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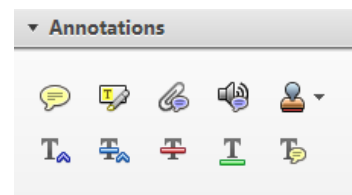
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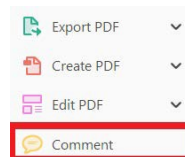
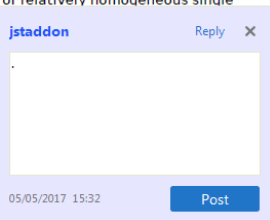### 1. Replace (Ins) Tool – for replacing text.

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. experimental data if available. For ORFs to be had to meet all of the following criteria:

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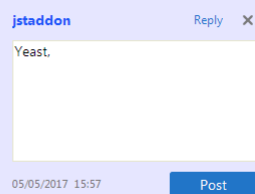
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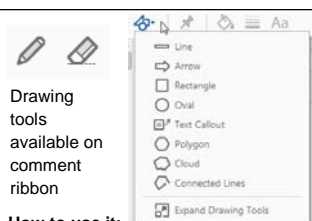
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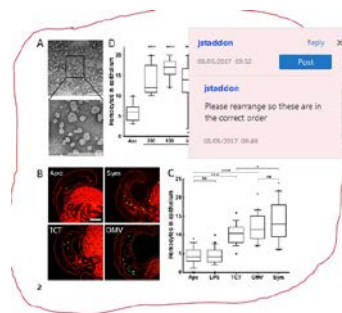
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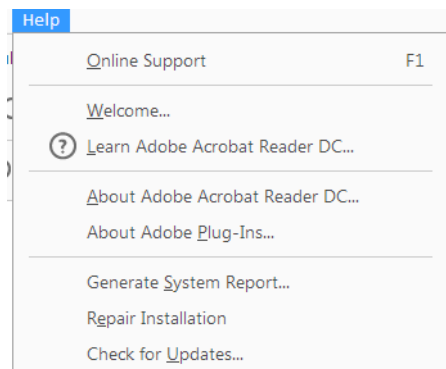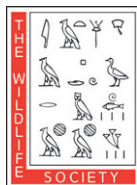
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THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Age, landscape, and arrival date explain ranging behavior of wintering red kites in southwest europe

Connor T. Panter[1] | Ivan Literák[2] | Rainer Raab[3] | Bryony A. Tolhurst[1] | Rachel L. White[1]

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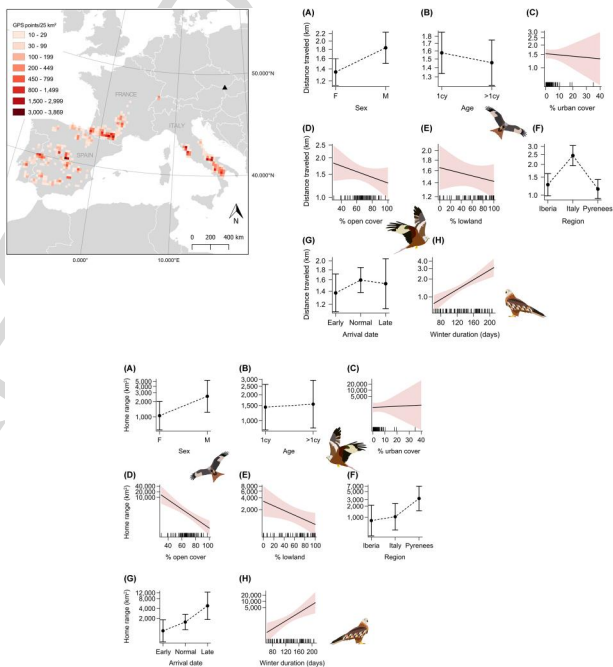
We fill knowledge gaps on ranging and survival for 36 red kites during winter. Older kites arriving late to over-wintering grounds ranged farther, and open, lowland landscapes were key predictors of winter space use.

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Abstract

Understanding intrinsic and extrinsic influences of movement behavior in migratory species, with the potential to recommend management actions for species of conservation concern, requires data from across the species' range. For some raptor species, such as the red kite (*Milvus milvus*; kite), existing data focus on breeding populations or movements *en route* to wintering areas without considering movements within the wintering areas. Here, we contribute to filling this knowledge gap by investigating landscape-level associations of kites in their southwestern European winter ranges between 2015 and 2020. We also explored aspects of the migration process in terms of geographical patterns in the location of over-wintering grounds, including time spent and distances traveled within them. We predicted that space use in over-wintering areas would be linked to the proportional amount of open, lowland, or urban land cover they contain at the landscape level. Specifically, we tested whether winter range sizes (95% kernel density estimators [KDE] home range and 50% KDE core area) would be smaller in areas with greater proportional open and urban land cover within kite ranges. Controlling for the effects of age and sex, we compared results in 3 over-wintering regions: the Iberian Peninsula, Italy, and the Pyrenean region of southern France. We tracked 36 kites by global positioning system-global system for mobile communications (GPS-GSM) telemetry over 70 individual winters between 2015 and 2020. Kites wintering in the Pyrenees had

larger home ranges and core areas but moved less than those wintering in Italy and the Iberian Peninsula. As predicted, ranges were smaller in areas with greater proportional open and lowland land cover; however, there was no effect of urban areas. Older kites that arrived late to the wintering areas had larger home ranges than those that arrived early or on time. During the study 20 kites died or the transmitter malfunctioned. Six of 13 confirmed deaths were due to anthropogenic activity; 5 kites were poisoned. Our results confirm that land use and elevation are key influences of kite space use in southwestern European over-wintering populations, but additional demographic intrinsic factors also affect ranging parameters. These data indicate that over-winter conservation action for kites, for example supplementary feeding with livestock carrion, should focus on open lowland landscapes throughout the species' winter range.

