Shift in proximate causes of mortality for six large migratory raptors over a century

Federico De Pascalis[a], Michele Panuccio[b,1], Giovanni Bacaro[c], Flavio Monti[b,d,*]

[a] *Department of Environmental Sciences and Policy, University of Milan, Via Celoria 2, 20133 Milano, Italy*
[b] *MEDRAPTORS (Mediterranean Raptor Migration Network), Via Mario Fioretti 18, 00152 Rome, Italy*
[c] *Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy*
[d] *Department of Physical Sciences, Earth and Environment, University of Siena, Via Mattioli 4, 53100 Siena, Italy*

ABSTRACT

Delayed maturity and low reproductive rate make raptors naturally sensitive to high mortality rates, yet a wide variety of human-related threats negatively affect their population dynamics and persistence over time. We modelled the variability in the proximate causes of mortality associated with six species of large migratory raptors characterized by different ecological traits. We tested the hypothesis that species-specific mortality signals occur owing to differential exposure to threats in space and time. We relied on an unprecedently large dataset of ring (band) recovery (31,269 records) over a period of > 100 years. Our findings suggested that mortality of these birds has declined dramatically since the late 1970s. We found species-specific seasonal patterns of mortality, with higher mortality rates during early life-stages. For Black Kite, Common Buzzard, and Osprey, mortality increased with distance travelled and decreased with distance from migratory bottlenecks. Human-related mortality was higher than natural mortality (47% vs 5.6%), but after 1979 indirect anthropogenic factors increased, while direct ones decreased. Raptors showed differential specific exposure to mortality causes (direct human: Honey Buzzard, Marsh Harrier; indirect human: Common Buzzard, Black Kite; direct and indirect human: Osprey; natural: Montagu's Harrier). Conservation efforts and international laws have helped lower mortality caused directly by humans, but new emerging human-related threats are impacting migratory raptors and call for advanced conservation efforts. In a fast-changing world, anticipating future threats is key to stemming losses and boosting future preservation.

1. Introduction

Raptors are a particularly threatened group of birds (Buechley et al., 2019), with 52% of global species in decline and 18% currently classified as threatened with extinction (McClure et al., 2018). The number of raptor species listed as of Least Concern, according to the IUCN Red List, is declining at an alarming rate (Ceballos et al., 2017) and in Europe nearly 80% of non-owl birds of prey have an unfavourable conservation status (Tucker and Heath, 1994; Stroud, 2003). Historically, large declines in raptor populations have been documented in many parts of the world, including the Western Palearctic (Newton, 2003). Such declines were associated with multiple threats, among which human-induced threats were particularly important, leading several raptor populations to the brink of extinction and raising concerns about the potential for population recovery (Madden et al., 2019). Delayed maturity (large raptors can require from 2 to 5 years to reach

sexual maturity and start breeding), high trophic levels and relatively low reproductive rates make these birds especially vulnerable to human-related threats and to high mortality rates (Owens and Bennett, 2000; Sergio et al., 2008). Because of these life-history traits, the cumulative effects of individual mortality have particularly important consequences for population dynamics and the resilience of populations over-time, with carry-over effects often diagnosed on local, regional, and continental scales (Klaassen et al., 2014; Oppel et al., 2015).

Among raptors, migratory populations are especially vulnerable (Bildstein, 2006), mainly because of the high mortality they often experience during migration. Recent studies have demonstrated how hazardous long-distance migratory journeys can be for these birds (Strandberg et al., 2009; Klaassen et al., 2014; Oppel et al., 2015). Long-distance migration is energetically demanding and exposes migrants to unfavourable conditions (e.g. poor resource availability at stop-over sites, harsh weather events, hazards), increasing the risk of

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mortality. Furthermore, in long-distance migrants, the migration period can cover up to 40–50% of the year, a significant part of the annual cycle (Alerstam et al., 2006). Thus negative effects on population dynamics are most severe for long-distance migrants relying on seasonal habitats (Both et al., 2010).

Twice a year, tens of thousands of migratory raptors move from northern/central Europe to wintering grounds in sub-Saharan Africa and vice versa, along the African-Eurasian flyway (Newton, 2010; BirdLife International, 2010). This flyway includes large tracts of open-sea (i.e. the Mediterranean Sea) and is characterized by a significant ecological barrier, the Sahara desert (Strandberg et al., 2009; Zwarts et al., 2009). In addition, the flyway crosses regions with intense human activities - commercial trade, industry, recreational tourism - and where much habitat has been converted to agriculture or building. Human artifacts such as electric cables and wind farms represent additional obstacles to safe journeys over these countries (Lehman et al., 2007), as do poaching and illegal shooting which still occur in some regions (Brochet et al., 2017). As a result, migratory raptors face many different threats in their journeys across this region, especially at some migratory bottlenecks where they congregate in large numbers (Panuccio et al., 2005).

Studying the proximate causes of mortality for migratory raptors at the flyway scale is particularly important, as local/regional threats can influence population dynamics even at broader scale: an increase in the mortality rate in one area could affect population persistence over time at species' scale. Furthermore, species adopting different migratory tactics (e.g. different travel distances, flight performances, time schedules, social behaviour during flight and diet; Panuccio et al., 2005, 2017) might be exposed to species-specific threats. For instance, a species unable to perform long sea-crossing flights (e.g. griffons, storks, large eagles) will congregate over bottlenecks to cross water bodies, often being more exposed to poaching than a species capable of flying long stretches over the open sea (e.g. osprey). Quantifying and mapping mortality causes is thus a key prerequisite to fully understanding how, where and why specific selective processes may affect each taxa (e.g. Sergio et al., 2019), and helps implement effective conservation measures.

In this study, we focused on six species of large migratory raptors (Osprey *Pandion haliaetus*, Black Kite *Milvus migrans*, Western Marsh Harrier *Cyrcus aeruginosus* (hereafter Marsh Harrier), Montagu's Harrier *Cyrcus pygargus*, Common Buzzard *Buteo buteo* and Honey Buzzard *Pernis apivorus*) characterized by different flight performances (Agostini et al., 2015) and migratory strategies (Mellone et al., 2012). We hypothesized that specific potential threats could differentially affect each one of them. Specifically, we developed a set of post-hoc species-specific predictions on space, time and sources of threats potentially affecting each species according to their main ecological traits (Table 1). To provide a comprehensive account of the diversity and distribution of the proximate causes of mortality for each species, we make use of a large dataset of ring recovery data on marked individuals (Du Feu et al., 2016), which includes data collected from 1906 onwards, over a period of ca. 100 years. More specifically, we aimed at quantifying the effect of mortality induced by human activities on overall mortality and at investigating changes over time. Analyses were conducted with two different approaches:

1) Patterns of mortality: we start with an examination of temporal variation in mortality. We predict that raptor mortality decreased after 1979 as key international treaties addressing the conservation of raptors in Europe (the 1979 EEC Council Directive 79/409/EEC on the Conservation of Wild Birds, the 1979 Convention on the Conservation of European Wildlife and Natural Habitats and the 1979 Convention on the Conservation of Migratory Species of Wild Animals) came into effect. We also investigated patterns of mortality in relation to time of year, migration distances travelled, and distance from migratory bottlenecks. Finally, we evaluated the effect of

age on mortality, following the general assumption that in birds of prey mortality decreases with experience and rises again with senescence (e.g. Newton et al., 2016);
2) Causes of mortality: the role of natural vs human-induced mortality was investigated in relation to ecology and migration strategy, to test whether the impacts of threats vary among different raptors.

Our analysis takes a broad perspective and provides insights into patterns and causes of mortality for six large migratory raptor species both historically and in more recent years with a focus at the intercontinental scale across the African-Eurasian flyway. The relative importance of natural versus human-induced mortality was given particular consideration, and its long-term effects discussed. By analysing the relationship between diversity and distribution of mortality, we shed light on the shifting balance of selection pressures affecting different species of large migratory raptors in Europe. Our findings could help in evaluating the effectiveness of ongoing conservation measures in this region.

2. Materials and methods

2.1. Ecological traits of target species

We selected six migratory raptor species characterized by different ecological traits and migratory strategies (Tables 1, 2).

I) The Osprey is a highly specialized fish-eating raptor dependent on aquatic environments. It is a versatile flyer capable of traversing several hundred kilometers of open water, exploiting thermal uplifts when available, and using continuous flapping flight when uplifts are not available (Duriez et al., 2018). It migrates on a broad front but where possible, tends to cross water bodies at straits. For European populations, autumn migration spans from late July to early November; spring migration occurs between mid-February and early April.

II) The Black Kite is a generalist forager and a long-distance migrant that uses narrow-front migration funnelled through straits (Sergio et al., 2011; Panuccio et al., 2013; Santos et al., 2020). It often travels within loose flocks and exploits thermal current uplifts (Sergio et al., 2014). Migration peaks occur between the end of August and the beginning of September in autumn and between March and May, according to the flyway, in spring (Panuccio et al., 2013).

III) Marsh and IV) Montagu's harriers are both generalist foragers and solitary long-distance broad-front migrants. While Montagu's Harrier selects specific migration routes with relatively narrow sea crossings (Trierweiler et al., 2014; Panuccio et al., 2013; Millon et al., 2019), the Marsh Harrier often undertakes long sea-crossings through powered flight and with considerable expenditure of energy (Strandberg et al., 2008b; Agostini and Panuccio, 2010; Agostini et al., 2017). Montagu's Harrier generally starts autumn migration in late August to early-September, arriving at wintering grounds in early-mid-September. Spring migration starts in mid-March with birds arriving back at breeding grounds in mid-April (Limiñana et al., 2012). The Marsh Harrier's migration peaks in late March/ early April (spring) and in September (autumn) (Agostini and Panuccio, 2010).

V) The Common Buzzard is a generalist forager (feeding on a large variety of prey belonging to different taxa such as mammals, birds, reptiles and amphibians; e.g. Selås et al., 2007) and a short-distance migrant that uses a combination of slow migration speed and short migration time (Strandberg et al., 2008a). Autumn migration spans from late August to early October, while spring migration takes place from the end of March to the beginning of April. VI) The Honey Buzzard is a long-distance migrant that flies in large flocks and feeds on honeybees and wasps (an insect specialist). Autumn

Table 1
Post-hoc predictions on space, time and sources of threats potentially affecting each species according to their main ecological traits (migration type and tactics, social behaviour during migration and diet).

