versus natural causes of mortality

The proportion of mortality events identified as human-induced was consistently higher than the proportion identified as natural mortality across taxonomic groups, geographic areas, and age classes (Fig. 2). When analysing the relationship between human induced and natural mortality (i.e., ratio human-induced/natural), we found that human-induced causes of mortality (37.38 %) were 1.64 times more commonly identified than natural causes of mortality (23.06 %). The ratio between human-induced (31.83 %) and natural mortality (13.28 %) was significantly higher in Africa (2.4 times) than in any other continent ($\chi^2 = 69.61$, $df = 4$, $p < 0.01$) (Fig. 2B). Non-adult birds showed a higher percentage of natural mortality (24.79 %) than adult birds (17.48 %) ($\chi^2 = 31.33$, $df = 4$, $p < 0.01$) (Fig. 2C). When considering mortality events with a known cause of mortality (i.e., human, and natural) the probability of a correct identification was as follows: "possible" = 4.56 %, "very probable" = 20.01 % and "confirmed" = 75.34 %. Since the proportion of mortality events with a known cause identified as "possible" was so low, we decided to keep all records in further analysis regardless of this category.

None of the three GLM models investigating the temporal trend in the proportion of human-induced and natural mortality detected any significant effect of year (Fig. 3) (Model 1: $\chi^2_1 = 0.88$, $p = 0.35$, Model 2: $\chi^2_1 = 1.42$, $p = 0.23$; Model 3: $\chi^2_1 = 0.02$, $p = 0.9$) (Supplementary material – Table S5). To reduce the influence of the probability of correct identification of mortality events, we fitted the same GLM model only including the "very probable" and "confirmed" cases of natural and human-induced mortality. Similar to the models using the full dataset, this model could not detect any significant effect of year ($\chi^2_1 = 2.88$, $p = 0.09$) (Supplementary material – Table S6).

3.3. Human-induced mortality

When pooling all species together, three main causes of mortality were the most frequently recorded: electrocution (40.5 %), illegal killing (21.66 %), and poisoning (16.33 %) (Fig. 4). For predatory raptors, and storks and cranes, the primary identified cause of mortality was

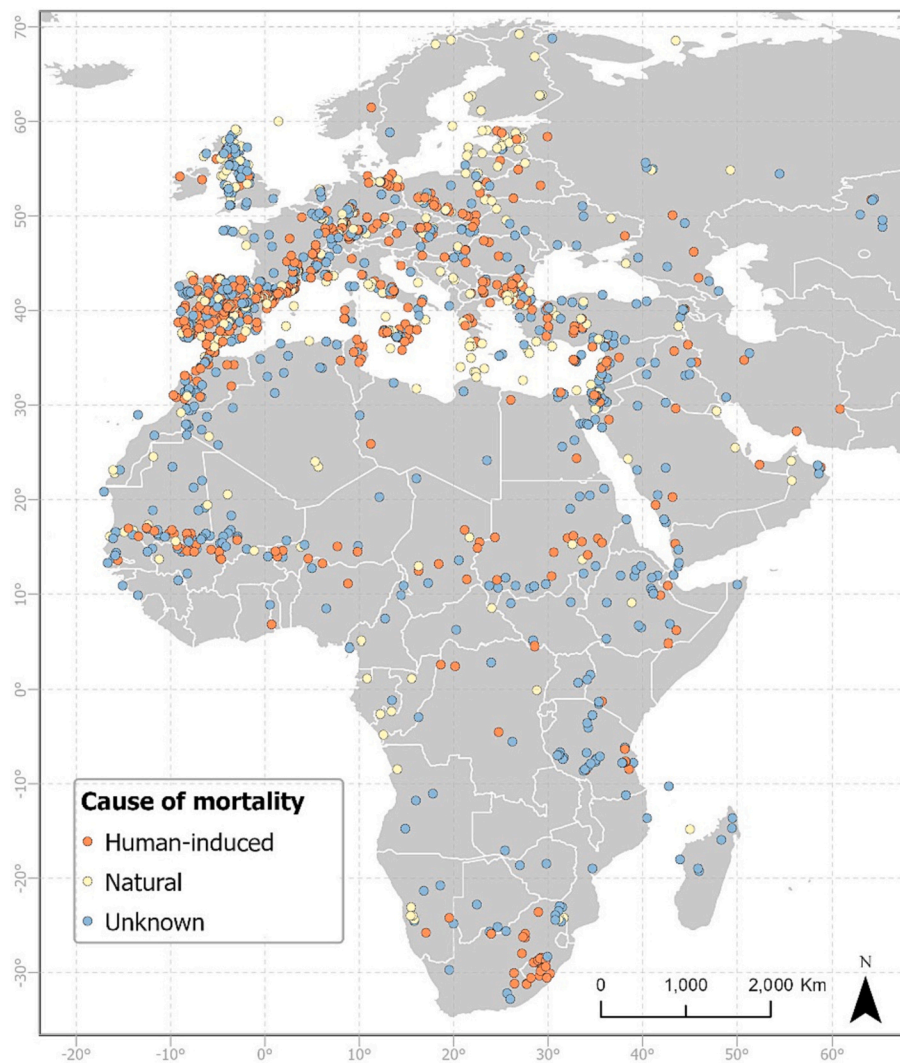


Fig. 1. Spatial distribution of mortality events in the study area, the African-Eurasian flyway.

electrocution (36.25 % and 54.47 %, respectively), followed by illegal killing (23.9 % and 21.27 % respectively). For vultures, poisoning was the main cause of mortality (39.74 %), followed by electrocution (25.83 %) and illegal killing (18.54 %). Illegal killing had the highest prevalence as a cause of mortality in Africa (48.03 %), while electrocution was most prevalent as a recorded cause of mortality in Europe (47.2 %). Energy infrastructure-related mortality (i.e., electrocution, power line collision, and wind-farm collision combined) accounted for 48.98 % of all mortalities across all species combined. Most human-induced mortality events were categorized as “confirmed” (77.86 %) and “very probable” (19.78 %), thus we decided to keep all records regardless of the classification category in subsequent analysis.

The RF model showed an overall accuracy of 73.4 % (Supplementary material – Table S8) in classifying whether a mortality event was natural or human-induced. The most important predictor was taxonomic group, followed by latitude, and human footprint index. Longitude, migratory status and origin had intermediate importance (Fig. 5), but no discernible pattern in the partial dependence plots (Fig. 6). Partial dependence plots showed that buzzards, harriers, and cranes had the lowest predicted probability of human-induced mortality, while eagles showed the highest. Human-induced mortality was highly likely across most latitudes but decreased substantially north of 40° N. Finally, human-induced mortality was highest at intermediate human footprint index values between 0.25 and 0.75, with very low probabilities in undeveloped regions (<0.25) and low probability in highly developed urban

regions (>0.75, Fig. 6). Two variables had no significant ($p > 0.01$) influence on whether a mortality event was human-induced or natural: age and year.