KEYWORDS

home range, migration, *Milvus milvus*, mortality, movement behavior, raptors, spatial ecology, telemetry

The identification of intrinsic and extrinsic factors predicting movement behavior is an important component of understanding animal ecology (McNab, 1963). In recent years the field of movement ecology has grown because of technological advances (Alarcón & Lambertucci, 2018; Cagnacci et al., 2010; Cooke et al., 2004; Tomkiewicz et al., 2010), allowing for improved characterization of movement behavior and its underlying influences. This has enhanced our understanding of how species, including those that range widely, traverse habitats and geographical areas (Hebblewhite & Haydon, 2010). Inference from detailed studies of animal movement can benefit biodiversity conservation and management (Allen & Singh, 2016; McGowan et al., 2016), for example, by making recommendations for protected area design (Choi et al., 2019) or guiding mitigation measures for development (e.g., windfarms; Vasilakis et al., 2016).

Raptors frequently feature within movement ecology research primarily because of their wide-ranging behavior and large body sizes (Alarcón & Lambertucci, 2018), use as ecological indicators (Buechley et al., 2019), and disproportionate extinction risk compared to other avian and non-avian groups as a result of their ecology and life histories (McClure et al., 2018). Satellite telemetry techniques allow for the study of raptor movement behavior throughout various lifecycle stages, including the characterization of intrinsic and extrinsic effects. These include age-related effects (Krüger et al., 2014) and seasonal variation in space use (Pérez-García et al., 2013) such as during the migratory (Kumar et al., 2020) and over-wintering periods (Limiñana et al., 2014; Morant et al., 2020). Migratory raptors are particularly challenging to study because of varying environmental conditions across broad geographical areas affecting their spatial behavior. Results from such studies can be important for management of raptor species of conservation concern, allowing quantification of threats, species movements through space and time (May et al., 2011), and the identification of suitable habitats to be prioritized for conservation (Limiñana et al., 2014).

The red kite (*Milvus milvus*; kite) is a large facultative scavenger native to Europe (Cereghetti et al., 2019; Cramp & Simmons, 1980; Mougeot et al., 2011; Pfeiffer & Meyburg, 2015; Seoane et al., 2003) but also occurs in scattered

populations in North Africa including Morocco (Radi et al., 2020) and Tunisia (BirdLife International, 2020; Literák et al., 2019b). Recent estimates indicate a global population of between 60,000 and 70,000 mature individuals and approximately 35,000 breeding pairs, with a stronghold in Germany, Switzerland, France, and Spain (BirdLife International, 2020; Génsbøl & Thiede, 2008). Northern breeding populations tend to be migratory, wintering in 3 key regions of southwestern Europe: Italy, the Iberian Peninsula, and the Pyrenean region of southern France (Evans & Pienkowski, 1991; Ferreira et al., 2015; Raab et al., 2017; Viñuela, 1997). They occasionally also over-winter as far east as Greece (Literák, 2017, 2019a; Maciorowski et al., 2019; Panter et al., 2020). Southern populations are mostly resident within the Mediterranean region (Crespo-Luengo et al., 2020; Knott et al., 2009) because of milder climates and sufficient local resources available for over-winter survival (García et al., 1998).

Until recently kites experienced population declines throughout their range, predominantly influenced by direct and indirect poisoning (Mateo-Tomás et al., 2020; Molenaar et al., 2017; Smart et al., 2010), and changes in agricultural and refuse treatment policies (BirdLife International, 2020; Blanco, 2014; Villafuerte et al., 1998). Organochlorine contamination (Gómara et al., 2008) and wind turbine collisions have also been identified as threats to kite populations (Bellebaum et al., 2013; Dürr, 2009; Schaub, 2012). Additionally, collisions and subsequent electrocutions with electrical power lines are well-documented threats to large raptors including kites (Bevanger, 1998; Crespo-Luengo et al., 2020; Janns, 2000; Kolnegari et al., 2020). Encouragingly, the species was recently down-listed from near threatened to least concern on the International Union for the Conservation of Natures' Red List of Threatened Species and is now reported to be increasing in the majority of countries within its geographic range following successful reintroductions and conservation action (BirdLife International, 2020; Carter, 2007; Orros & Fellowes, 2014; Pain et al., 2007). Nevertheless, a sustained stable or increasing future population trend is necessary for kite persistence and continued monitoring is required to infer population status where necessary. Winter is arguably one of the most important periods of the year as over-winter stochastic events (Newton, 2004), such as periods of low food availability associated with low rainfall (Amat, 1986), negatively affect migratory raptor populations including kites (Blanco et al., 1990).

While kites are relatively well studied, past limitations of technology, such as the use of very high frequency radio-telemetry, have led to previous underestimations of home range sizes (Kenward, 2001; López-López et al., 2014). Further, current knowledge on kite spatial behavior is focused towards periods of breeding (Hötker et al., 2017; Maciorowski et al., 2021; Mougeot et al., 2011; Pfeiffer & Meyburg, 2015) and migration (Maciorowski et al., 2019; Pfeiffer & Meyburg, 2009; Schwitter, 2020) or restricted to local scales across the species' winter range (Blanco et al., 1990; Heredia et al., 1991 [Spain]; Nachtigall et al., 2003; Pfeiffer & Meyburg, 2009 [Germany]; Ferreira et al., 2015 [Portugal]). Because animal movements vary intra-annually in response to changes in prevailing environmental and lifecycle-related conditions (Powell, 2000), an important knowledge gap persists around migratory kite space use across large areas of the species' winter range.