Species	Migration type	Migration tactic	Social behaviour	Diet	Post-hoc predictions on mortality
Osprey	Long-distance	Broad front + Sea-crossing	Solitary	Specialist *Exclusively fish species living close to water surface*	• Increases with distance travelled • Does not concentrate at bottlenecks • Mortality due to human causes occurring at water bodies • Greater in juveniles • Greater during migration/winter
Black Kite	Long-distance	Narrow front + Bottlenecks	Group (flocks)	Generalist *Arthropods, rodents, birds, small reptiles, carrions*	• Increases with distance travelled • Concentrates at bottlenecks • Mortality due to shooting and electrocution • Greater in juveniles • Greater during migration/winter
Marsh Harrier	Long-distance	Broad front + Over land/sea	Solitary	Generalist *small mammals, birds, insects, reptiles, amphibians and occasionally fish*	• Increases with distance travelled • Does not concentrate at bottlenecks • Mortality due to shooting and collision with infrastructures • Greater in juveniles • Greater during migration/winter
Montagu's Harrier	Long-distance	Broad front + Over land/sea	Solitary	Generalist *small rodents, small birds, bird eggs, reptiles (including snakes) and large insects*	• Increases with distance travelled • Does not concentrates at bottlenecks • Mortality due to shooting and collision with infrastructures • Greater in juveniles • Greater during migration/winter
Common Buzzard	Short-distance	Over land	Solitary	Generalist *small rodents, birds, reptiles, amphibians, large insects and earthworms, carrions*	• Highly increases with distance travelled • Does not concentrate at bottlenecks • Mortality due to electrocution, collision with infrastructures and vehicles (close to roads) • Greater in juveniles • Equally distributed over the year
Honey Buzzard	Long-distance	Narrow front + Bottlenecks	Group (flocks)	Specialist *Exclusively arthropods such as wasps and hornets*	• Increases with distance travelled • Concentrates at bottlenecks • Mortality due to shooting • Greater in juveniles • Greater during migration

Table 2
Euring dataset details of six raptor species after the cleaning phase (see Material and methods). Ringing data period, number of records of birds found alive and dead and total number of records (N) are reported for each species.

Species	Period	Alive	Dead	N
Osprey	1906–2014	1764	5047	6811
Black Kite	1906–2014	314	1195	1509
Marsh Harrier	1920–2009	232	1885	2117
Montagu's Harrier	1920–2009	81	437	518
Common Buzzard	1906–2014	2981	16,805	19,786
Honey Buzzard	1906–2014	58	470	528
Total	108 years	5430	25,839	31,269

migration takes place between August and October and spring migration between April and May (Hake et al., 2003; Panuccio et al., 2005). As this species relies on thermal updrafts to fly over great distances, it tends to concentrate at high-density spots for sea-crossings (Agostini and Panuccio, 2005; but see also Nourani et al., 2020).

2.2. Euring dataset

All the following statistical analyses were performed with R Software (R Core Team, 2016 - Version 3.2.4), using data from EURING Data Bank, which holds copies of recovery records from bird ringing schemes throughout Europe (Du Feu et al., 2016; https://euring.org/). Six EURING datasets were used, covering ringing data from 1906 to 2014 for Osprey, Black Kite, Common Buzzard and Honey Buzzard, and from 1920 to 2009 for Marsh Harrier and Montagu's Harrier. The datasets allowed an analysis on a continental scale and over a period of

maximum 108 years. The datasets were prepared to data analysis using the "Birdring" R package (Korner-Nievergelt and Robinson, 2014). More specifically, since we were interested in mortality patterns rather than survival and given that most individuals were recaptured just one time (only 8% individuals in the dataset were recaptured more than 1 time), only first (ringing occasion) and last encounter (0 bird encountered alive, 1 bird encountered dead) were retained. Records where the status of the bird at last encounter was unclear (sick, unknown, etc.) were discarded. Birds found dead as chicks were excluded from the analysis, not to alter the patterns with nest mortality (except for the analysis of mortality related to age -and the maps of mortality locations - see below). After the cleaning phase, we gathered 31,269 records, among which 5430 and 25,839 were for bird encountered alive and dead, respectively (Table 2). We acknowledge that our approach (see below) investigates patterns in the probability of observing an individual alive or dead, rather than the actual probability of mortality. Therefore, an underlying bias is that the probability of observing an individual dead or alive heavily relies on the number of observers and the effort in marking birds, both varying spatio-temporally. However, given the very large and long-term dataset, and given that aim of our work is to investigate patterns, we believe that the probability of observing an individual alive or dead represent a good proxy to understand changes in mortality over time/distances/ages.

2.3. Statistical analyses

To investigate patterns in the probability of observing an individual alive or dead (hereafter referred simply as "mortality"), GAMs (Generalized Additive Models) were applied to each dataset using a binomial family distribution (0 bird encountered alive, 1 bird

encountered dead) with logit link function, and response curves (i.e. smoothers) were plotted on the response scale using Visreg.R package (Breheny and Burchett, 2017). GAMs were chosen due the high non-linear relationship between response and explanatory variables (Zuur, 2012). When an explanatory variable showed a strong linear relationship with the response variable, it was fitted in the model as a linear variable (Zuur, 2012). A visual inspection of model Pearson's residuals using an autocorrelation function did not reveal temporal autocorrelation (Zuur et al., 2009). To test when birds were exposed to enhanced risk and mortality during their annual cycle, we calculated the day of year from 1st of January and we fitted it as a circular variable in the model. To minimize sea-crossing, they usually concentrate at bottlenecks such as straits or isthmus. To test if mortality events occurred at migratory bottlenecks we calculated, for each last encounter of an individual, the distance in kilometers from the closest migratory bottleneck (See Supplementary information 4 for a complete list of bottlenecks considered) and we included it in the models. To test the effect of distance travelled we included in the model the distance between the first and the last observation of an individual, under the general prediction that mortality risks increase with the migration length and duration. Greater distances require higher energetic costs and can expose individuals to multiple threats for a longer time, than when migrating for shorter distances (Klaassen et al., 2014). To check eventual trends in mortality over time, the year of last encounter was included in the model. The best minimum adequate model for each species was identified with a backwards model selection (starting from a full model including all variables) based on significativness of variables (variables with P values > 0.05 removed) coupled, when necessary, with minimization of UBRE score.

The relationship between age and mortality was tested using binomial GLMs with logit link function. A subset of data, with known age classes, was used and nest mortality in this case was included. Significance was tested with likelihood ratio tests.

To qualitatively assess and visualize mortality at a coarse spatial level (e.g. continental), for each species, ringing location of dead individuals (all data, including unknown mortality causes) were plotted. To understand ringing effort and location, animated maps showing both ringing and recovery of dead individuals were created using gganimate R package (Pedersen and Robinson, 2019). One recovery of a Common Buzzard (found in the Russian far east) and one ringing occasion of a Black Kite (ringed in Mongolia) were discarded in the maps to keep them at an acceptable spatial scale.

To better understand the causes and origin of mortality, data were grouped into 4 broad categories: "Natural" (mortality due to natural causes), "Human direct" (bird intentionally killed; e.g.: shot, hunted, trapped, etc.), "Human indirect" (not intentionally killed, but mortality due to human activity/presence; e.g.: by catch, electrocution, collision, etc.) and "Unknown" (mortality causes unknown). The percentage of each broad mortality cause (overall and in respect to two historical periods pre- and post-1979) was then calculated and plotted. The percentages of the main four mortality causes pre- and post-1979 (all species together) were also calculated and plotted, as well as the main 10 natural mortality causes.

To reveal differences and different impact of broad mortality causes between species post-1979, a Principal Component Analysis (PCA) was applied on the proportion of mortality of the four broad categories per species. To aid the interpretation of PCA's results, the percentage of the main two mortality causes per each species (post-1979) was calculated and plotted.

3. Results

3.1. Patterns of mortality

The minimum adequate models for each species are shown in Table 3. Overall, mortality decreased with time, roughly from the end

of the 1970s, for all species (Fig. 1, $P < 0.01$ for all response curves). Mortality was higher during migratory and wintering periods and lower during the reproductive period for all species (Fig. 2, $P < 0.01$ for all response curves), with the exception of the Common Buzzard for which highest mortality occurred during the breeding season (April–June; Fig. 2). However, slight differences in mortality patterns during the year were noticeable among species, in relation to their phenology (Fig. 2). Response curves were not significant for the Montagu's Harrier, probably owing to lack of data. Osprey, Black Kite and Common Buzzard showed a slight positive linear increase of probability of mortality with distance travelled (Osprey: $\beta = 0.00031$ $SE = 0.00004$ $P < 0.001$; Black Kite: $\beta = 0.0003$, SE $= 0.0001$, $P = 0.01$; Common Buzzard: $\beta = 0.0014$, $SE = 0.0001$, $P < 0.001$; Supplementary information 1). They also showed a slight negative linear effect of distance from migratory bottleneck on mortality (Osprey: $\beta = -0.00035$, $SE = 0.00008$, $P < 0.001$; Black Kite: $\beta = -0.0004$, $SE = 0.0001$, $P = 0.003$; Common Buzzard; $\beta = -0.0006$, $SE = 0.0001$, $P < 0.001$; Supplementary information 2). Geographically, mortality patterns were different for each species (Fig. 3), reflecting main migratory flyways and wintering areas. Common Buzzard mortality occurred mainly in Europe, roughly concentrating between 30° and 70° N (Fig. 3E). For all the species, interactive maps showing ringing locations and recovery locations of dead individuals are available in supplementary materials (Supplementary information 3).

3.2. Mortality causes

Causes of mortality are mainly due to human factors rather than to natural causes (47% vs 5.6%; Fig. 4). Before 1979, however, the main mortality causes were linked to direct human activities; after 1979 indirect human activity was the most common cause of death (Fig. 4). The percentage of death from natural causes remained roughly constant throughout the historical period (Fig. 4).