4. Discussion

Tracking technologies can be a powerful tool to investigate avian mortality in wild populations. Our study shows how these data can be used to quantify the extent of human-induced mortality among populations of large birds. Investigating mortality can be challenging, both because of the necessary time and expertise to evaluate and analyse this type of data, and because of the cost and time needed to investigate this in the field. However, data on mortality have great value, not only for scientific research but also for conservation. The large numbers of birds tagged in recent years could contribute important information on this topic if additional efforts were made to gather and analyse these data, particularly during the design stage of tagging projects.

Our results agree with previous studies on the high importance of human-induced mortality over natural mortality, but the strength of this importance varies. For instance, De Pascalis et al. (2020) using ringing data, found that natural mortality was just c.5–8 % of total mortality events registered, a much lower percentage than our findings. However, these numbers could be highly influenced by the increased likelihood of finding and reporting a bird dying from human-induced causes close to human settlements. Data on raptor mortality from wildlife rehabilitation

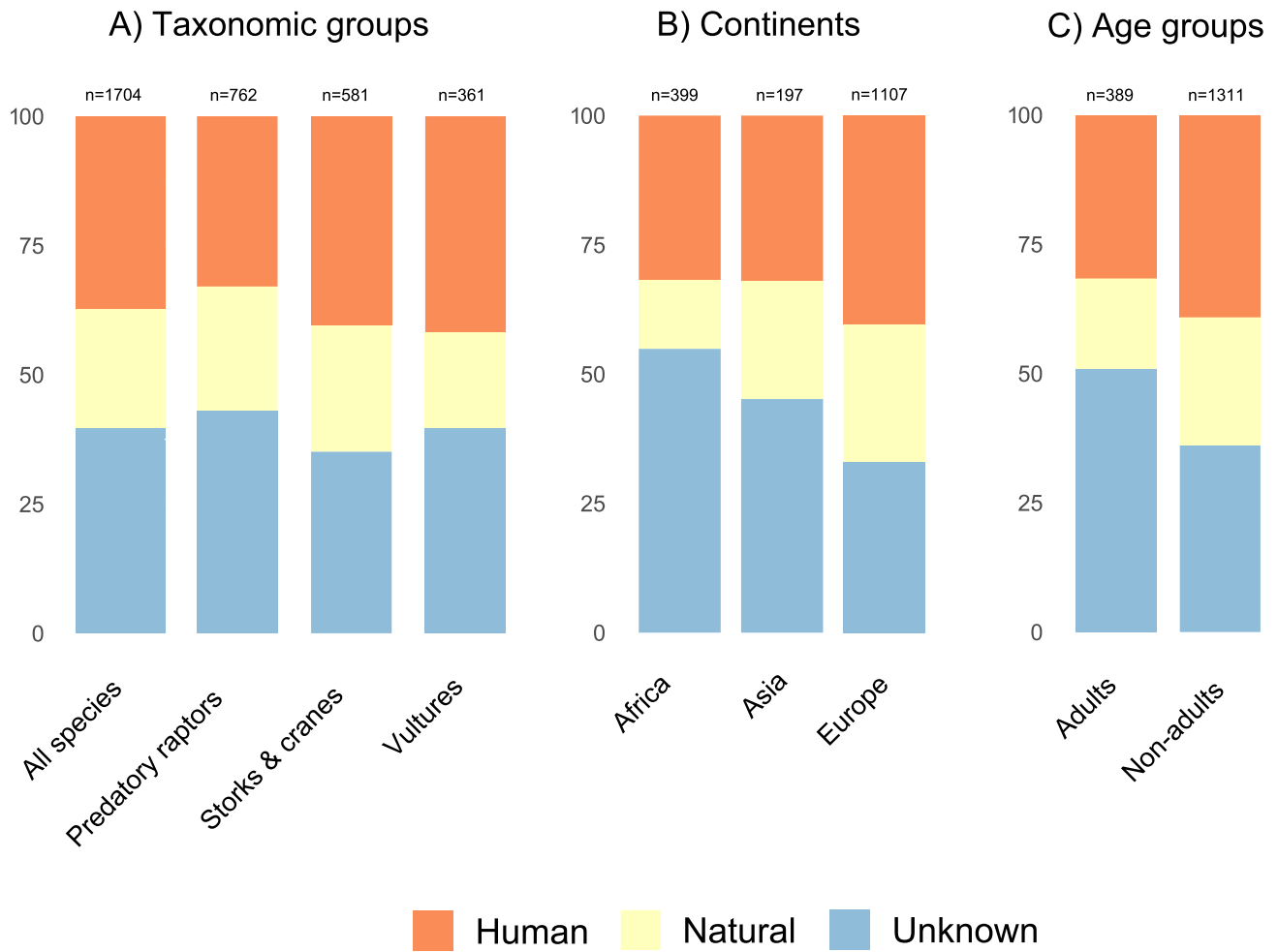


Fig. 2. Percentages of human-induced, natural, and unknown causes of mortality for all mortality events recorded depicted by: A) taxonomic groups, B) continents, and C) age groups. All age classes not considered as adults were classified as non-adults. One mortality event recorded in the middle of the Atlantic Ocean could not be assigned to a continent and four other events did not include age.