Key features of kite ecology such as hunting and scavenging behavior and dietary preferences would be expected to similarly influence habitat selection and movement behavior across the lifecycle and range. Throughout their breeding ranges, kites are usually associated with medium-low elevations (Seoane et al., 2003; Sergio et al., 2005), being most common between 400–600 m above sea-level (Sergio et al., 2019). Kites, however, are not fully restricted to lowland areas (García et al., 1998). Researchers also report reduced traveling distances, home ranges, and core areas in open landscapes with high lagomorph, rodent, and livestock carrion availability (Blanco et al., 1990; García et al., 1998). In the Pyrenean region of southern France and across northern Iberia, regional administrations maintain a large network of long-term supplementary feeding stations linked to vulture conservation programs, where avian scavengers congregate (Margalida et al., 2013; Oro et al., 2008). During winter, these feeding stations are provisioned with sheep limbs and other bone matter (Margalida et al., 2011), yielding potentially greater carrion availability to kites than in Italy. In addition, throughout their range, kites use urban areas and landscapes directly adjacent to them (Knott et al., 2009), which provide food resources particularly at waste disposal facilities (e.g., garbage dumps; Literák et al., 2017, 2019a; Panter et al., 2020; Zduniak et al., 2021), and intentionally or unintentionally provided by householders in residential yards (Cereghetti et al., 2019; Orros & Fellowes, 2014, 2015). These resources may be particularly abundant or important for kite survival in winter when

food in adjacent natural landscapes is disproportionately scarce (Cereghetti et al., 2019). Additionally, across taxa, home range size tends to be smaller in urban than more natural environments (O'Donnell & del Barco Trillo, 2020). This reflects evolutionary theory on resource distribution and territoriality (e.g., the resource dispersion hypothesis; Macdonald & Johnson, 2015), a corollary of which is that organisms will be contractors, occupying the smallest area containing all necessary resources over a particular period (O'Donnell & del Barco Trillo, 2020). The contractor pattern of kite space use appears to be mediated by intrinsic factors such as age, with older kites reported to occupy smaller home ranges and core areas than first calendar-year birds because of higher rates of winter site fidelity to areas with abundant food resources identified in previous years (McKinley & Mattox, 2010; Shiu et al., 2006). Winter arrival date may also affect space use if kites arriving earlier secure high-quality winter territories, spending less time searching for areas with high resource availability. Age-related differences, for example relating to differential previous experience, may affect other spatio-temporal aspects of the migration process (e.g., arrival date at wintering areas, distances traveled to reach them).

Understanding the limiting factors affecting kite space use throughout the entire year is important for improving our knowledge on the species' ecology and for continued conservation across its geographic range. In this study, we fill knowledge gaps on kite winter space use by exploring the movement behavior of a sample of kites tracked with global positioning system-global system for mobile communications (GPS-GSM) devices originating from a central European population over-wintering in 3 key regions of southwestern Europe previously described. Specifically, we tested the following hypotheses: H1) the Pyrenees and Iberian Peninsula would be associated with smaller ranges and shorter distances traveled relative to Italy because of greater carrion availability; H2) kite winter ranges would be smaller, and distances traveled shorter, following earlier arrival to areas where open, lowland, and urban land cover types predominate, in accordance with contractor-space-use theory; H3) younger kites would arrive later to wintering areas and occupy larger ranges because they lack of knowledge of or competitive ability at sites containing concentrated, rich resources.

STUDY AREA

Italy

The Italian peninsula covers a land mass of 294,140 km^2 lying between 35° and 48°N, and 6° and 18°E and includes the islands of Sicily and Sardinia. Approximately 40% of Italian territory is mountainous, with the Alps at the northern boundary and the Apennine Mountains extending southwards for 1,350 km. The Po and Venetian plains are the largest lowland areas, exceeding 46,000 km^2 (Fratianni & Acquaotta, 2017). Winter air temperature differs considerably between the north and south, from −2°C in Milan (45°28′N, 9°11′E), 8°C in Rome (41°53′N, 12°30′E), to 20°C in Palermo, Sicily (38°7′N, 13°22′E). Mean annual precipitation ranges from <300 mm through >3,000 mm (Fratianni & Acquaotta, 2017). Rainfall is generally higher along the western Ligurian-Tyrrhenian coast than the eastern Adriatic-Ionian (Fratianni & Acquaotta, 2017). Broadly, more than half of Italy's landscape is agricultural land, followed by forested (41%) and urban areas (5%; Sambucini et al., 2010). In the northern temperate climates, the natural vegetation consists of broad-leaved forests dominated by oak (*Quercus* spp.), beech (*Fagus* spp.), and hornbeams (*Carpinus* spp.). In the southern Mediterranean climate, the area is dominated by mixed woodland and shrubland characterized by densely growing evergreen species of the Mediterranean maquis, which also includes small trees comprising olives (*Olea* spp.) and figs (*Ficus* spp.; Costantini & Dazzi, 2013).

France

France covers a land mass of 548,826 km^2 between 41° and 51°N, and 4° and 8°E, including mainland France and the island of Corsica. Topography mostly consists of flat plains and rolling hills in the north and west, and mountains

in the south (including the Massif Central and the Pyrenees) and east (Alps). Generally, the climate is temperate, with oceanic and semi-continental climates present in the west, north, and northeast. Mediterranean climates occur in the lower Rhône Valley in the south and on the island of Corsica, and mountainous climates in the Alps and Pyrenees. Annual precipitation ranges from 635 mm through 1,016 mm, with the Atlantic coast receiving the highest rainfall and mountainous regions regularly experiencing snowfall. Winter air temperatures range from 2°C in Lorraine and Alsace (48°87′N, 6°20′E), 4.5°C in Paris (48°86′N, 2°35′E), to 9°C in Corsica (42°4′N, 9°1′E) and the lower Rhône Valley (43°18′N, 4°50′E). Agricultural landscapes total 52% of land, of which 36% is used for arable crops and 16% for livestock, 31% of land is covered by forests, and approximately 16% is urban areas (World Bank, 2021). Towards the Pyrenees, more natural landscapes are present following mass land abandonment of previously productive agricultural areas (Etienne et al., 1998). Natural vegetation in the south is characterized by chestnut (*Castanea* spp.), beech, oak, and pine (*Pinus* spp.), along with Mediterranean maquis on Corsica (Etienne et al., 1998).