Examining the main causes of death pre- and post-1979 in more detail, the decrease in number of birds shot and the increase in birds hit by vehicles between the two historical periods is striking (Fig. 5). The main natural mortality causes were individuals being taken by a wild animal (37%, obtained pooling together causes listed as "taken by an animal", "taken by owl or raptor", "taken by predatory bird", "taken by wild mammal" and "taken by bird") and poor conditions (33%), likely a proxy for starvation, a common cause of mortality during migration (e.g. Oppel et al., 2015). The top 10 natural mortality causes are shown in Fig. 6.

When investigating mortality causes on single species (post-1979) in detail, common drivers emerged (Fig. 7A). Honey Buzzard and Marsh Harrier shared an important component of direct killing (i.e. shot, Fig. 7B), while Common Buzzard and Black Kite tended to die owing to indirect causes (e.g. collision with infrastructure and electrocution, Fig. 7B). For Ospreys, causes of death fell between these two groups, revealing both direct and indirect sources of mortality (Fig. 7B). Montagu's Harrier showed an important natural component of mortality: predation by wild mammals.

3.3. Effect of age on mortality

Mortality decreased with age for all species. The only exception was the Osprey which showed an increase of mortality with age (Table 4). For Montagu's Harrier there was no effect of age on mortality, probably owing to the low number of known age classes.

4. Discussion

4.1. Temporal patterns of mortality

Our analysis of long-term ring-recovery data of six migratory European raptor species revealed that rates of mortality have declined

continuously since the end of the 1970s. This suggests an interplay of different factors, but especially international treaties that helped ban the hunting of birds of prey. While European treaties have promoted conservation mainly in breeding areas, different policies and international agreements under the Convention on Migratory Species (CMS) have fostered conservation in wintering areas and across migratory
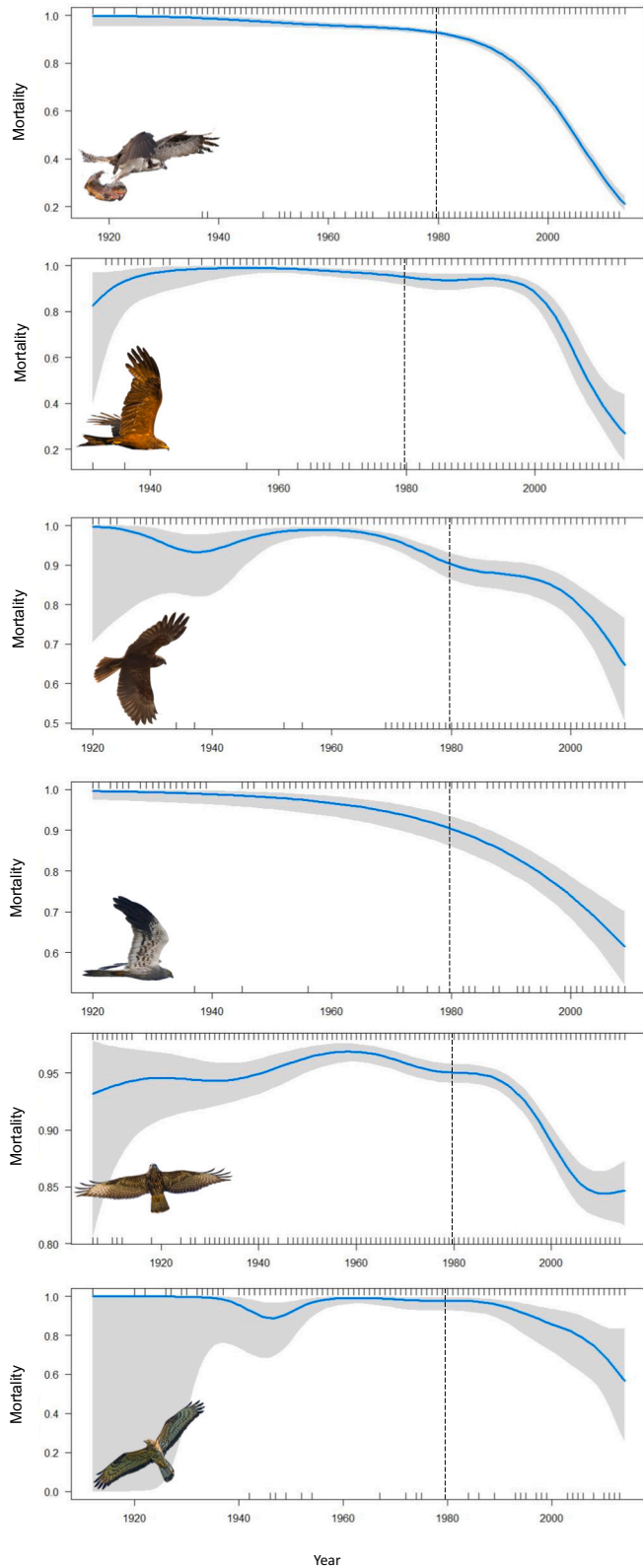

Fig. 1. Response curves from the fitted Generalized Additive Models showing probability of mortality over time (years) for six raptor species. From top to bottom: Osprey (*Pandion haliaetus*), Black Kite (*Milvus migrans*), Marsh Harrier (*Cyrcus aeruginosus*), Montagu's Harrier (*Cyrcus pygargus*), Common Buzzard (*Buteo buteo*), Honey Buzzard (*Pernis apivorus*). Ringing data range from 1906 to 2014 for Osprey, Black Kite, Common Buzzard and Honey Buzzard, and from 1920 to 2009 for Marsh and Montagu's harriers. The dotted line represents the year 1979 to distinguish between pre- and post- adoption of the international treaties addressing the conservation of raptors and that prohibited their deliberate killing or trapping. Ticks on the upper and lower horizontal axis show the distribution of the data (0: individual recovered alive, 1 individual recovered dead).

flyways. For example, the Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia (Raptors MoU) promotes internationally coordinated actions to preserve migratory raptors throughout their range in the African-Eurasian region, in an effort to reverse their decline.

In addition, although not directly related to raptors, the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) - an intergovernmental treaty dedicated to the conservation of migratory waterbirds and their habitats across Africa, Europe, the Middle East, Central Asia, Greenland and the Canadian Archipelago, developed under the framework of the CMS and administered by the United Nations Environment Programme (UNEP) - has since 1995 promoted the coordinated conservation of 255 species of birds ecologically dependent on wetlands as well as the management of a network of suitable sites on which raptors also rely to support their annual journeys. Combined, all of these policies contributed significantly to reduce mortality of raptors throughout their range and annual cycle.

Despite these conservation measures, however, illegal killing of birds still occurs in many countries along the Eurasian-African flyways (Hirschfeld and Heyd, 2005; Brochet et al., 2017), although its current impact on overall mortality rates of birds of prey seems to be of minor concern, compared to the past. The six raptor species we studied showed differing exposure to threats at a temporal scale, a fact that can be explained by their different migratory strategies, phenology and ecological traits (Table 1). However, some care must be taken when interpreting our results. Given the nature of the data, the decrease in mortality we observed could be related to an increase in the recoveries of live animals, owing to increasing number of observers (both ringers and birdwatchers). However, the steady trend since 1970/80 (when the recoveries of live animal are more frequent and uniform) suggests a generally consistent decrease in mortality.

Overall mortality was higher during migration and wintering periods, although the Common Buzzard showed higher mortality during the breeding period, a fact we attribute to the sedentary behaviour of this species and possibly a bias associated with higher sampling effort at reproductive sites, i.e. Germany. Honey Buzzard had low mortality levels during breeding but showed high mortality outside that period, possibly because of its long and extended migrations (Hake et al., 2003; Panuccio et al., 2005). Osprey showed an opposite trend to that of the Common Buzzard: mortality peaks occurred in winter and gradually decreased during migration, with minimum values during the breeding season. This is in line with other studies reporting high mortality rates in winter months (Monti et al., 2018a; Poole, 2019) and during migration (Klaassen et al., 2014).