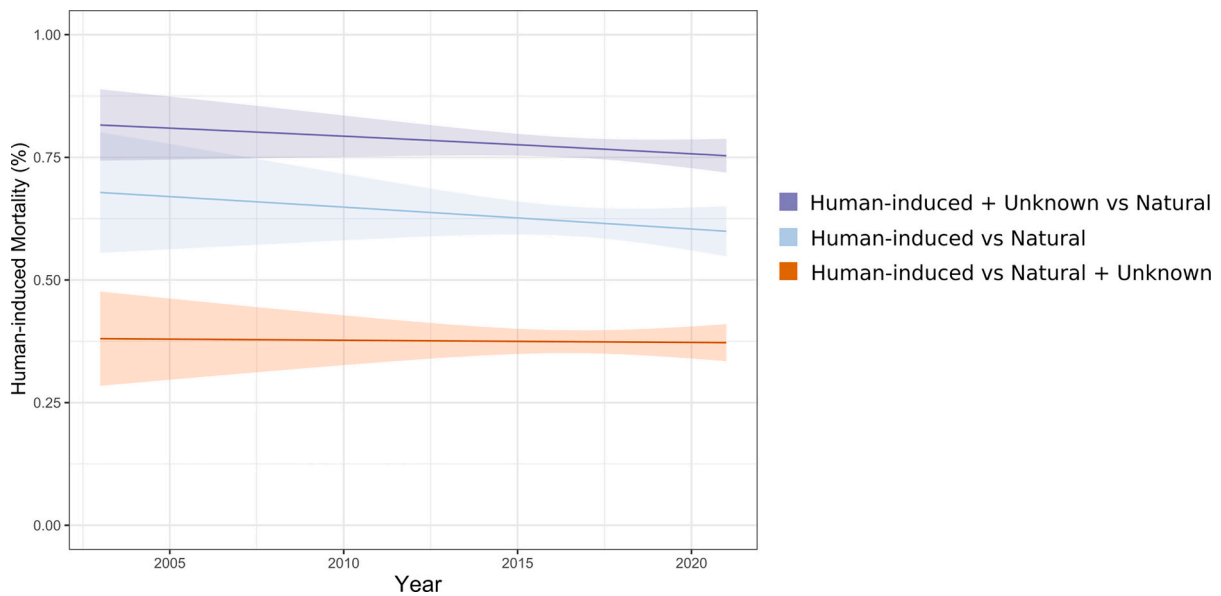


Fig. 3. Probability of human-induced mortality $\pm 95\%$ CI in relation to year, calculated as the proportion of this kind of mortality in relation to total mortalities. Three different GLM models were built to incorporate unknown causes of mortality in the analysis. None of the resulting models were significant ($p > 0.01$).

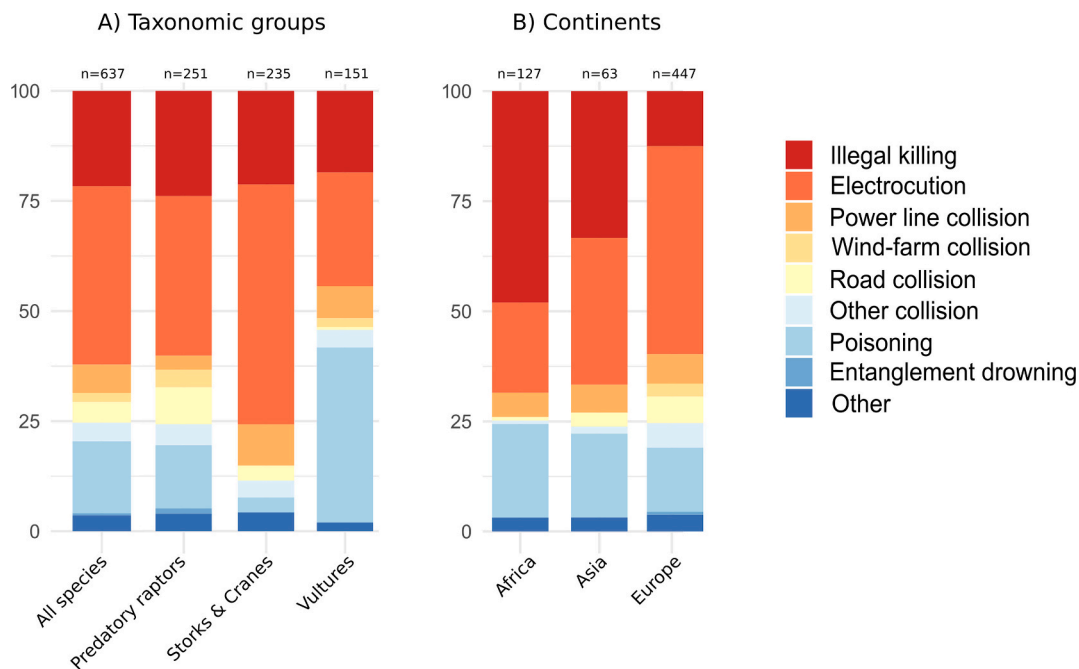


Fig. 4. Percentages of human-induced causes of mortality by: A) taxonomic groups and B) continents, calculated from all known human-induced causes of mortality (n = 637).

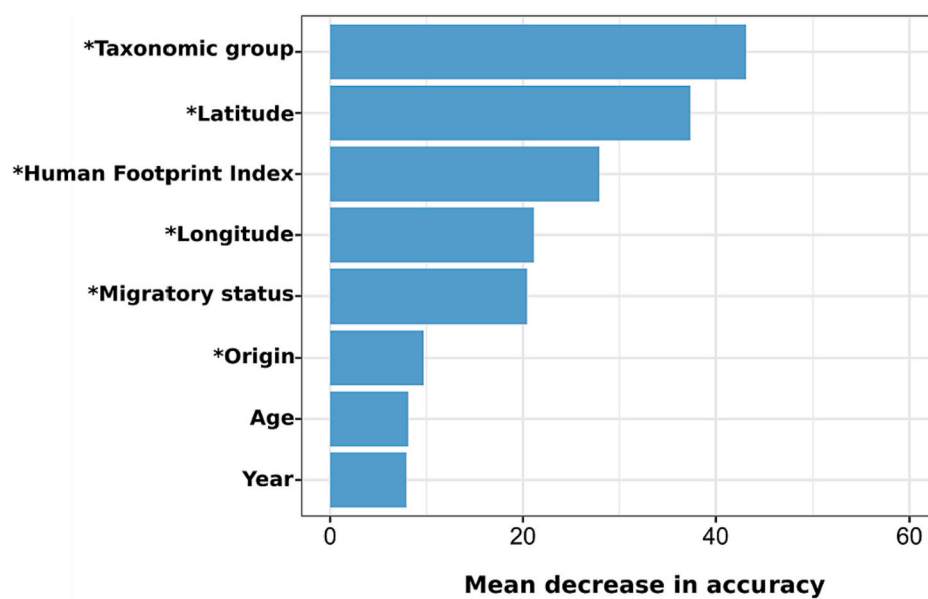


Fig. 5. Relative variable importance influencing a random forest model’s accuracy in classifying whether a mortality cause was human-induced or not. Mean decrease in accuracy measures the reduction in the accuracy of the model when randomly permuting that particular variable while maintaining the rest. Variables marked with an asterisk were significant ($p < 0.01$) after 1000 permutations.

centres in Spain, which could be biased in a similar way, showed similar figures of natural mortality (Martínez et al., 2016). Remote tracking devices provide an opportunity to reduce this bias by revealing locations of dead individuals away from human settlements. Studies carried out using tracking data provide similar results to ours. For instance, Buechley et al. (2021) reported that for Egyptian vultures tracked across the African-Eurasian flyway, 51.1 % of the total known causes of mortality were human-induced, and Monti et al. (2023) found that 60 % of mortality causes for GPS-tracked Griffon vultures in central-southern Italy were also human-induced, like our overall results.