Iberian Peninsula

The Iberian Peninsula comprises a land mass similar to France, with an area of 583,254 km^2, lying within 36° and 43°N, and 9°W and 3°E (Lorenzo-Lacruz et al., 2011). It includes mainland Spain, Portugal, and the Pyrenean state of Andorra. The region is mainly mountainous and includes the Pyrenees (42°37′N, 0°39′E) and Cantabrian Mountains (43°11′N, 4°51′W) in the north, the Sistema Central (40°14′N, 5°17′W), which continues into Portugal and divides the peninsula latitudinally, through to the Sierra Morena (38°22′N, 3°50′W) and the Baetic System (37°0′N, 5°0′W) in the south. The Meseta Central, an expansive plateau ranging from 610 m through 760 m is located centrally (Fischer, 1920). Because of geography, topography, and the effects of large atmospheric circulation patterns, a northwest to southeast gradient of annual precipitation occurs ranging from 2,000 mm to 300 mm, respectively. Winters are mild with mean air temperatures ranging from 9.3°C in the north (Bilbao 43°15′N, 2°55′W), 6.3°C in the center (Madrid; 40°25′N, 3°43′W), to 12.6°C in the south (Almería; 36°50′N, 2°28′W). Agriculture comprises 47% of land, followed by shrubland (27%), forests (22%), and urban areas (14%; Ferández-Nogueira & Corbelle-Rico, 2018; World Bank, 2021). Natural vegetation of the northern regions consists of heathland and broadleaved woodland including oak, pine, beech, and juniper (*Juniperus* spp). In the mountains of the northern Meseta and the Baetic and Iberian cordilleras, Portuguese oak (*Q. faginea*) forests occur (Loidi, 2017). In the south and across Portugal, cork oak (*Q. suber*), holm oak (*Q. ilex*), pine, and carob (*Ceratonia* spp.) form the characteristic natural vegetation (Loidi, 2017). Throughout all study regions, December marks the start of the annual winter season with temperatures generally at their lowest through to the end of February.

METHODS

Telemetry data and temporal variables

Between 2015 and 2019, we tagged first calendar-year (1 cy) kites in the nest prior to fledging, during the pullus growth stage, between 31 May and 23 July each year. Kites originated from the same central European population distributed throughout a tri-border zone of approximately 60 km^2 located between Austria, Slovakia, and the Czech Republic (48°40′N, 16°56′E; Figure 1). We tagged all birds with 20-g Saker H loggers (Ecotone, Gdynia, Poland) weighing on average 2% of the kites' body mass. We fitted loggers onto the back of the birds and secured them with a 6-mm Teflon ribbon harness encircling the body in 2 loops around the base of the wings and joining in front of the breastbone following similar methodology to Literák et al. (2019*a*, 2019*b*, 2019*c*). The loggers operated in GPS-GSM systems and received signals every 3 hours depending on signal strength. We determined sex via DNA
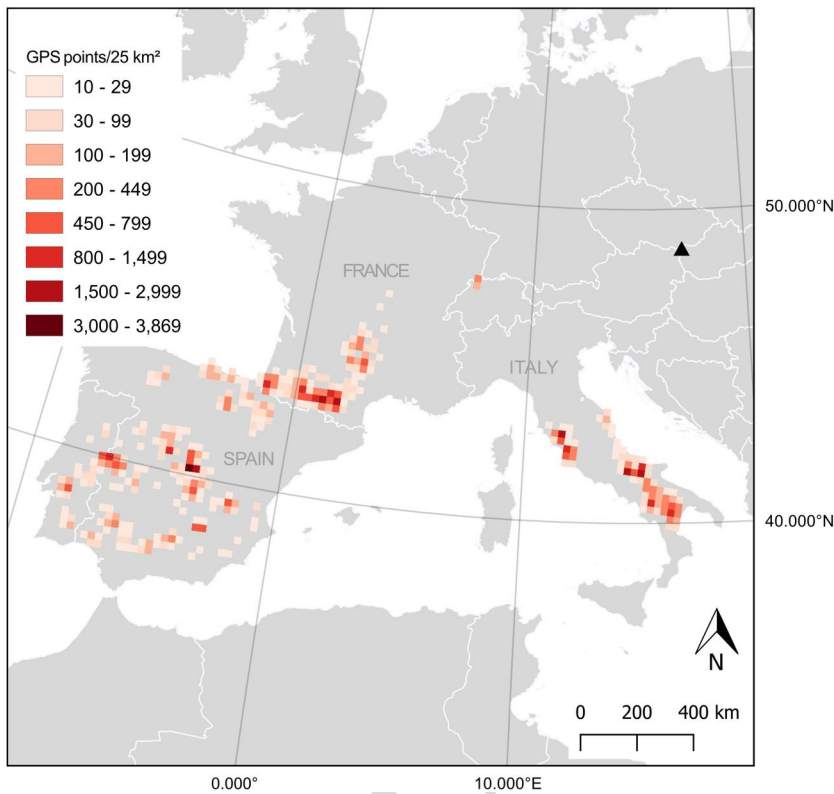
FIGURE 1 Kernel density estimators showing highly used areas by 36 red kites tagged with global positioning system-global system for mobile communication (GPS-GSM) transmitters wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. We calculated GPS point densities using 25-km radii and 25-km^2 grid cells in QGIS version 3.2.3 with the GRASS 7.4.1 extension. We pooled data points together for all kites over all winters and do not show low frequency points (those <10 within a 25-km radius). The black triangle shows the approximate nest and tagging locations of kites used in this study

analysis using a growing breast feather sample taken from each bird (Suh et al., 2011). We tracked kites in their wintering grounds in Italy, the Iberian Peninsula, and the Pyrenees (Figure S1, available in Supporting Information).