Like the Honey Buzzard, the Marsh Harrier showed fairly high mortality during extended periods of the year, with a minimum detected in summer. In this case, however, mortality peaks were associated with spring and autumn migrations as well as with the winter season. The Marsh Harrier spends winters in Sahelian areas, a semiarid transition zone of 3 million km^2, where mortality rates have been reported to be high, especially in dry years (Zwarts et al., 2009). It is a wide strip (~500 km, ranging North from the Sahara desert to the Guinea coast rainforest in the South) and extending for 5500 km from
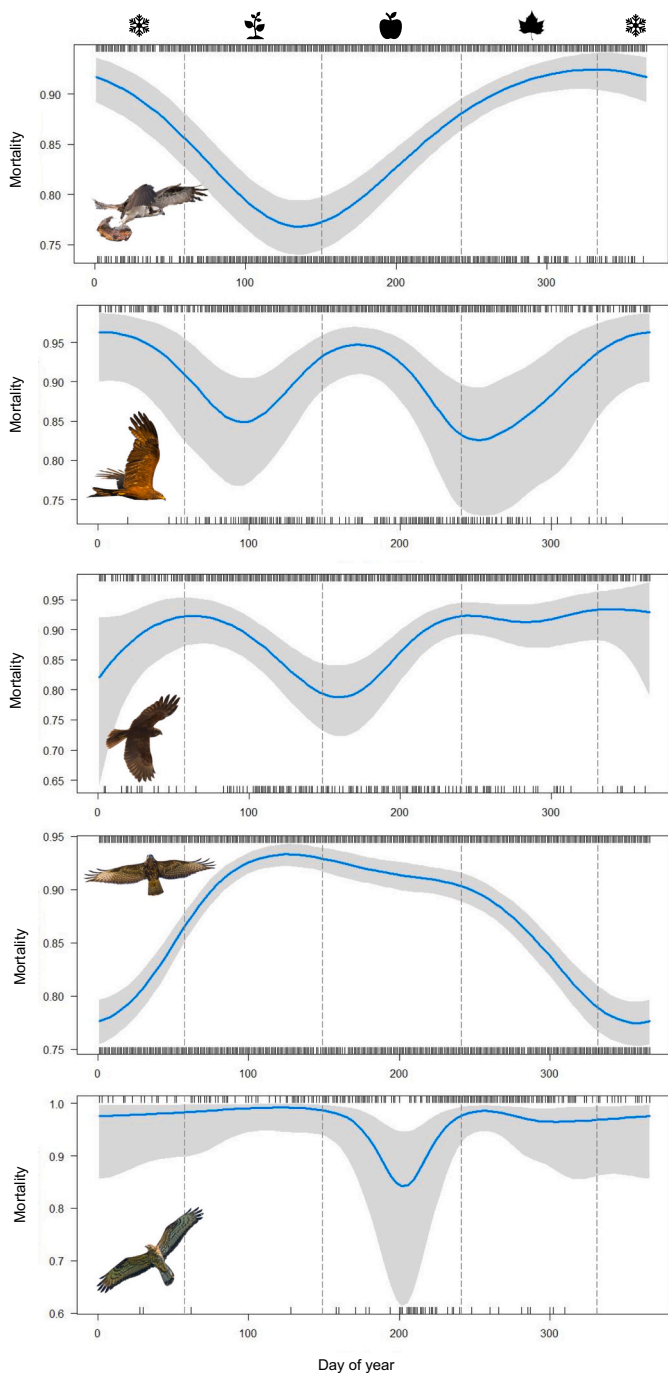
Fig. 2. Response curves from the fitted Generalized Additive Models showing probability of mortality within the year for five raptor species. From top to bottom: Osprey (*Pandion haliaetus*), Black Kite (*Milvus migrans*), Marsh harrier (*Cyrcus aeruginosus*), Common Buzzard (*Buteo buteo*), Honey Buzzard (*Pernis apivorus*). Ringing data range from 1906 to 2014 for all the species except the Marsh Harrier (1920–2009). Dotted lines show the start/end date of meteorological seasons, each one indicated with a symbol. From left to right: Winter, Spring, Summer, Fall, Winter. Ticks on the upper and lower horizontal axis show the distribution of the data (0: individual recovered alive, 1 individual recovered dead).

the Atlantic coast to the Red Sea, characterized by high variability in rainfall (Zwarts et al., 2009). Under conditions of drought, birds gather in the few remaining wetlands, enhancing the risk of being shot or trapped (Zwarts et al., 2009).

The Black Kite showed reduced mortality in spring and autumn, with higher rates in winter/summer. This might be explained by

specific threats occurring in breeding and wintering grounds, when local low-altitude movements (compared to altitudes reached during migratory flights; > 250 m as per Panuccio et al., 2014) might favour electrocution fatalities (i.e. its main cause of mortality - see below). Moreover, electrocution risk is higher for gregarious species such as kites, which are more likely to be in physical contact while perching in groups on electric-utility structures (e.g. Harness and Wilson, 2001; Lehman et al., 2007).

4.2. Spatial patterns of mortality

At a coarse spatial level, the distribution of recovery locations has illuminated prevalent migratory flyways and related wintering grounds, as well as where mortality occurred. Dead Common Buzzard were found over much of Europe, with eastern limits in the Middle East and western/central Russia. Interestingly, 26 records (ca. 0.14% of the total) were found in western Sahel and even in equatorial and South Africa, indicating some extraordinary long-distance movements (Fig. 3E). These recoveries likely belong to the subspecies-group of the Common Buzzard known as the Steppe Buzzard (*Buteo buteo vulpinus*) that from eastern Europe is known to migrate in large numbers to Africa via Israel (Herremans, 2000; Väli and Vainu, 2015), while the nominal subspecies (*Buteo buteo buteo*) in western Europe usually does not cross Gibraltar.

Mortality records of Honey Buzzards were concentrated in central Europe, but present as well at bottlenecks such as Gibraltar Strait, Messina Strait, Batumi, and the coast of Israel (Fig. 3F). On the east, a few records from the coast of Black Sea showed that some individuals migrated along the eastern European flyway, while records from equatorial Africa are in line with the known winter range of the species. The distribution of recovery locations for Ospreys was broad (Fig. 3A). The huge ringing effort in northern European countries has resulted in a plethora of recoveries, not only in Europe but also in Africa (Zwarts et al., 2009). Discovery locations were spread across the Western Palearctic, from Lapland to the coast of North Africa and from Mediterranean islands on the west to Arabian Peninsula on the east. Recovery locations at sub-Saharan countries formed a broad belt covering all major and many minor water bodies of the Sahel, including salt and brackish water in the coastal zone. This confirms that Ospreys from various parts of Europe show extensive overlap on their wintering grounds, even if an east-west cline is nevertheless prevalent (Zwarts et al., 2009; Monti et al., 2018b). Many recoveries from Mediterranean islands indicate the capacity with which this species is able to cross large water bodies.

A marked NW-SE migratory flyway, along which dead recoveries are spread, is evident for the Black Kite (Fig. 3B). Particularly, a massive concentration of records between Spain and Morocco could be an effect of a long-term ringing effort in the area (Sergio et al., 2011). Unlike other species, few African recoveries were available for the Montagu's Harrier (Fig. 3D). They mainly come from dry savanna-like habitats confined in the Sahel, where birds commonly winter relying on local sources of food and outbreaks of locusts and grasshoppers (García and Arroyo, 1998; Zwarts et al., 2009). More recent studies of this species using satellite telemetry and radar monitoring have identified three main migration routes towards wintering areas in sub-Saharan Africa (Trierweiler et al., 2014), with wintering areas and migration routes of different breeding populations overlapped (e.g. weak connectivity). Marsh Harrier recoveries were distributed broadly across the Mediterranean Sea (Fig. 3C), with few recoveries found at migratory bottlenecks on either side of the Mediterranean. Recoveries of dead birds in West Africa were largely associated with large floodplains and inland and coastal marshlands.

4.3. Distance travelled

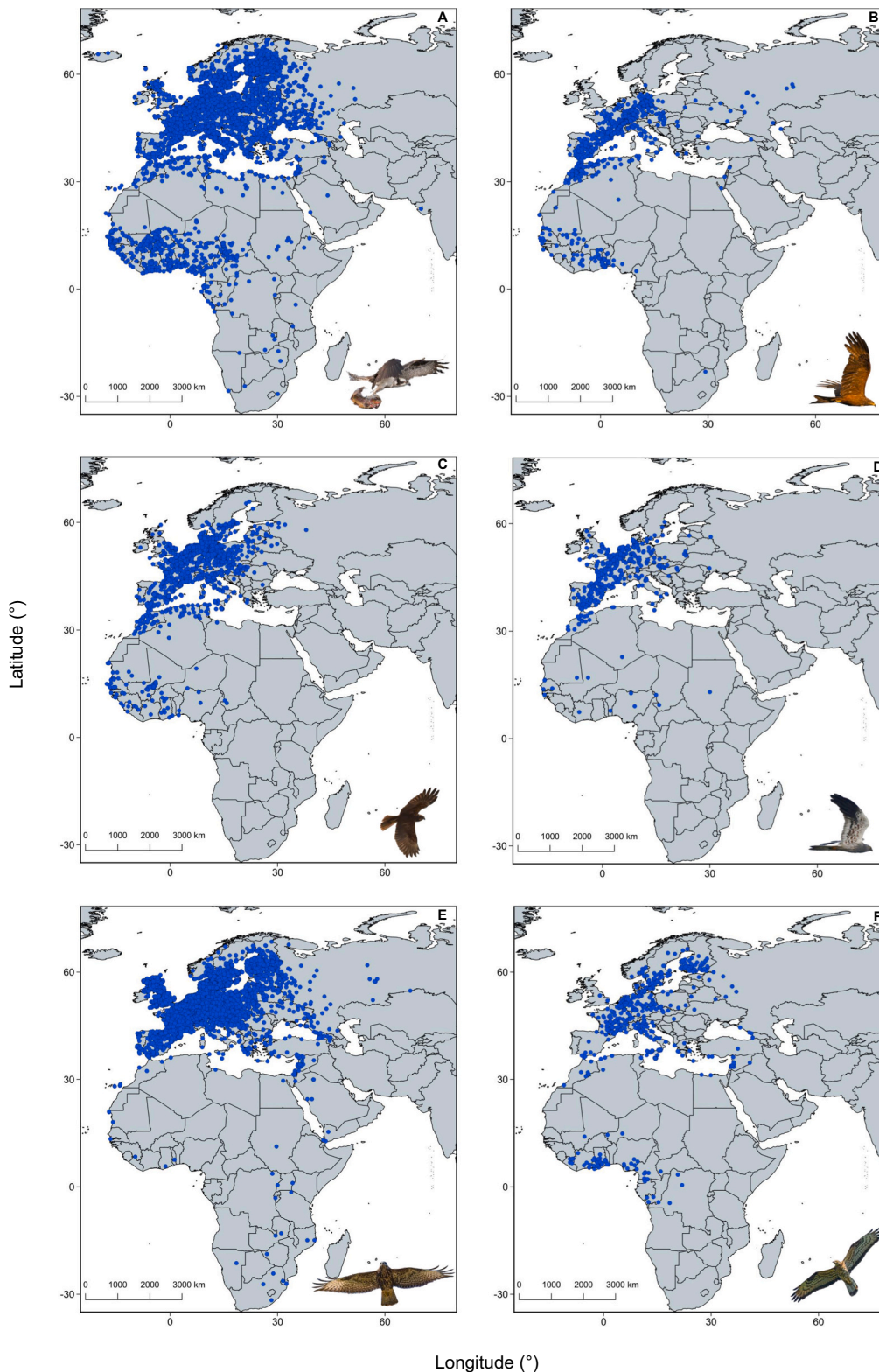Migration distance was related to mortality in some (Osprey, Black

Fig. 3. Locations where individuals were recovered dead. All data, including unknown mortality causes, were plotted. A: Osprey (*Pandion haliaetus*), B: Black Kite (*Milvus migrans*), C: Marsh Harrier (*Cyrcus aeruginosus*), D: Montagu's Harrier (*Cyrcus pygargus*), E: Common Buzzard (*Buteo buteo*), F: Honey Buzzard (*Pernis apivorus*). Animated maps showing both ringing location and recovery location are present in Supplementary information 3.