Our models could not detect any change in the frequency of human-

induced mortality in the last 15 years. Although events with an unknown cause of mortality generate uncertainty in our results, none of the different scenarios we modelled indicated that human-induced mortality is declining. It is possible that we did not detect any change because both (natural and human-induced) have increased or decreased at the same rate. Likewise, it is also possible that some threats have been replaced by others across time and/or geographical areas. For instance, previous studies from Spain indicate that in recent decades the number of cases of illegal killing has decreased, while fatalities related to energy infrastructure have increased (Martínez et al., 2016; Martínez-Abraín et al., 2009). New threats have also emerged. For instance, intentional

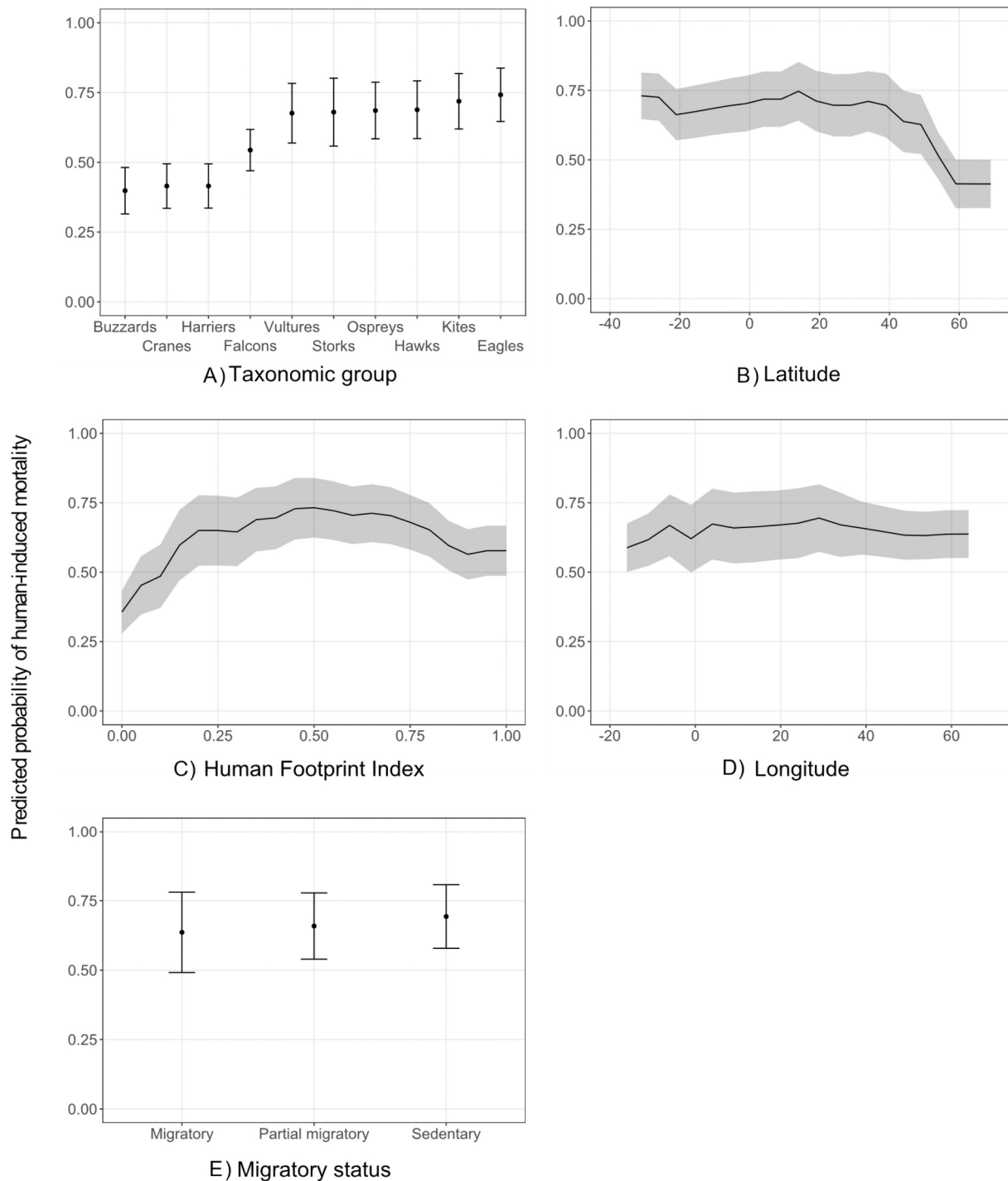


Fig. 6. Partial dependence plots showing the relationship between the most important variables detected by a random forest model and the probability of human-induced mortality if all other variables were held at their actual values. Shadowed areas and error bars represent the standard deviation around predicted mean probability.

poisoning has increased sharply in Africa, having a major impact on vulture populations (Henriques et al., 2020; Ogada et al., 2016a). These new emerging threats may have counteracted the reduction of previous ones.

Our analysis shows that not all bird species are equally at risk of human-induced mortality. The importance of taxonomic groups in our RF model reflects ecological and biological characteristics of species that make them particularly sensitive to certain causes of mortality. Secondly, the importance of latitude indicates that threats are not evenly

distributed across space but vary geographically in intensity and persistence (Buchan et al., 2022; Gauld et al., 2022). This is consistent with our findings of a spatial variation in the importance of threats between continents. For instance, according to our results, illegal killing is higher in Africa than in any other continent. This finding could be related to the combination of several factors like direct persecution of vultures for belief-based uses (Ogada et al., 2016b), a high level of hunting pressure in some African countries like Egypt (Brochet et al., 2016), and/or the increasing demand of hunting for bushmeat in sub-

Saharan countries (Whytock et al., 2016). Lastly, the importance of the human footprint index reflects the strong association between human presence and avian mortality. Interestingly, we did not find a monotonic increase in the probability of human-induced mortality with the footprint index, but a peak at intermediate values. This relationship indicates that even moderate human presence can have large impacts on avian mortality, but that human-induced mortality events are not more likely in extremely modified urban landscapes. We speculate that most large bird species simply do not find suitable habitat in highly developed or urbanized areas, and thus limit the time they spent there.