For the purposes of this study, we refer to the seasonal term winter as any period from the beginning of December until the end of February. Our definition of kite winter refers to the period where individual behavior of kites resulted in the initiation of their over-wintering period. We calculated kite winter by sub-setting GPS relocations between 1 September and 30 April because of the variation in winter durations amongst individual birds. We only included data for kites that survived entire winters. We included day and night fixes in our analyses, representing the full extent of kite space use during winter, including foraging, hunting, perching, and roosting behaviors. We plotted all GPS relocation coordinates in a geographic information system (GIS) using the program QGIS version 3.2.3 (http://www.qgis.org, accessed 15 Jun 2020) with the GRASS version 7.4.1 extension enabled and visually examined coordinates to check for outliers. We used the software package RANGES version 9.0 (https://www.anatrack.com; accessed 15 Jun 2020; Kenward et al., 2014) to process the telemetry data, using the inbuilt incremental area analysis (IAA) feature to determine kite winter start and end date. We calculated kite winter start date as the first point on the incremental plot where the kites' percentage area usage plateaued for the longest period on the plots indicating arrival at the winter grounds. On the plots, short plateaus indicated stopover sites during the autumn and spring migrations, which we excluded from winter start and end dates. To calculate kite

winter end date, we identified the last point on the longest plateau (Figure S2, available in Supporting Information). We calculated kite winter duration as the number of days between and including the start and end dates identified by IAA. Arrival dates at the wintering areas ranged from 22 September to 28 December for all kites across all years. We identified the median arrival date (9 Nov) and calculated the first (Q1) and third (Q3) interquartile date ranges (16 Oct and 3 Dec, respectively). We categorized dates between the first winter arrival date and up to and including Q1 as early, those arriving after Q1 and up to and including Q3 as normal, and those arriving after Q3 but before the last winter arrival date as late. To control for sampling biases, we included the number of GPS relocations throughout each kite winter period as one of our continuous explanatory variables.

Distance traveled, home range, and core areas

We used point kernel density estimators (point KDEs; Seaman & Powell, 1996) to estimate kite space-use metrics. Point KDEs are robust statistical tools that are intuitive, easy to compute, and widely used, allowing comparability between studies (Kie et al., 2010). Kernel density estimators generate a utilization distribution (UD), which is a probability density distribution in 2-dimensional space, for the relocations of each animal (van Winkle, 1975). For comparability with other studies, we used the standard metrics of 95% and 50% of each kite's relocations to represent entire home ranges minus outliers and most used core areas, respectively (Miller et al., 2017; Watson et al., 2014). We explored the relative performance of various smoothing parameter (bandwidth) estimators, including the least squares cross-validation (LSCV) method (Horne & Garton, 2010), to best represent kite relocations, via scrutinizing the resultant isopleths. We found the reference bandwidth to be the most resilient to either over or under smoothing, and therefore selected it for all analyses. We also calculated total distance traveled (km) within the wintering areas following arrival using the inter-location measures feature to generate the distances traveled between consecutive winter relocations. We totaled these distances to derive overall distance traveled per kite per winter. We computed all analyses in RANGES version 9.

Distances traveled by kites within wintering areas (distance traveled) were unlikely to be fully independent of distances traveled by kites from their tagging location to the wintering areas (migration distance) because the latter is likely to affect body condition, with consequences for movements throughout winter (Duijns et al., 2017). Explicit inclusion of migration distance in statistical models was beyond the scope of the current study because of the complexity of associated factors, including departure timing, presence of stopover sites, and varying environmental conditions along flight routes (Alerstam, 2011). Instead, we opted to control for any bias arising from variable migration distance by standardizing the distance traveled variable. We did this by merging all home range and core area isopleths by winter region and computing the geographic center of each merged regional polygon using GIS. We then calculated the shortest, straight-line distance between a reference point (48.67957, 16.94634; latitude, longitude) located within the tagging area, and each winter region's (Italy, Iberian, Pyrenean) geographic center. Following this, we converted the distances between points into kilometers and standardized our distance traveled values by dividing these by the distance between the reference point and geographic center for each winter region.

Land cover and topographic environmental data

We downloaded land cover data on 9 March 2020 from the COPERNICUS Land Monitoring Service's CORINE Land Cover (https://land.copernicus.eu/pan-european/corine-land-cover, accessed 1 Apr 2020) database at a 100-m resolution in raster format. We obtained 43 land cover types from the CORINE Land Cover dataset. Following a similar methodology to Miller et al. (2017), we reclassified the 43 land cover types into broad categories: open, urban, and closed land cover types (Table S1, available in Supporting Information). We performed this using the r.reclass function within QGIS version 3.2.3 with the GRASS version 7.4.1 extension GIS program. We produced a

new binary raster layer for each land cover type (open, urban, closed) with 1 = grid cells containing target land cover type and 0 = all other non-target land cover types. We extracted land cover scores for each home range and core area isopleth for each bird per winter using the zonal statistics feature. We calculated percentage land cover type within each 95% and 50% isopleth by dividing the land cover cell count by the number of cells within each.

We downloaded raw elevation data, in the form of a digital elevation model at 25-m resolution, from the COPERNICUS Land Monitoring Service's EU-DEM version 1.1 (https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1; accessed 1 Apr 2020). Following the same method of extracting land cover scores, we obtained elevation scores using zonal statistics. We classified elevations ≤500 m as lowland (Seoane et al., 2003; Sergio et al., 2005, 2019) and calculated a new continuous variable (% lowland) for each 95% and 50% isopleth (Figure S3, available in Supporting Information).