Kite and Common Buzzard), but not all, species. For the Common Buzzard (a short-distance migrant, Strandberg et al., 2008a) greater distances probably reflected extra energy costs and risks, influencing survival. Osprey mortality correlated with migration distance. In this sense, recovery locations reflect the important role of the Sahara desert as a severe ecological barrier for migrants (Zwarts et al., 2009; Klaassen et al., 2014). It should be noted that some Mediterranean breeding Ospreys are partial migrants (and some permanent residents - Monti

et al., 2018b). By migrating over limited distances and for short periods of time, individuals from these populations potentially reduce both energy expenditure and risk compared to long-distance migratory individuals from Northern populations. However, important winter mortality rates are known even for these Mediterranean Ospreys wintering at temperate latitudes, owing to multiple factors, including poaching (e.g. Monti et al., 2018a).

In the Black Kite, there was an effect of distance travelled on

Table 3

Generalized Additive Models of probability of mortality in relation to time and distance for six raptor species. Explained deviance and adjusted R^2 values for each model are shown. State at recapture was a binary variable where 0 is bird encountered alive and 1 is bird encountered dead. The day of the year starts from 1st of January and was fitted in the model as a circular variable. Distance was the linear distance in kilometers from the first and the last encounter. Distance from (migratory) bottleneck was the linear distance in kilometers from last encounter and geographically closest migratory bottleneck.

Species	Explained deviance (%)	Adjusted R^2	Best fitted model
Osprey	34.7	0.40	State at recapture ~ s(day of year) + s(year) + distance + distance from bottleneck
Black Kite	35.7	0.40	State at recapture ~ s(day of year) + s(year) + distance + distance from bottleneck
Marsh Harrier	11.0	0.08	State at recapture ~ s(day of year) + s(year)
Montagu's Harrier	14.8	0.12	State at recapture ~ s(year)
Common Buzzard	9.6	0.09	State at recapture ~ s(day of year) + s(year) + distance + distance from bottleneck
Honey Buzzard	37.4	0.37	State at recapture ~ s(day of year) + s(year)

mortality, likely acting differently according to age (see below- Sergio et al., 2014). Unexpectedly, no effects on distance travelled were retained by the model selection for the other species (Honey Buzzard, Montagu's and Marsh Harriers). This implies high mortality before having travelled a significant amount of the migratory route. This is further supported by the absence of an effect of distance from bottleneck on mortality (see below), and it is confirmed by the analysis of mortality causes, that revealed these three species as belonging to a cluster oriented differently to the former three species. Honey Buzzard and Marsh Harrier were mainly associated with direct killing, while Montagu's Harrier had a strong component of natural mortality, probably owing to predation during the breeding season.

4.4. Distance from bottlenecks

The same three species (Common Buzzard, Osprey and Black Kite) showed mortality decreased as distance from migratory bottlenecks increased. For the Common Buzzard and the Black Kite, large sea crossings were a severe barrier to cope with, resulting in recovery locations of dead individuals concentrated inland and/or at straits or isthmuses (Supplementary information 3). However, the broad front migration of the Osprey suggests no effect on mortality associated with distance from migratory bottlenecks, perhaps reflecting the difficulty in detecting dead Ospreys on the open sea or on islands (e.g. Monti, 2020). In fact, bottlenecks are known sensitive areas where birds concentrate but where illegal killing activities also occur more frequently (Brochet et al., 2017). On the other hand, it is also true that most raptor banding/watching stations occur at bottlenecks. Thus, more birds are likely to be
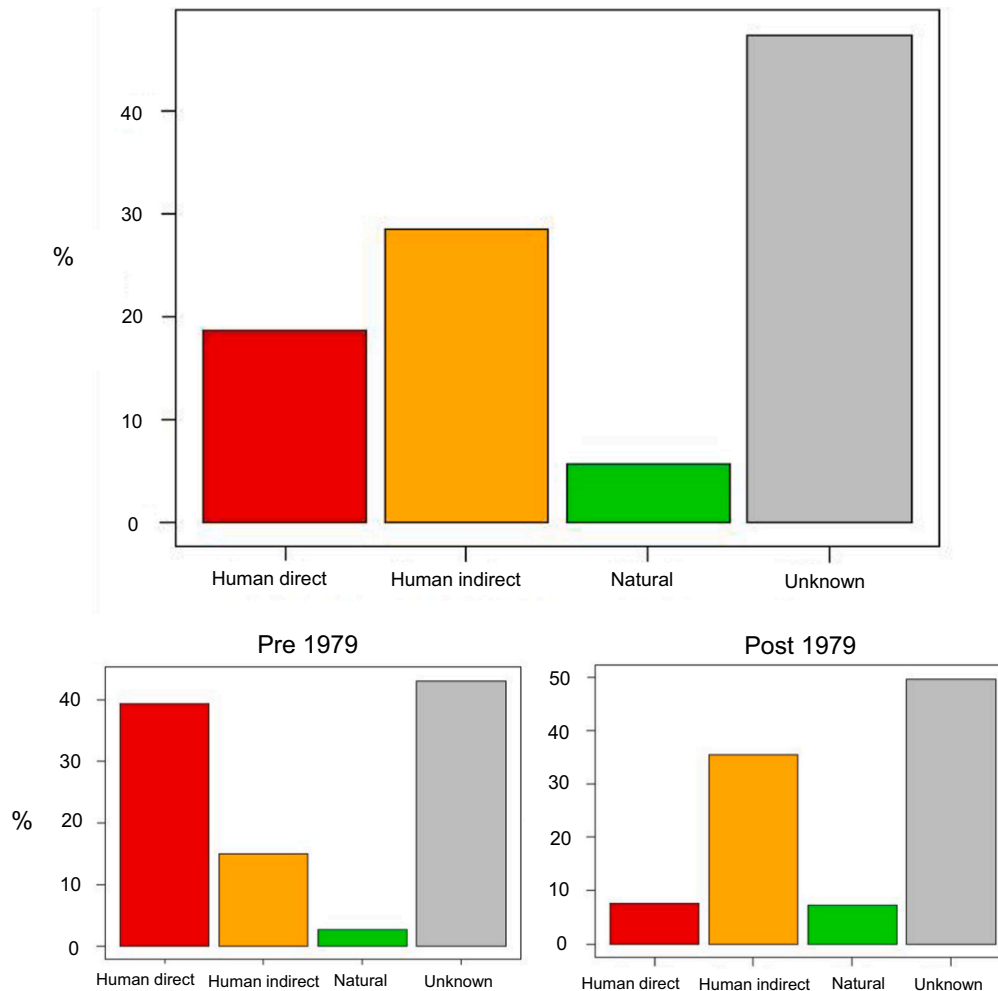

Fig. 4. Main broad mortality causes for six raptor species. Broad causes of mortality (all the species together), were grouped in 4 categories and percentages calculated. "Human direct" (bird intentionally killed; e.g.: shot, hunted, trapped – in red), "Human indirect" (not intentionally killed, but mortality due to human activity/presence; e.g.: bycatch, electrocution, road casualty – in orange), "Natural" (mortality due to natural causes – in green) and "Unknown" (mortality causes unknown – in gray). Percentage of causes of raptors mortality are reported also for the two historical periods, before and after the 1979. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
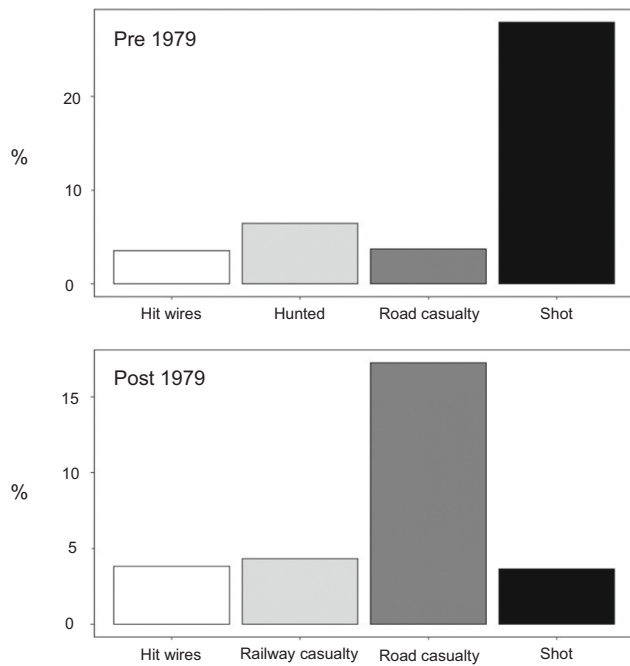
Fig. 5. Main four mortality causes for six raptor species. Main four causes of mortality, represented as percentage and considered for all the species together are shown, pre- and post-1979.

banded and encountered at these stations. This could be an additional bias in these types of data and represent another possible explanation for the bottleneck distance patterns observed. These factors combined may explain why mortality increases at these spots. Again, we did not find an effect of distance from bottleneck for the Marsh Harrier, Montagu's Harrier or the Honey Buzzard, suggesting that for these species other mortality sources play an important role before the species reach migratory bottlenecks.

4.5. Patterns and causes of mortality per species

We found that human-induced mortality played an important role in the mortality of the birds we studied, and was always higher than natural mortality. This is corroborated by the fact that after 1979 the

mortality associated with indirect human activities increased notably (7.66% direct vs 35.47% indirect). Thus in more recent decades, mortality from direct human activities (e.g. shooting) has been replaced by mortality from indirect human activities (e.g. collisions), whereas mortality associated with natural causes has remained constant over time (ca. 5–8%). We note, however, that natural causes of mortality are probably under-reported compared to human-related causes, probably because the latter happen near human settlements, increasing the likelihood of finding and reporting a dead bird, and because natural mortality causes (such as starvation) can be difficult to assess. We suspect that many unknown mortality causes could be in fact natural mortality causes that were difficult to detect. We recommend care when reporting causes of mortality of ringed individuals, and when possible a necropsy would be helpful.