We acknowledge that our study presents some limitations. First, we could not estimate absolute mortality rates and thus quantify demographic impacts. Capture-mark-recapture or recovery models applied to tracking data could be used to estimate mortality rates and relative contributions of mortality causes (Buechley et al., 2021; Schaub and Pradel, 2004; Swift et al., 2020). However, our focus was on identifying broad scale spatiotemporal patterns in mortality rather than estimating species-specific demographic parameters. Our estimates are conditional on the probability of finding and reporting a mortality event from a particular cause, which may lead to bias if certain mortality causes have a higher probability of being detected and diagnosed than others (Tavecchia et al., 2012). However, mortality information derived from tracking data has a higher probability of detection and fewer potential sources of bias than that from other sources (e.g., Bro et al., 2001). Lastly, since we collected data from multiple studies there is a large heterogeneity in the methods used to determine the mortality events. Nevertheless, from all mortality events included in our analysis of known causes of mortality, 95.4 % were classified as “confirmed” or “very probable”. We are therefore confident that the main conclusions of our study are robust.

In the coming decades, investment and development in renewable energy is expected to grow substantially worldwide. With much of the expected growth relying on solar and wind energy (70 %), this means that by 2050 we can expect a ten-fold increase in the current total onshore wind energy capacity (IEA, 2021; IRENA, 2019). This massive expansion of renewables will require a proportional growth of the electricity transmission grid to distribute this energy. With almost 50 % of all human-induced mortality events being related to energy infrastructure, our results highlight the impact that this source of mortality already has on birds. Therefore, the expected expansion of this infrastructure could have dramatic consequences for the conservation of these species (Serrano et al., 2020). Currently, the proportion of mortality events that are energy-related is lower in Africa (26 %) than in Europe (57 %). This may be related to the smaller size of the energy infrastructure network in Africa compared to Europe. However, the rapid expansion of electricity networks in developing countries will likely increase energy infrastructure-related mortality. This is already evident in some countries like Kenya and Ethiopia, where collisions/electrocutions have been identified as an important threat for raptors (Ogada et al., 2022; Opper et al., 2022). Birds could benefit from careful planning to minimise these impacts, and tracking technologies can help us in this task, providing opportunity for energy investors and developers to take account of the important areas and routes for migratory birds, and to build bird-safe infrastructures (Gauld et al., 2022; Opper et al., 2021).

5. Conclusions

Our study, covering 45 species across 91 countries, reveals that human-induced factors—predominantly electrocution, illegal killing, and poisoning—constitute the major threats to bird mortality, highlighting a critical issue in global biodiversity conservation. Our results further support targeted actions as an important mechanism to combat these threats. For example, insulating power lines and strategically shutting down wind turbines during bird migrations can substantially reduce deaths due to infrastructure (Chevallier et al., 2015; Ferrer et al.,

2022; McClure et al., 2021). Tackling illegal killing and poisoning can be based on robust law enforcement, widespread awareness campaigns, and community involvement to instil conservation values (Badia-Boher et al., 2019; Opper et al., 2023). Comprehensive environmental assessments for new infrastructural projects can prevent potential harm to avian populations. These practical measures will benefit specific species and have wider implications. The insights gained from this extensive study can guide international conservation efforts, informing policy adjustments and fostering cross-border collaborations to safeguard avian species. In doing so, they contribute to broader objectives of maintaining ecological balance and protecting global biodiversity, resonating with the goals of international environmental agreements and conservation strategies.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

WCS Tanzania are grateful to the Wyss Foundation and Disney Conservation Fund for funding our vulture monitoring program.

Aldina M. A. Franco's work was financed by the FEDER Funds through the Operational Competitiveness Factors Program — COMPETE and by National Funds through FCT – Foundation for Science and Technology within the scope of the project Birds on the move ‘POCI-0145-FEDER-028176’, by InBIO (UID/BIA/50027/2013 and POCI-0145-FEDER-006821), and by the Natural Environment Research Council (NERC), via the EnvEast DTP, and NERC and Engineering and Physical Sciences Research Council (EPSRC), via the NEXUSS CDT Training in the Smart and Autonomous Observation of the Environment. Funding for the development of the GPS tracking devices was provided by NERC (NE/K006312), Norwich Research Park Translational Fund, University of East Anglia Innovation Funds and Earth and Life Systems Alliance funds.

Andrea Santangeli acknowledges support from the European Commission through the Horizon 2020 Marie Skłodowska-Curie Actions individual fellowships (Grant no. 101027534).

Alessandro Andreotti thanks for the funding received by the European Commission through the Egyptian vulture LIFE project “Measures for the conservation of the Egyptian vulture in Italy and in the Canary Islands” (LIFE16/NAT/IT/000659) and the support provided by Carabinieri Forestali, Stazione Ornitologica Calabrese and De Rerum Natura.

Tagging and tracking of Eleonora's falcons from Greece were conducted in the framework of the projects ‘LIFE13 NAT/GR/000909 Conservation measures to assist the adaptation of Falco eleonorae to climate change’ with the financial support of the European Union LIFE Instrument and the Green Fund and ‘Survey and Conservation of Seabirds in Greece’ funded by A.G. Leventis foundation. We would like to thank Marion Gschweng, Jakob Fric and Thord Fransson for assistance in field surveys and bird handling. The latter complied with current laws in Greece. The Ministry of Environment and Energy (Greece) kindly granted permission for capturing and tagging Eleonora's falcons (License numbers: 6XΨA0-OKT, Ψ9Θ24653Π8-PT3). This is contribution No. 39 from Antikythira Bird Observatory – Hellenic Ornithological Society/BirdLife Greece.

Flavio Monti acknowledges support from “Progetto Falco pescatore” (and project collaborators) and wants to thank the Tuscan Archipelago National Park, the Maremma Regional Park, the Diaccia Botrona Natural Reserve, the WWF Orbetello Lagoon Natural Reserve and the WWF Orti-

Bottagone Marsh Natural Reserve, under the Tuscany Region administration, in Italy.

Joan Real and Antonio Hernández-Matías are deeply grateful to Grup de Naturalistes d'Osona-ICHN, Grup d'Anellament de Calldetenes-Osona (GACO), Servei de Biodiversitat de la Generalitat de Catalunya, Ferrovial S.A., Consoci per a la Gestió de Residus Urbans d'Osona, Ministerio de Transición ecológica de Spain (V. Matarranz and A. Díaz). Funding was provided by project PID2020-117909RBI00 funded by MCIN/AEI/10.13039/501100011033 from the National Plan of the Ministry of Science, Innovation and Universities and Red Eléctrica de España SAU, Fundació Catalunya-La Pedrera and Diputació de Barcelona.

Joao L. Guilherme was funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Actions grant agreement no. 766417.

Beneharo Rodríguez thanks SEO/BirdLife as the organization leading the project of Barbary Falcon GPS-PTT tagging on Lanzarote.