Statistical analysis

We generated a series of generalized linear mixed models (GLMMs) in R (R Core Team, 2018) using the lme4 package (Bates et al., 2015). We fitted distance traveled (km), home ranges (95%), and core areas (50%) as response variables and the following 10 measures as explanatory variables: 1) sex, 2) age (1 cy vs. >1 cy), 3) percent urban land cover, 4) percent open land cover, 5) percent closed land cover, 6) percent lowland, 7) region (Italy, Pyrenees, or Iberia), 8) arrival date (early, normal, or late), 9) winter duration, and 10) number of GPS fixes from first to last winter date.

Prior to the statistical analysis, we explored response variable distributions using the gnlm package (Swihart & Lindsey, 2019), with distance traveled best approximating a gamma distribution, and a bimodal shape for both home ranges and core areas. Computing the analysis for each categorical explanatory variable separately (sex, age, region, arrival date) did not resolve the bimodal distribution. Four kites (AUKI07 [2015–2016], AUKI88 [2017–2018], AUKO22 [2017–2018], KITE07 [2015–2016]) had large home range sizes of 37,320 km^2, 74,230 km^2, 127,513 km^2, and 39,812 km^2, respectively. Visual examination of residual diagnostic plots suggested our data were an improved fit for the models following the removal of these outliers prior to home range and core area analyses.

We tested for multicollinearity between continuous explanatory variables via a correlation matrix using the package Hmisc (Harrell, 2020). We identified collinear variables ($P < 0.05$) using the subsequent correlation matrix and 1 of the 2 collinear variables (i.e., the least biologically relevant was removed [% closed land cover, number of GPS fixes]; Table S2, available online in Supporting Information). We checked for data heteroscedasticity with the F test feature using the fitted values of each model in the package olsrr (Hebbali, 2020). We standardized and centered continuous explanatory variables, with the number of iterations increased to 200,000 to prevent model non-convergence. We ran all models using a gamma data distribution and included kite individual identification as a random effect.

Following the recommendations of Kernohan et al. (2001), we used an information-theoretic approach to select the most appropriate model for each response variable. Following Burnham and Anderson (2002), we assumed a model was plausible if the difference from the top model in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c) was <4 and likely if <2. If multiple models generated ΔAIC_c values of <2, we select the model with the lowest AIC_c. Using the package MuMIn (Barton, 2020), we quantified the variation accounted for by the fixed (marginal R^2 value; R^2_m) and both the fixed and random variables (conditional R^2 value; R^2_c) for these models.

To test the prediction that younger kites arrive later than adults, affecting home range sizes and distance traveled, we fitted a separate model with age and arrival date as interaction terms. We then repeated the model selection process and selected the model with the lowest AIC_c for each response variable. We performed additional *post hoc* contrasts between kite ages and arrival dates using the LSMEANS package (Lenth, 2016).

Lastly, we quantified patterns of kite mortality similar to van Eeden et al. (2017), exploring associations between mortality, sex, and wintering region using Fisher's exact tests. For the contingency analyses, we only used

data for identified causes of mortality confirmed by post-mortem autopsies and subsequently excluded unknown causes for termination of data retrieval ($n = 7$). We categorized kite mortality attributed to poisoning and gunshots as anthropogenic, and that relating to predation and disease as natural.

RESULTS

We tracked 36 kites (19 females and 17 males) throughout winter between 2015 and 2020, yielding data for 70 individual winters (43 and 27, respectively for females and males; Table S3, Figures S4–S6, available in Supporting Information). We tracked 21 kites for >1 winter period, hence multiple distance traveled, home range, and core area values were available for these birds. Of the 36 tagged birds, 36 out of 70 winters worth of data were derived from 1 cy birds and 34 were from birds in their second calendar year or older. Of the 70 winters of data, 30% ($n = 21$) came from kites that wintered in the Iberian Peninsula, 31% ($n = 22$) from Italy, and 39% ($n = 27$) from the Pyrenees (Figure 1; Table S3). These data included kites that spent >1 season in each winter region. One kite (AUKI51 2017–2018) wintered in the eastern part of central France close to the border with Switzerland (Figure 1; Figure S5).

Tracking yielded a mean of 900 ± 529 ($\pm$SE) GPS fixes/kite/winter with a mean of 6.5 ± 0.3 fixes/day (Table S3). Kites arrived at their wintering areas between 22 September and 28 December, departing between 10 February and 30 April. Open land cover was the dominant landscape type in kite home ranges with a mean ($\pm$ SD) of $67 \pm 13\%$, followed by closed ($29 \pm 15\%$) and urban ($4 \pm 5\%$). Similarly, core areas were mostly composed of open land cover ($\bar{x} = 69 \pm 18\%$), followed by closed ($28 \pm 19\%$) and urban ($3 \pm 5\%$). Lowland comprised on average $58 \pm 34\%$ of kite home ranges and $56 \pm 39\%$ of core areas.

The best model predicting distance traveled by wintering kites was the global model, containing all variables (this was the single model with <4 ΔAIC_c; Table 1). Distance traveled varied between individuals, with a mean ($\pm$SD) of $2,326 \pm 1,319$ km ($n = 70$; range = 450–6,802 km). Kites wintering in the Iberian Peninsula traveled on average $2,986 \pm 1,674$ km, approximately 1.19 and 1.79 times farther than those wintering in Italy ($\bar{x} = 2,504 \pm 1,122$ km) and the Pyrenees ($\bar{x} = 1,667 \pm 825$ km), respectively (Figure 2; Table 2). Males traveled 1.13 times farther than females, averaging $2,279 \pm 1,074$ km with females averaging $2,010 \pm 1,052$ km throughout the winter period (Figure 2); although the proportional variance associated with sex was low (Table 2). Confidence intervals for percentage urban, open and lowland, and winter duration bounded zero and the proportional variance contributed by each of these variables was low; therefore, we considered these variables non-influential within the distance traveled model (Table 2).