The species we have considered showed differences in the causes of their mortality, according with their ecological traits. The main cause of death for the Common Buzzard was collision with vehicles ("road casualty"), in line with this species' habit of perching and hunting from light poles and fences along roads (Wuczyński, 2005), and by its feeding on roadkills. Road casualty have been poorly considered as source of mortality (Bujoczek et al., 2011), but recent findings and studies adopting specific sampling methods (Schwartz et al., 2018) shed new light on the potential of this threat. The Honey Buzzard was the most actively killed species, as shooting represented the main cause of mortality, even after 1979 (Fig. 7). This is likely due to this species forming large flocks during migration, which makes individuals easy to find and kill in areas where poachers are active. Ospreys were accidentally caught in fishing nets along water bodies and also directly shot, in line with recent literature (e.g. Monti et al., 2018a). Black Kites died especially because of indirect threats such as electrocution and road casualty (Fig. 7), as the species commonly perches on wires and light poles in busy human landscapes. Most Marsh Harrier recoveries were of individuals shot or killed by impact with road vehicles along roads, in line with its typical ground-hugging hunting flights, while Montagu's Harrier recoveries showed birds shot or the prey of terrestrial predators in agricultural environments, likely during the breeding season while nesting on the ground (i.e. natural causes).

Unexpectedly, we did not find that wind farms killed many of these raptors, although wind power may be a cause of mortality too new (developed only over the last 20 years) to show detectable patterns in our analytic framework. Even though mortality of raptors has been documented at wind farms (e.g. Drewitt and Langston, 2008), we suspect that
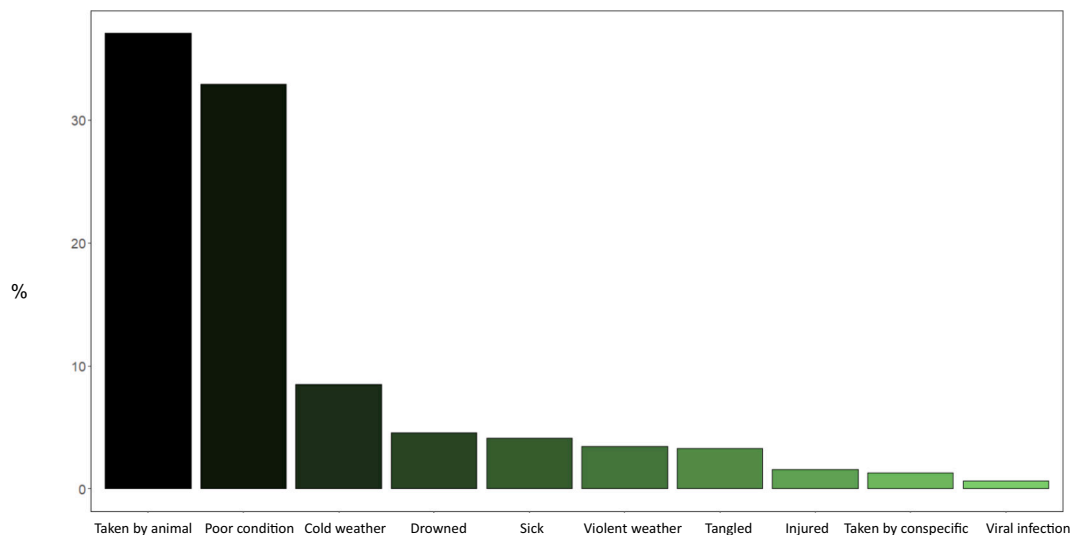

Fig. 6. Main ten natural mortality causes for six raptor species. Mortality causes represented as percentage and considered for all the species together are shown. Mortality causes where the individual was killed by a wild animal were pooled together (i.e. mortality causes listed in the dataset as "taken by an animal", "taken by owl or raptor", "taken by predatory bird", "taken by wild mammal" and "taken by bird").
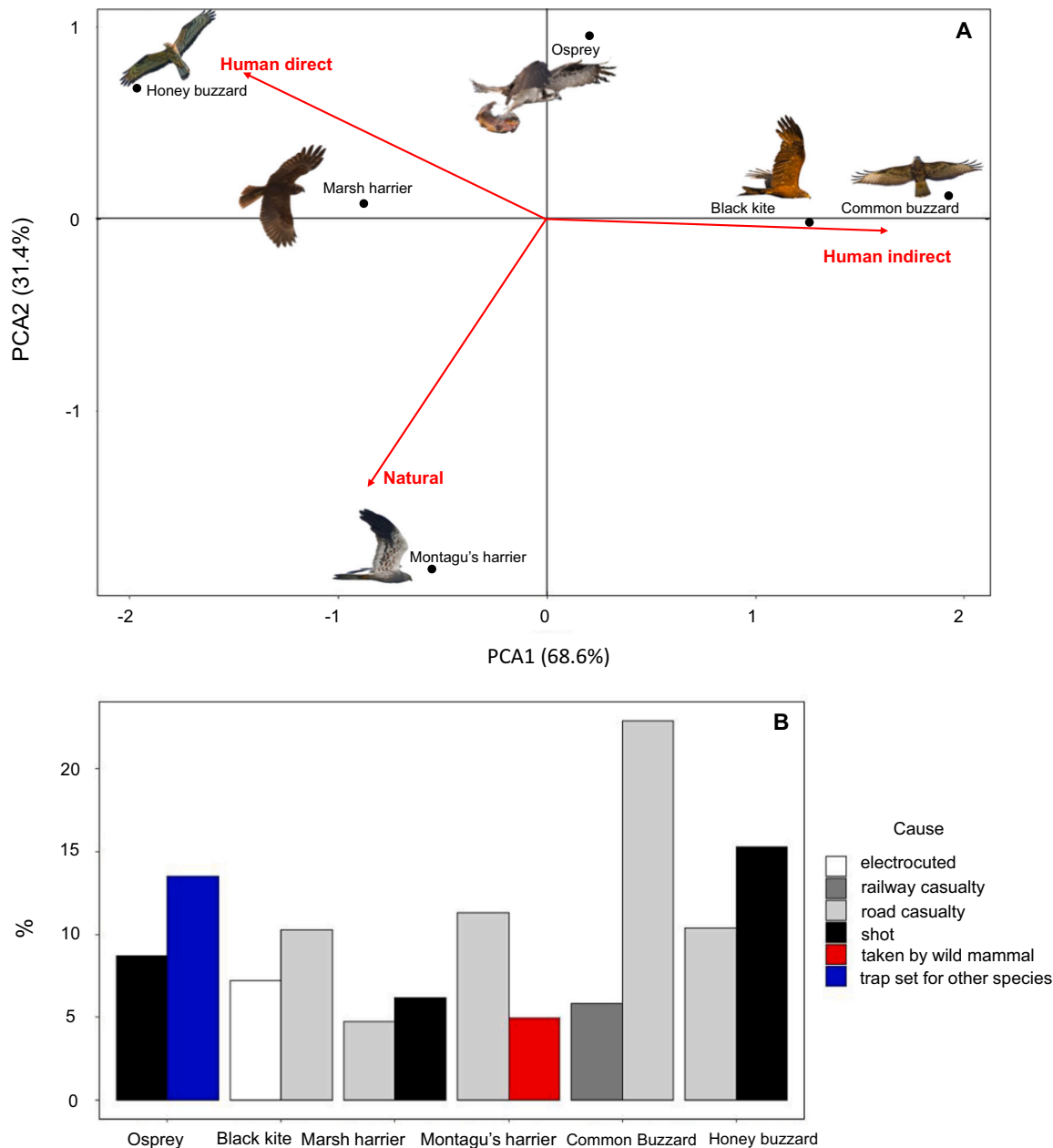
Fig. 7. Panel A: Principal Component Analysis (PCA) plot showing the multivariate causes of mortality for six raptor species after 1979. Vectors indicate mortality causes of different nature (Human direct, Human indirect, Natural), and each species is plotted in the multivariate space as a black dot. The first two principal axes (PC1 and PC2) explained the 100% of the variance. Panel B: main two mortality causes for six raptor species after 1979. The percentages of the main two mortality causes for each species after 1979 are shown.

this is the product of a combination of site-specific and species specific factors (e.g. Janss, 2000; Barrios and Rodriguez, 2004), such as flight and avoidance behaviours. For example, Montagu's Harrier in the Netherlands approached turbines less often than expected, showing a high rate of avoidance (93.5%; Schaub et al., 2020). From our analyses, only a small fraction of individuals seems actually exposed to turbines fatalities (0.04% of indirect mortality events, all species pooled together). However, we do not exclude significant impacts at certain sites (and in future years), where local conditions of wind installations do not respect mapping of migration routes and passage concentrations, thus augmenting the risk of fatalities (Janss, 2000).

4.6. Effects of age on mortality

In general, it is expected that young birds have lower survival than older ones, owing to their inexperience and low social status, with mortality decreasing as age increases (Newton et al., 2016). However, mortality increases again at very old age, reflecting individual senescence (Sergio et al., 2014). Our results confirm this trend, with some differences that can be linked to the nature of the data analysed. We found that mortality was higher during the first years of life, with most species having the higher mortality at age class 1 (chick at nest). The Osprey, however, was the only exception, showing an opposite trend. This could be due to the low number of recoveries of dead Osprey's chicks, a result of its peculiar lifestyle. Most nests are built on sites overlooking water (Poole, 2019), making recovery of dead chicks difficult or even impossible. However, osprey mortality was higher for juveniles (e.g. first calendar year) compared to adults, in line with other studies (e.g. Wahl and Barbraud, 2014). Generally, passage at bottlenecks and social grouping during migration (e.g. Honey Buzzards and

Table 4
Binomial Generalized Linear Model of probability of mortality in relation to age for six raptor species. Age was fitted in the model as a numeric variable. Only know age classes were used. Chicks (age 1) were included in the model. Significance of fixed effect terms was tested by likelihood ratio tests.