Çağan H. Şekercioğlu and Kyle D. Kittelberger are grateful to Turkey's Department of Nature Conservation and National Parks and the Iğdır Ministry of Agriculture and Forestry for providing us with the permits used for this study. We are grateful to E. Çoban, N. Güven, KuzeyDoğa Society, Iğdır University, the residents of Yukarı Çıyıklı, and the dozens of volunteers at the Aras River Ornithological Research Station for their support. This research was supported by generous donors, including B. Bahar, S. İşmen, Ö. Külahçioğlu, B. Över, B. Özkan, A. Peterson, E. Özgür, S. Reyent, C. Sertoğlu, B. Watkins, the Sigrid Rausing Trust and the Whitley Fund. Ç.H.S is grateful to H. Batubay Özkan and Barbara Watkins for their support of the Biodiversity and Conservation Ecology Lab at the University of Utah School of Biological Sciences.

Research permission in Tanzania was granted by the Tanzania Wildlife Research Institute, Tanzania Commission for Science and Technology, Tanzania National Parks and Tanzania Wildlife Authority. NCST/5/002/R/817. Vulture research in southern Tanzania was funded by North Carolina Zoo and Wildlife Conservation Society (WCS). Corinne J. Kendall and collaborators are very grateful for the donor support provided by Association of Zoos and Aquariums (AZA), AZA SAFE (Saving Animals From Extinction), Dallas Zoo, Disney Conservation Fund, Leiden Conservation Foundation, National Geographic Society, Taronga Conservation Society Australia, and The Mohamed bin Zayed Species Conservation Fund. Many thanks to Singira Ngoishiye, TAWA Selous Game Reserve, for their invaluable contributions to ensure successful deployment of satellite tags. Work in Selous Game Reserve (now Nyerere National Park) was conducted in collaboration with Frankfurt Zoological Society, and we appreciate their support. Corinne J. Kendall tagged vultures in Masai Mara National Reserve, Kenya as part of The Peregrine Fund's Pan African Raptor Conservation Program as part of her PhD at Princeton University and thanks Narok County Council, Mara Conservancy and neighbouring group ranches as well as Africa Ecocamps, Kenya Wildlife Service, National Museums of Kenya, Simon Thomsett, Wilson and Jon Masek, and Wilson Kilong. Work was covered under permit NCST/5/002/R/448 issued by the National Council for Science and Technology.

Damijan Denac thanks Comita d.d. and Elektro Ljubljana d.d. for supporting White Stork telemetry in Slovenia.

David R. Barber is grateful to Wallace Research Foundation, The Acopian Family, Hawk Mountain Sanctuary, VulPro (South Africa), Clive Barlow, The Gambian Department of Parks and Wildlife Management, Endangered Wildlife Trust (South Africa).

Evan Buechley would like to thank the following collaborators that enabled tracking of Egyptian Vultures: KuzeyDoğa Society (Turkey), Iğdır Directorate of Nature Conservation and National Parks (Turkey), American University of Armenia, Ethiopia Wildlife Conservation Authority, Ethiopia Wildlife and Natural History Society, and our colleagues who assisted with Egyptian vulture trapping, including Emrah Çoban, Lale Aktay, Kayahan Ağırkaya, Berkan Demir, Mete Türkoğlu (Turkey); Anush Khachatryan, Garo Kurginyan (Armenia); Sisay Seyfu,

Alazar Daka Rufo, Yilma Dellelegn Abebe, Girma Ayalew (Ethiopia). This work was financially supported by the US National Science Foundation, the Christensen Fund, National Geographic Society, the Whitley Fund for Nature, Faruk Yalçın Zoo and KuzeyDoğa's donors, Turkey's Ministry of Forestry and Water Affairs General Directorate of Nature Conservation and National Parks, NorthStar Science and Technology, HawkWatch International, the University of Utah, and The Peregrine Fund.

Gradimir Gradev acknowledges funding by Project LIFE for Lesser Kestrel, LIFE19 NAT/BG/001017.

Hristo Peshev thanks funding provided by the projects; 'Recovery of the Populations of Large European Vultures in Bulgaria' (LIFE08 NAT/BG/000278), 'Vultures back to LIFE - Bright Future for Black Vulture in Bulgaria' (LIFE14 NAT/BG/000649) funded by the European Union and project 'Saving the Balkans' last vultures: introducing Vulture Safe Areas as a model for scavenger conservation in the Anthropocene' funded by Whitley Fund for Nature.

Inês Catry was funded by contract 2021.03224.CEECIND.

Funding for the work on rough-legged buzzards in Norway was provided by the Norwegian Environment Agency and the Environment departments at the Office of the County Governors of Troms and Finnmark, Trøndelag, Innlandet, Vestfold and Telemark, Oslo and Viken, Agder and Vestland.

Ivan Pokrovsky is very grateful to everyone who helped collecting data in the field. This study was funded by the Max-Planck Institute of Animal Behavior and the German Air and Space Administration (DLR). Partial funding was provided by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2117–422037984.

Tagging of common cranes in Estonia was supported by institutional research funding (IUT21-1) at the Estonian Ministry of Education and Research, by the Environmental Investment Centre Projects 2015–2017, and by Research Development Projects from Estonian University of Life Sciences.

A significant proportion of the GPS birds provided by Ana Bermejo-Bermejo and Javier de la Puente were marked as part of the Migra programme developed by SEO/BirdLife between 2011 and 2021 and funded by Fundación Iberdrola España.

José M. Fernández-García thanks rangers and practitioners from Diputación Foral de Gipuzkoa (Í. Mendiola, A. Lekuona, F. Diez, M. Olano, F. Ansoregi, E. Iriarte, J. Ugarte, A. Galdos, T. Aierbe, J. Vazquez, H. Beñaran) who performed most of the fieldwork. Licenses were issued by Diputación Foral de Gipuzkoa. Technical support by SEO/BirdLife, IREC and governments of Aragón and Navarre. Funding was provided by Interreg POCTEFA Ecogyp (EFA 089/15).

Julien Terraube thanks Dr. Beatriz Arroyo for assistance with data collection.

The telemetry of Montagu's Harrier in the Czech Republic was supported by the European Union under the Operational Program Environment, project No. CZ.05.4.27/0.0/0.0/19_130/0010743.

Lindy Thompson would like to thank John Davies, Colin Rowles, The Endangered Wildlife Trust and Hawk Mountain Sanctuary. Ethical approval was granted by the University of KwaZulu-Natal Animal Ethics Subcommittee (AREC/094/015PD). Fieldwork was done with provincial research permits (ZA/LP/HO/2937, MPB. 5557 and MPB. 5581).