The best model predicting 95% home range sizes of wintering kites was again the global model, with <2 ΔAIC_c and the lowest AIC_c value (Table 1). Range sizes were also variable, with a mean ($\pm$ SD) of $4,032 \pm 6,450$ km^2 ($n = 66$; range = 1.7–32,942 km^2). Kites that wintered in the Pyrenees occupied the largest home ranges, averaging $5,141 \pm 8,537$ km^2, compared to those that wintered in Italy ($\bar{x} = 2,843 \pm 3,887$ km^2) and the Iberian Peninsula ($\bar{x} = 3,882 \pm 5,650$ km^2). Pyrenean home ranges were approximately 1.81 and 1.32 times larger than in Italy and the Iberian Peninsula, respectively. In contrast to distance traveled, home ranges were smaller where open land cover and lowland areas predominated (Figure 3; Table 2). An interactive effect of age and arrival date indicated that older kites arriving late to their wintering grounds occupied larger home ranges than those arriving early (Table S4, available in Supporting Information). Only age was influential in predicting range size in the main effect models (Table 2) with, conversely, little apparent difference in fitted plots (Figure 3). The small sample size for 1 cy kites in the early category precluded robust assessment of the effect of arrival date on range size in juveniles, potentially confounding the results. Lastly, winter duration was positively associated with home range size (Figure 3; Table 2), but sex was not influential, as confidence intervals bounded zero (Table 2).

The global model best predicted kite wintering core areas (<2 ΔAIC_c; lowest AIC_c value). Mean winter kite core areas (50% KDE) were $1,536 \pm 3,932$ km^2 ($n = 66$; range = 0.4–29,549 km^2). As for the other response

TABLE 1 Generalized linear mixed models used to explore distance traveled, home ranges (95% kernel density estimators; KDE), and core areas (50% KDE) of 36 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. Models shown are those with a change in Akaike's Information Criterion for small sample size (ΔAIC_c) <4 with 2–4 providing plausible and <2 providing substantial evidence (Burnham & Anderson, 2002). Where there is substantial evidence for multiple models, we chose the model with the lowest AIC_c to be the best model. We present the number of model parameters (K), log-likelihood (logLik), model weights, marginal R^2 (R_m^2), and conditional R^2 (R_c^2). Sample sizes for models relating to distance traveled = 70, home ranges = 66, and core areas = 66 (because of the removal of 4 outlier birds)

Response variable[a]	Model	K	logLik	AIC_c	ΔAIC_c	Weight	R_m^2	R_c^2
Distance traveled (km)	Sex + age + urban (HR) + open (HR) + lowland (HR) + region + arrival + duration	13	−46.0	124.6	0.0	1.000	0.65	0.84
Home range (95%)	Sex + age + urban (HR) + open (HR) + lowland (HR) + region + arrival + duration	13	−584.0	1201.0	0.0	0.441	0.31	0.78
	Sex + age + urban (HR) + open (HR)	7	−593.3	1202.5	1.5	0.210		
	Sex + age + urban (HR) + open (HR) + lowland (HR)	8	−592.2	1202.8	1.8	0.177		
	Sex + age + urban (HR) + open (HR) + lowland (HR) + region	10	−589.7	1203.4	2.4	0.132		
Core areas (50%)	Sex + age + urban (core) + open (core) + lowland (core) + region	10	−479.6	983.1	0.0	0.563	0.39	0.71
	Sex + age + urban (core) + open (core) + lowland (core) + region + arrival + duration	13	−476.0	985.0	1.9	0.222		
	Sex + age + urban (core) + open (core) + lowland (core)	8	−483.7	985.9	2.8	0.143		