Species	Estimate $\pm$ SE	df	χ^2	P	Age classes[a]
Osprey	1.03 $\pm$ 0.13	1	86.0	< 0.001	1,3,5,7
Black Kite	−0.26 $\pm$ 0.10	1	7.1	0.007	1,3,5,7,9
Marsh Harrier	−0.87 $\pm$	1	32.9	< 0.001	1,3,5,7
Montagu's Harrier	0.11 $\pm$ 0.15	1	0.54	0.46	1,3,5,7
Common Buzzard	−0.77 $\pm$ 0.03	1	1016.0	< 0.001	1,3,5,7,9
Honey Buzzard	−0.71 $\pm$ 0.31	1	5.1	0.02	1,3,5

[a] Age classes available per species are provided according to EURING codification: 1 = Pullus: nestling or chick, unable to fly freely, still able to be caught by hand. 3 = First-year: full-grown bird hatched in the breeding season of this calendar year. 5 = 2nd year: a bird hatched last calendar year and now in its second calendar year. 7 = 3rd year: a bird hatched two calendar years before, and now in its third calendar year. 9 = 4th year: a bird hatched three calendar years before, and now in its fourth calendar year. EURING – The European Union for Bird Ringing (2010). The EURING Exchange Code 2000+. Thetford, U.K. ISBN 978-1-9085581-51-8

Black Kites) could increase the high mortality rate of inexperienced juveniles (Sergio et al., 2011). The development of migratory behaviour is promoted by individual improvements and selective mortality, mainly operating at early life-stages (Strandberg et al., 2009; Sergio et al., 2014). This trend was present even in a short-distance migrants like the Common Buzzard, as suggested by other studies (e.g. Kenward et al., 2000). Finally, the extremely low number of birds recovered dead at age > 7/9 suggests that, even if life expectancy for raptors species is around 15–25 years (Cramp and Simmons, 1980), most adult birds die prematurely. Therefore, a drastic reduction in human-related cause of mortality could lead to an increase in survival, with more birds reaching senescence.

4.7. Conclusions: implications for conservation

Our study, despite some limitation in the dataset and in the statistical framework used, highlights the importance in understanding mortality patterns using long-term datasets results that can help to prioritize and address effective conservation strategies (e.g. González et al., 2007). Despite the net improvements in the conservation of raptors have been achieved in the last century, a large set of lethal agents that requires some targeted conservation measures still exists. Large-bodied migratory raptors, because of their size and limited manoeuvrability, are exposed to a wide variety of human-related mortality agents, both direct and indirect. Deliberate killing is still a common threat to several species. Tougher sanctions and an increase in monitoring effort in specific places (e.g. sensitive areas) could help relieve the direct killing pressure (BirdLife International, 2014). Collisions with vehicles and trains represent a major source of mortality to most species, especially the ones hunting from perches along the roads or scavenging for roadkills (e.g. Common Buzzard). Pole barriers have been proofed as an effective tool in the mitigation of collisions with vehicles (Zuberogoitia et al., 2015). Their use, coupled with the removal of roadkills (e.g. Schwartz et al., 2018), could be an important strategy in the reduction of indirect mortality events in these birds. For some species, however, specific conservation measures are needed owing to their unique lifestyle. Many Osprey are killed by entanglement in fishing nets (e.g. trapped and drowned in nets at fish ponds). Protection measures at aquacultures facilities that help prevent accidental entanglement, such as overhead lines instead of nets laid over water surface, could be an effective measure for reducing Osprey mortality. Black Kites are strongly affected by electrocution: mitigation measures for electrocution such as a review of pylon design and the use of suspended insulators with elongated strings (following Guil et al., 2011

and Martín Martín et al., 2019) could improve the efficacy of mitigation measures and help minimize electrocution cases. Given that the number of human infrastructures is set to rise in the coming years, specific measures are urgently needed to mitigate the risks posed by these infrastructures (Hunt et al., 2017).

Therefore, more studies considering both general and species-specific mortality causes would be helpful. Actions on the ground should focus on areas where the threats are acute, and efforts should be scaled-up to produce an impact at broader scales. In this sense, several projects have been funded by the European Union through the Life programme (the EU's funding instrument for the environment and climate action) to protect raptors and to support activities aiming at significantly reduce the impact of deaths due to collision and similar sources of threats (BirdLife International, 2013). An additional concern is that individual unmarked animals that have been found dead might not be recorded in any official database, and important data could be lost. Many cases still remain unreported/undetected (BirdLife.org), so that the phenomenon is largely underestimated and makes the work of conservationists more complicated, thus calling for further conservational efforts.

Gaining a clearer understanding of how humans impact migratory raptor populations will help forecast population trends in many threatened species (Sergio et al., 2014) and help to focus adequate conservation measures, especially for those species with delayed maturity and naturally low reproductive rates. In a changing world, where the human population is increasing rapidly and where climate change represents a further challenge to survival, the need of anticipating future impacts is inextricably tied to the preservation of all living organisms.

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CRediT authorship contribution statement

Declaration of competing interest

Acknowledgments

References

Agostini, N., Panuccio, M., 2005. Analysis of the spatial migration patterns of adult honey buzzards (*Pernis apivorus*) during spring and autumn in the Central Mediterranean. Ring 27 (2), 215–220.

Agostini, N., Panuccio, M., 2010. Western Marsh harrier (*Circus aeruginosus*) migration through the Mediterranean Sea: a review. Journal of Raptor Research 44, 136–142.

Agostini, N., Panuccio, M., Pasquaretta, C., 2015. Morphology, flight performance, and water crossing tendencies of Afro-Palearctic raptors during migration. Current Zoology 61, 951–958.

Agostini, N., Panuccio, M., Pastorino, A., Sapir, N., Dell'Omo, G., 2017. Migration of the western marsh harrier to the African wintering quarters along the central Mediterranean flyway: a 5-year study. Avian Research 8 (24), 2–7.

Alerstam, T., Hake, M., Kjellén, N., 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. Anim. Behav. 71, 555–566.

Barrios, L., Rodriguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. J. Appl. Ecol. 41, 72–81.

Bildstein, K.L., 2006. Migrating Raptors of the World: Their Ecology and Conservation. Cornell University Press, Ithaca, New York, USA.

BirdLife International, 2010. Spotlight on Flyways. Presented as Part of the BirdLife State of the World's Birds Website. Available from: http://www.birdlife.org/datazone.

BirdLife International, 2013. Wind turbines can cause significant deaths in bird species. Downloaded from: http://www.birdlife.org on 08/08/2019.

BirdLife International, 2014. Important bird and biodiversity areas in danger - priority sites for immediate action. http://datazone.birdlife.org/userfiles/file/IBAs/pubs/IBAsInDanger2014.pdf.

Both, C., van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., van Strien, A.J., Foppen, R.P.B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc. R. Soc. B 1685, 1259–1266.

Breheny, P., Burchett, W., 2017. Visualization of regression models using visreg. R J. 9 (2), 56.

Brochet, A., Van Den Bossche, W., Jones, V., Arnardottir, H., Damoc, D., Demko, M., Driessens, G., Flensted, K., Gerber, M., Ghasabyan, M., Gradinarov, G., Hansen, J., Horvath, M., Karlonas, M., Krogulec, J., Kuzmenko, T., Lachman, L., Lehtiniemi, T., Lorge, P., Lotberg, U., Lusby, J., Otten, G., Paquet, J.-Y., Rukhaia, A., Schmidt, M., Shimmings, P., Stipnieks, A., Sultanov, E., Vermouzek, Z., Vintchevski, A., Volke, V., Willi, G., Butchart, S., 2017. Illegal Killing and Taking of Birds in Europe Outside the Mediterranean: Assessing the Scope and Scale of a Complex Issue. Bird Conservation International, pp. 1–31. https://doi.org/10.1017/S0959270917000533.

Buechley, E.R., Santangeli, A., Girardello, M., Neate-Clegg, M.H., Oleyar, D., McClure, C.J., Şekercioğlu, Ç.H., 2019. Global raptor research and conservation priorities: tropical raptors fall prey to knowledge gaps. Divers. Distrib. 25, 856–869.

Bujoczek, M., Ciach, M., Yosef, R., 2011. Road-kills affect avian population quality. Biol. Conserv. 144, 1036–1039.

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. U. S. A. 114, E6089–E6096.

Cramp, S., Simmons, K.E.L., 1980. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. vol. 2. Oxford University Press, Oxford, pp. 265–277.

Drewitt, A.L., Langston, R.H.W., 2008. Collision effects of wind-power generators and other obstacles on birds. Ann. N. Y. Acad. Sci. 1134, 233–266.

Du Feu, C.R., Clark, J.A., Schaub, M., Fiedler, W., Baillie, S.R., 2016. The EURING Data Bank - a critical tool for continental-scale studies of marked birds. Ringing and Migration 31, 1–18. https://doi.org/10.1080/03078698.2016.1195205.

Duriez, O., Peron, G., Grémillet, D., Sforzi, A., Monti, F., 2018. Migrating ospreys use thermal uplift over the open sea. Biol. Lett. 14, 20180687.

García, J.T., Arroyo, B.E., 1998. Migratory movements of western European Montagu's harrier Circus pygargus: a review. Bird Study 45, 188–194.

González, L.M., Margalida, A., Mañosa, S., Sánchez, R., Oria, R., Molina, J.I., Aranda, A., Caldera, J., Prada, L., 2007. Causes and spatio-temporal variations of non-natural mortality in the vulnerable Spanish Imperial Eagle (Aquila adalberti) during a recovery period. Oryx 41, 495–502.

Guil, F., Fernández-Olalla, M., Moreno-Opo, R., Mosqueda, I., Gómez, M.E., Aranda, A., Arredondo, A., Guzmán, J., Oria, J., González, L.M., Margalida, A., 2011. Minimising mortality in endangered raptors due to power lines: the importance of spatial aggregation to optimize the application of mitigation measures. PLoS One 6, e28212.

Hake, M., Kjellen, N., Alerstam, T., 2003. Age-dependent migration strategy in Honey Buzzards Pernis apivorus tracked by satellite. Oikos 103, 385–396.