Mansoor H. AlJahdhami thanks the Office for Conservation of the Environment, Diwan of Royal Court.

Manuel Galán is grateful to Ministerio para la Transición Ecológica y Reto Demográfico.

Marcin Tobolka thanks funding from National Science Centre (Poland), 2016/23/D/NZ8/01902.

Māris Strazds acknowledges funding by Administration of Latvian Environmental Protection Fund, and the Latvian Ornithological Society. The following people have contributed to data download and/or recovery of tags from dead birds: Ivars Brediks, Zanda Briķe, Raimonds Celms, Henrijs Eikens, Dainis Freimanis, Ginta Gotfridsone, Helmut

Hofmanis, Lelde Jagmina, Raivis Jasinskis, Didzis Jurciņš, Rolands Kāpostiņš, Jānis Ķuze, Līga Laurenoviča, Dagnija Lāce-Ate, Jānis Legzdīņš, Edgars Lediņš, Solvita Martinšone, Inga Skrūzmane, Elīze Spridzāne, Pēteris Strautiņš, Anita Tauriņa, Edgars Tauriņš, Marina Dmitrenok, Pavel Pakul, Olga Lukshitsc, Konstantin Gomel, Hissein Abdoulaye, Mahamat Hassan Hacha, Sven Kapelj, Vedran Lucić, Milan Obranić, Darko Podravec, Urmis Sellis, Shay Rotics, Vaidas Palinauskas, Emanuel Baltag, Petrisor Galan, Zsolt Hegyeli, Laurentiu Petrencu, Zoltan Szabo, Tamara Astafyeva, Kristina Chaika, Nikita Chernetsov, Dmitry Grishanov, Gennady Grishanov, Yulia Grishanova, Il'ya Ishenko, Mikhail Markovets, Andrey Mukhin, Vladimir Salikhov, Ibrahim M. Hashim, Nasir Gaboush, Moutasim Eisa, Andriy Bokotey, Leonid Taranyenko, Larisa Tel'nova, Sergei Grigorenko, Kerem Ali Boyla, Sevim Karabiyik, Lider Sinav, Lincoln Fishpool, John Newby, Richard Porter, Tim Wachter, and Joost Brouwer.

Mario Posillico acknowledges Eliseo Strinella, Rosario Balestrieri, Stefano Laurenti, Enzo Savo, Elisa Mancuso, Giancarlo Opramolla, Antonello Pascazi, Rosita Giuliani, Elena Di Filippo, Filippo La Civita, Samuele Spacca and Annalisa Brucoli, for their invaluable support in capture and ringing griffon vultures.

Marta Acácio, from the Black Stork Portugal project, wants to thank Carlos Pacheco and Luís Venâncio for their valuable help in the field.

Martin Wikelski acknowledges partial funding by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's ExcellenceStrategy – EXC 2117–422037984.

Michael J. McGrady thanks the Environment Authority of Oman for issuance of permits and field support and the Environment Society of Oman for administrative and logistical support.

Munir Z. Virani thanks the Band Foundation, The Peregrine Fund, Whitley Fund for Nature, National Geographic Society, Simon Thomsett, Narok County Government, Kenya Wildlife Service and Matira Safaris.

Nili Anglister is grateful for the support of the Israeli Nature and Parks authority.

Oliver Krone thanks the “Eagle Club”, Estonia.

Orr Spiegel acknowledges funding by the Binational Science Foundation (BSF) 822/2019 grant.

Pauline L. Kamath thanks support from NSF-BSF Ecology and Evolution of Infectious Diseases (EEID) Grant 2015904; USDA—National Institute of Food and Agriculture Hatch Project Nos. ME021908 and ME022402 to PLK.

Peter Palatitz was funded by LIFE11/NAT/HU/000926 and would like to thank Zsófia Nyerjak-Sumegi, Eva Horvath, Szabolcs Solt and Dr. Peter Fehervari for their help.

Rainer Raab thanks the support from LIFE EUROKITE project (LIFE18 NAT/AT/000048).

Ralph Buij, Richard Stratton Hatfield, and Shiv Kapila would like to thank the Narok County Government, National Museums of Kenya, the Wildlife Research and Training Institute and the Kenya Wildlife Service for their support of this project. Our work would not have been possible without the field expertise of Simon Thomsett and Lemein Parmuntoro and the technical expertise of the late Theo Gerrits. Finally, we are grateful for the support and help accorded by numerous camps and individuals within the Mara who made this work possible. Ralph Buij wishes to thank the Province of Flevoland for providing financial support for the Marsh Harrier study. Ralph Buij and Kjell Janssens thank Gerard Müskens, Reinhard Vohwinkel, Jan Nagel, Jacques van der Ploeg, and the NOP Birds of Prey Working Group for their cooperation. They acknowledge funding through the WUR Knowledge Base Program: KB36 Biodiversity in a Nature-Inclusive Society (project number KB36-5200044844) - which is supported by the Dutch Ministry of Agriculture, Nature and Food Quality.

Ran Nathan thanks the Minerva Centre for Movement Ecology and Grants BSF-255/2008, BSF-904/2015, DIP NA 846/1-1, GIF-999-66.8/2008, JNF-KKL 14-093-01-6, ISF 2525/16 to RN for their kind support.

Ron Efrat thanks people who helped with field work in Israel, especially to Walter Naser and Korin Reznikov. This work was supported

by grant no. I-1465-413.13/2018 of the German-Israeli Foundation for Scientific Research and Development (GIF). Ron Efrat was supported by the Israeli Academy of Science's Adams Fellowship and the Ben-Gurion University's Negev Fellowship.

Thanks to Professor Oded Berger-Tal for his help leading the Egyptian vulture project in Israel.

Salim Javed would like to thank the Environment Agency-Abu Dhabi for their support.

Simeon A. Marin thanks the Project Greater chance for Lesser Kestrel (*Falco naumanni*) in Bulgaria - Lesser Kestrel Recovery, LIFE11 NAT/BG/360.

Simon Krejčí was supported by the University of Veterinary Sciences Brno grant no. IGA 204/2023/FVHE.