Harness, R.E., Wilson, K.R., 2001. Electric-utility structures associated with raptor electrocutions in rural areas. Wildl. Soc. Bull. 29, 612–623.

Herremans, M., 2000. The 'chaotic' flight feather moult of the Steppe Buzzard Buteo buteo vulpinus. Bird Study 47, 332–343.

Hirschfeld, A., Heyd, A., 2005. Mortality of migratory birds caused by hunting in Europe: bag statistics and proposals for the conservation of birds and animal welfare. Ber. Vogelschutz 42, 47–74.

Hunt, G.W., Wiens, D.J., Law, P.R., Fuller, M.R., Hunt, T.L., Driscoll, D.E., Jackman, R.E., 2017. Quantifying the demographic cost of human-related mortality to a raptor population. PLoS ONE 12 (2), e0172232. https://doi.org/10.1371/journal.pone.0172232. PMID: 28234926.

Janss, G.F.E., 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biol. Conserv. 95, 353–359.

Kenward, R.E., Walls, S.S., Hodder, K.H., Pahkala, M., Freeman, S.N., Simpson, V.R., 2000. The prevalence of non-breeders in raptor populations: evidence from radio-tagging and survey data. Oikos 91, 271–279.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.M., Bairlein, F., Alerstam, T., 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J. Anim. Ecol. 83, 176–184.

Korner-Nievergelt, F., Robinson, R.A., 2014. Introducing the R-package 'birding'. Ringing and Migration 29, 51–61.

Lehman, R.N., Kennedy, P.L., Savidge, J.A., 2007. The state of the art in raptor electrocution research: a global review. Biol. Conserv. 126, 159–174.

Limiñana, R., Soutullo, A., Urios, V., Reig-Ferrer, A., 2012. Migration and wintering areas of adult Montagu's Harriers (Circus pygargus) breeding in Spain. J. Ornithol. 153, 85–93.

Madden, K.K., Rozhon, G.C., Dwyer, J.F., 2019. Conservation letter: raptor persecution. Journal of Raptor Research 53 (2), 230–233.

Martín Martín, J., Barrios, V., Clavero Sousa, H., Garrido López, J.R., 2019. Les oiseaux et les réseaux électriques en Afrique du Nord. Guide pratique pour l'identification et la prévention des lignes électriques dangereuses. UICN Gland, Suisse et Malaga, Espagne.

McClure, C.J.W., Westrip, J.R.S., Johnson, J.A., Schulwitz, S.E., Virani, M.Z., Davies, R., Symes, A., Wheatley, H., Thorstrom, R., Amar, A., Buij, R., Jones, V.R., Williams, N.P., Buechley, E.R., Butchart, S.H.M., 2018. State of the world's raptors: distributions, threats, and conservation recommendations. Biol. Conserv. 227, 390–402.

Mellone, U., Klaassen, R.H.G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., Strandberg, R., Urios, V., Vardakis, M., Alerstam, T., 2012. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. PLoS One 7, e39833.

Millon, A., Danovaro, C., Printemps, T., Leroux, A.B., Schlaich, A.E., Villers, A., Bourriou, J.L., Bretagnolle, V., 2019. Disentangling the effects of environmental conditions on wintering and breeding grounds on age-specific survival rates in a trans-Saharan migratory raptor. J. Avian Biol. 50. https://doi.org/10.1111/jav.02233.

Monti, F., 2020. Oil contamination of Osprey (Pandion haliaetus) in the Mediterranean Sea: an underestimated threat for the species? Journal of Raptor Research 54 (3), 000.

Monti, F., Grémillet, D., Sforzi, A., Sammuri, G., Dominici, J.M., Triay Bagur, R., Muñoz Navarro, A., Fusani, L., Duriez, O., 2018a. Migration and wintering strategies in vulnerable Mediterranean Osprey populations. Ibis. https://doi.org/10.1111/ibi.12567.

Monti, F., Grémillet, D., Sforzi, A., Dominici, J.M., Triay Bagur, R., Muñoz Navarro, A., Fusani, L., Klaassen, R.H.G., Alerstam, T., Duriez, O., 2018b. Migration distance affects stopover use but not travel speed: contrasting patterns between long- and short-distance migrating ospreys. J. Avian Biol. 49, e01839. https://doi.org/10.1111/jav.01839.

Newton, I., 2003. Population Limitation in Birds. Academic Press, San Diego.

Newton, I., 2010. Bird Migration. Collins, London.

Newton, I., McGrady, M.J., Oli, M.K., 2016. A review of survival estimates for raptors and owls. Ibis 158, 227–228.

Nourani, E., Vansteelant, W.M.G., Byholm, P., Safi, K., 2020. Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. Biol. Lett. https://doi.org/10.1098/rsbl.2019.0797.

Oppel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Velevski, M., Stoychev, S., Nikolov, S.C., 2015. High juvenile mortality during migration in a declining population of a long-distance migratory raptor. Ibis 157, 545–557.

Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences U.S.A. 97, 12144–12148.

Panuccio, M., Agostini, N., Mellone, U., 2005. Autumn migration strategies of honey buzzards, black kites, marsh and montagu's harriers over land and over water in the Central Mediterranean. Avocetta 29, 27–32.

Panuccio, M., Chiantante, G., Tarini, D., 2013. Two different migration strategies in response to an ecological barrier: Western marsh harriers and juvenile European honey buzzards crossing the central-eastern Mediterranean in autumn. Journal of Biological Research-Thessaloniki 19, 10–18.

Panuccio, M., Agostini, N., Mellone, U., Bogliani, G., 2014. Circannual variation in movement patterns of the Black Kite (Milvus migrans migrans): a review. Ethology, Ecology & Evolution 26 (1), 1–18.

Panuccio, M., Duchi, A., Lucia, G., Agostini, N., 2017. Species-specific behaviour of raptors migrating across the Turkish straits in relation to weather and geography. Ardeola 64 (2), 305–324.

Pedersen, T.L., Robinson, D., 2019. Gganimate: a grammar of animated graphics. See. https://CRAN.R-project.org/package=gganimate.

Poole, A.F., 2019. Ospreys: The Revival of a Global Raptor. Johns Hopkins University Press, Baltimore.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Retrieved from. http://www.R-project.org/.

Santos, C.D., Silva, J.P., Muñoz, A.R., Onrubia, A., Wikelski, M., 2020. The gateway to Africa: what determines sea crossing performance of a migratory soaring bird at the strait of Gibraltar? J. Anim. Ecol. 89, 1317–1328.

Schaub, T., Klaassen, R.H.G., Bouten, W., Schlaich, A.E., Koks, B.J., 2020. Collision risk of Montagu's Harriers Circus pygargus with wind turbines derived from high-resolution GPS tracking. Ibis 162, 520–534. https://doi.org/10.1111/ibi.12788.

Schwartz, A.L., Williams, H.F., Chadwick, E., Thomas, R.J., Perkins, S.E., 2018. Roadkill scavenging behaviour in an urban environment. Journal of Urban Ecology 4, 1–18.

Selås, V., Tveiten, R., Aanonsen, O.M., 2007. Diet of Common Buzzards (Buteo buteo) in southern Norway determined from prey remains and video recordings. Ornis Fennica 84, 97–104.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F., 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. Ann. Rev. Ecol. Evol. Syst. 39, 1–19.

Sergio, F., Tavecchia, G., Blas, J., López, L., Tanferna, A., Hiraldo, F., 2011. Age-structured vital rates in a long-lived raptor: implications for population growth. Basic and Applied Ecology 12, 107–115.

Sergio, F., Tanferna, A., De Stephanis, R., Jimenez, L.L., Blas, J., Tavecchia, G., Preatoni, D., Hiraldo, F., 2014. Individual improvements and selective mortality shape lifelong

migratory performance. Nature 515, 410–413.

Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G., Hiraldo, F., 2019. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. Scientific Report 9, 17352. https://doi.org/10.1038/s41598-019-54026-z.

Strandberg, R., Alerstam, T., Hake, M., Kjellén, N., 2008a. Short-distance migration of the common buzzard *Buteo buteo* recorded by satellite tracking. Ibis 151, 200–206.

Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P., Thorup, K., Alerstam, T., 2008b. Complex timing of Marsh Harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. Ardea 96, 159–171.

Strandberg, R., Klaassen, R.H.G., Hake, M., Alerstam, T., 2009. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol. Lett. https://doi.org/10.1098/rsbl.2009.0785.

Stroud, D.A., 2003. The status and legislative protection of birds of prey and their habitats in Europe. In: Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M., Galbraith, C.A. (Eds.), Birds of Prey in a Changing Environment. TSO, Edinburgh, pp. 51–84.

Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K.M., Komdeur, J., Bairlein, F., Koks, B.J., 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. Proc. Biol. Sci. 281, 20132897.

Tucker, G.M., Heath, M.F., 1994. Birds in Europe: Their Conservation Status. Birdlife International, Cambridge.

Väli, Ü., Vainu, O., 2015. Short-distance migration of Estonian Common Buzzards *Buteo buteo*. Ringing Migration 30 (2), 81–83. https://doi.org/10.1080/03078698.2015.1128246.

Wahl, R., Barbraud, C., 2014. The demography of a newly established Osprey *Pandion haliaetus* population in France. Ibis 156, 84–96.

Wuczyński, A., 2005. Habitat use and hunting behavior of Common Buzzards *Buteo buteo* wintering in south-western Poland. Acta Ornithol. 40, 147–154.

Zuberogoitia, I., del Real, J., Torres, J.J., Rodríguez, L., Alonso, M., de Alba, V., Azahara, C., Zabala, J., 2015. Testing pole barriers as feasible mitigation measure to avoid bird vehicle collisions (BVC). Ecol. Eng. 83, 144–151.

Zuur, A.F., 2012. A beginner's Guide to Generalized Additive Models With *R*. Highland Statistics Limited, Newburgh, NY.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York, NY.

Zwarts, L., Bijlsma, R.G., van der Kamp, J., Wymenga, E., Zwarts, J., Visser, D., 2009. Living on the Edge: Wetlands and Birds in a Changing Sahel, Édition: 1. KNNV Publishing, Zeist, The Netherlands.