Steffen Oppel and Volen Arkumarev highlight that their work was carried out in the framework of the LIFE projects “The Return of the Neophron” (LIFE10 NAT/BG/000152) and “Egyptian Vulture New LIFE” (LIFE16 NAT/BG/000874, www.LifeNeophron.eu) funded by the European Union and co-funded by the A. G. Leventis Foundation, MAVA Foundation, and the BirdLife GEF/UNDP Migratory Soaring Birds project. The project team that carried out the work reported above was coordinated by Stoyan Nikolov and included: Vladimir Dobrev, Kristi Bashmili, Taulant Bino, Anastasios Bounas, Alexis Chardin, Dobromir Dobrev, Klea Duro, Eleftherios Kapsalis, Elzbieta Kret, Marie-Pia Marchant, Slave Nakev, Nenad Petrovska, Haritakis Papaioannou, Georgi Popgeorgiev, Ledi Selgjekaj, Theodora Skartsi, Anton Stamenov, Stoycho Stoychev, Mirjan Topi, Dimitrios Vavylis, Metodija Veleviski, Zydjon Vorpsi, Erald Xeka, Xhemal Xherri, Emil Yordanov, Samuel Bakari, Solomon Adefolu, Lale Aktay Sözüer, Paul T. Apeverga, Şafak Arslan, Yahkat Barshep, Turan Çetin, Maher Dayyoub, Laith El-Moghrabi, Hana ElSafoury, Ahmed Endris, Nabegh Ghazal Asswad, Junior H. Harry, Sam T. Ivande, Sharif Jbour, Bruktawit A. Mahamued, Shiiwua A. Manu, Solomon Mengistu, Abdoul R. Moussa Zabeirou, Sulaiman I. Muhammad, Slave Nakev, Alex Ngari, Joseph Onoja, Maher Osta, Serdar Özuslu, Cloé Pourchier, Tareq Qaneer, Alazar Ruffo, Mohammed Shobrak, Panagiotis Kordopatis, Theodora Skartsi, Özgün Sözüer, Million Tesfaye, Mengistu Wondafraash, Can Yeniurt, Emil Yordanov, Khaled Noby, Haitham Mossad, Sherif Baha El Din, Nouran Elbolkin, Tariq Abdalla, Ben Jobson, William Hayward, Salisha Chandra, Lubomir Peske, Clementine Bougain, Mekonnen Kassa, Samson Zelleke, Behailu Abraham, Nora Juhar, and Amin Seid. We acknowledge the support of field assistants helping to guard and supply supplementary food and monitoring Egyptian vulture territories, in particular Ivaylo Angelov, Tzvetomira Angelova, Nikolai Terziev, Sanie Mumun, Vanya Angelova, Yanina Klimentova-Nikolova, Ivayla Klimentova, Sylvia Dyulgerova, Emil Yordanov, Polina Hristova, Atanas Delchev, Hristo Hristov, Georgi Georgiev, Dimitar Nedelchev, Krasimir Manev, Medzhunun Ademov, Mitko Angelov, Svetoslav Cvetanov, Pencho Penchev, Jivko Barzov, Ivailo Ivanov, Marin Kurtev, Albena Kurteva, Kralju Kraljev, Rusko Petrov, Yordanka Vasileva, Dimitar Slavov, Stefka Dimitrova, Andreana Dicheva, Giannis Chondros, Giorgos Greousiotis, Lavrentis Sidiropoulos, Ali Abtourachman, Theodoris Christodoulou, Konstantinos Christodoulou, Paschalis Seitani, Katerina Demiri, Vasilis Papavasiliou, Nikos Maroukas, EVS and Greek volunteers hosted by WWF Greece.

Steven R. Ewing would like to thank the private individuals and organisations that funded the RSPB's Hen Harrier tagging programme, particularly the European Commission's LIFE programme through the Hen Harrier LIFE project (LIFE13 NAT/UK/000258), Northern England Raptor Forum (NERF), Lothian and Borders Raptor Study Group, Lush Retail Limited, Natural Resources Wales, Scottish and Southern Energy and the Welsh Government. We thank past and present RSPB staff that were involved in the LIFE project, as well as the licenced raptor workers, taggers and members of NERF and the Scottish Raptor Study Groups (too many to name individually) who monitored harrier breeding attempts and facilitated tagging efforts, as well as the many land managers and owners that permitted access to their land.

Tracking of Imperial eagle in Bulgaria was funded by the LIFE Program of the European Union under the project “Conservation of Imperial Eagle and Saker Falcon in key Natura 2000 sites in Bulgaria” (LIFE07 NAT/BG/000068).

Tomáš Veselovský acknowledges support from the Pannon Eagle LIFE project (LIFE15/NAT/HU/000902).

Tagging of short-toed eagles in Italy was funded by Parco Regionale Gallipoli Cognato e Piccole Dolomiti Lucane.

Wayne M. Getz was funded by the National Science Foundation, Grant/Award Number: 1617982; United States-Israel Binational Science Foundation, Grant/Award Number: 904/2015.

Rigas Tsiakiris is grateful to the FWFF-Fund for Wild Flora and Fauna (<https://www.fwff.org/>) with special thanks to Hristo Peshev and Emilian Stoynev for their technical support and advice.

Sonja Krüger would like to thank Ezemvelo KZN Wildlife and the Maloti Drakensberg Transfrontier project for their support.

Pietro Serroni would like to thank GREFA for their support and collaboration throughout the reintroduction project, Ministero dell’Ambiente e della Sicurezza Energetica for funding the gps tracking activity, Dipartimento Ambiente - Regione Calabria for funding the reintroduction project, and Dr. Giuseppe Cortone for ringing and marking of birds.

Stoycho Stoychev would like to thank Dimitar Demerdzhiev.

Ülo Väli acknowledges support from the EC LIFE programme (project LIFE04NAT/EE/000072), Estonian Environmental Investments Centre (Projects No. 15432 and 15632), the Estonian Environmental Board, Estonian Ministry of Foreign Affairs (Project no. 79-2017) and the Estonian University of Life Sciences (Project No. P180271).

Tracking of saker falcons in Slovakia was funded by the LIFE projects LIFE09 NAT/HU/000384 Conservation of Falco cherrug in NE Bulgaria, Hungary, Romania and Slovakia, and LIFE06 NAT/H/000096 Conservation of saker (Falco cherrug) in the Carpathian Basin. Vladimír Nemček would like to thank Jozef Chavko, Lucia Deutschová, Boris Maderič, Marcel Uhrin, Michal Noga, Mátyás Prommer, David Horal, Martin Dobrý and local ornithologists from Bulgaria and Germany, who helped us in the field and provided information for us.

Support for title page creation and format was provided by Author-Arranger, a tool developed at the National Cancer Institute.

We would also like to thank Jonas Waldenström and BirdLife International science team for their help and support.

We are grateful to two anonymous reviewers for their constructive comments that helped to improve the manuscript.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

This article is Hawk Mountain Conservation Science Contribution number 398.

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Funding

This work was funded by the MAVA Foundation through the MAVA Safe Flyways Energy project, specifically the M7 Birds – Reducing mortality of migratory birds and vultures in the Mediterranean 2016–2022.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110525>.

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