[a]Urban = % urban landcover, open = % open landcover, lowland = % lowland, arrival = winter arrival date, duration = winter duration (days), HR = home range, and core = core areas.
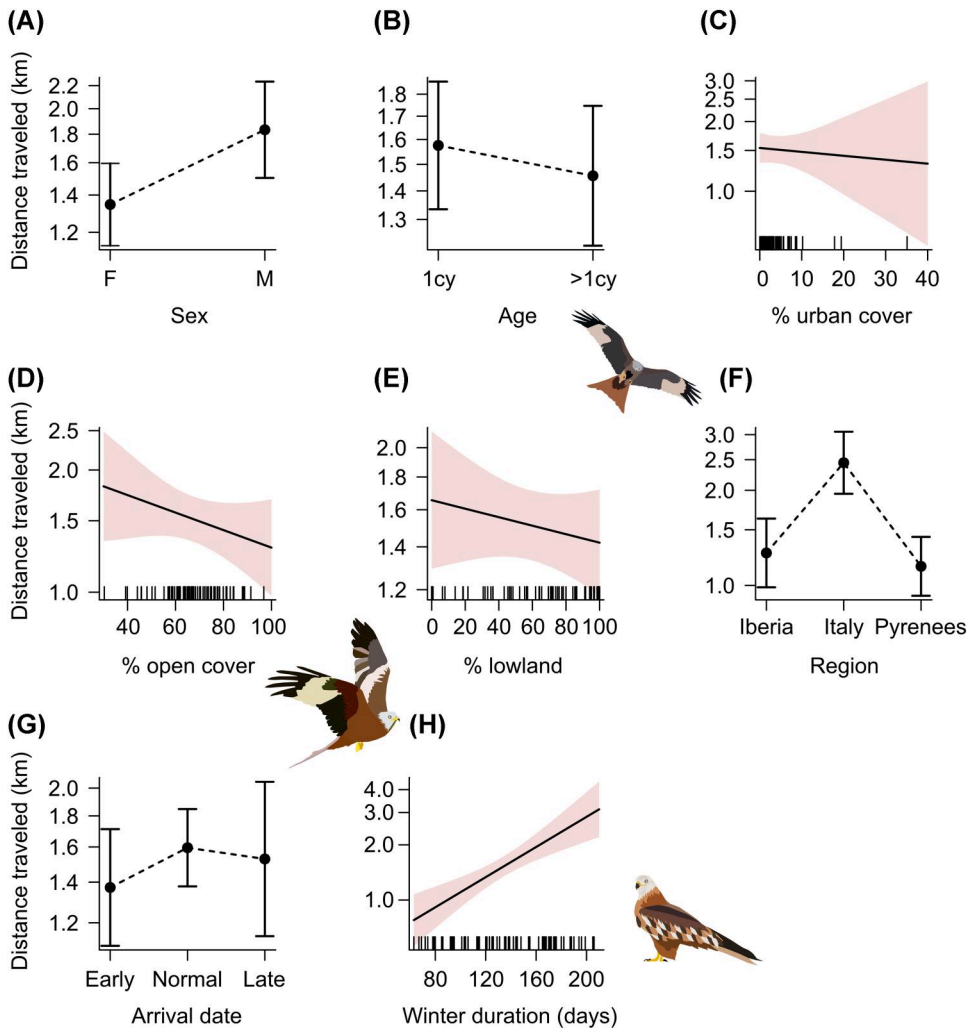
FIGURE 2 Predicted effects with 95% confidence intervals for distance traveled (km) model variables: (A) sex, (B) age, (C) percent urban land cover, (D) percent open land cover, (E) percent lowland, (F) winter region, (G) winter arrival date, and H) winter duration (days; F = female, M = male, 1 cy = first calendar year individuals, >1 cy = individuals in their second calendar year or older) for 36 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. We standardized the distance traveled variable to control for potential migration route length biases

variables, on average, kites that wintered in the Pyrenees occupied larger core areas ($\bar{x}$ = 1,011 ± 1,644 km^2) than those wintering in Italy ($\bar{x}$ = 519 ± 629 km^2) or the Iberian Peninsula ($\bar{x}$ = 784 ± 1,147 km^2; Table 2). Pyrenean core areas were nearly twice the size of those from Italy and 1.12 times larger than kites wintering in the Iberian Peninsula. Both percentage open cover and lowland had negative effects on kite winter core area size (Table 2). Age also predicted core area size (Table 2) with 1 cy birds occupying core areas ($\bar{x}$ = 863 ± 1,205 km^2) that were 1.21 times larger than their older conspecifics ($\bar{x}$ = 712 ± 1,300 km^2). Adult (>1 cy) kites that arrived later again had larger core areas than those that arrived early or on time (Table S4), but we were unable to perform an equivalent robust analysis for 1 cy kites that arrived early because of small and unequal sample sizes between categories. Confidence intervals spanned zero and variance was low for sex, suggesting that this variable had a minimal effect (Table 2).

TABLE 2 Generalized linear mixed model coefficients and proportion of variance for explanatory variables used to explain distance traveled, home ranges (95% kernel density estimators; KDE) and core areas (50% KDE) for 36 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. We present the proportion of variance calculated for each explanatory variable disregarding levels within variables. Cells with an asterisk (*) are associated with confidence intervals that excluded zero, and cells with daggers (†) show contributing proportional variance >10

Variable	Distance traveled (km)					Home range (95%)					Core areas (50%)				
	Coefficient	SE	95% CI (lower)	95% CI (upper)	Proportion of variance	Coefficient	SE	95% CI (lower)	95% CI (upper)	Proportion of variance	Coefficient	SE	95% CI (lower)	95% CI (upper)	Proportion of variance
(Intercept)	0.056	0.194	-0.324	0.436		8.893	2.353	4.281	13.505		8.707	1.527	5.714	11.699	
Demographic															
Sex(male)	0.309	0.140	0.035*	0.583*	0.039	0.677	0.483	-0.270	1.625	2.443	0.638	0.329	-0.008	1.283	4.441
Age(>1 cy)[a]	-0.079	0.125	-0.323	0.165	38.301†	-0.254	0.571	-1.373	0.865	32.512†	-0.638	0.363	-1.349	0.073	25.911†
Environmental															
% urban	-0.020	0.058	-0.135	0.094	6.172	0.013	0.037	-0.059	0.085	0.832	0.008	0.025	-0.042	0.057	0.142
% open	-0.065	0.050	-0.164	0.034	0.021	-0.055	0.014	-0.083*	-0.027*	26.427†	-0.044	0.008	-0.059*	-0.029*	32.915†
% lowland	-0.053	0.063	-0.177	0.071	1.968	-0.012	0.007	-0.025	0.001	5.291	-0.018	0.005	-0.027*	-0.009*	19.500†
Region(Italy)	0.657	0.178	0.309*	1.006*	33.359†	0.273	0.683	-1.066	1.611	7.584	0.011	0.367	-0.615	0.825	17.091†
Region (Pyrenees)	-0.098	0.176	-0.443	0.248	1.39	0.649	0.118*	2.662*	1.436	0.374	0.703*	2.169*			
Temporal															
Arrival(late)	0.108	0.201	-0.286	0.502	4.584	1.746	0.672	0.428*	3.064*	4.410					
Arrival (normal)	0.151	0.128	-0.101	0.402	0.649	0.452	-0.237	1.535							
Duration	0.367	0.084	0.203	0.531	15.556†	0.025	0.007	0.010*	0.039*	20.503†					

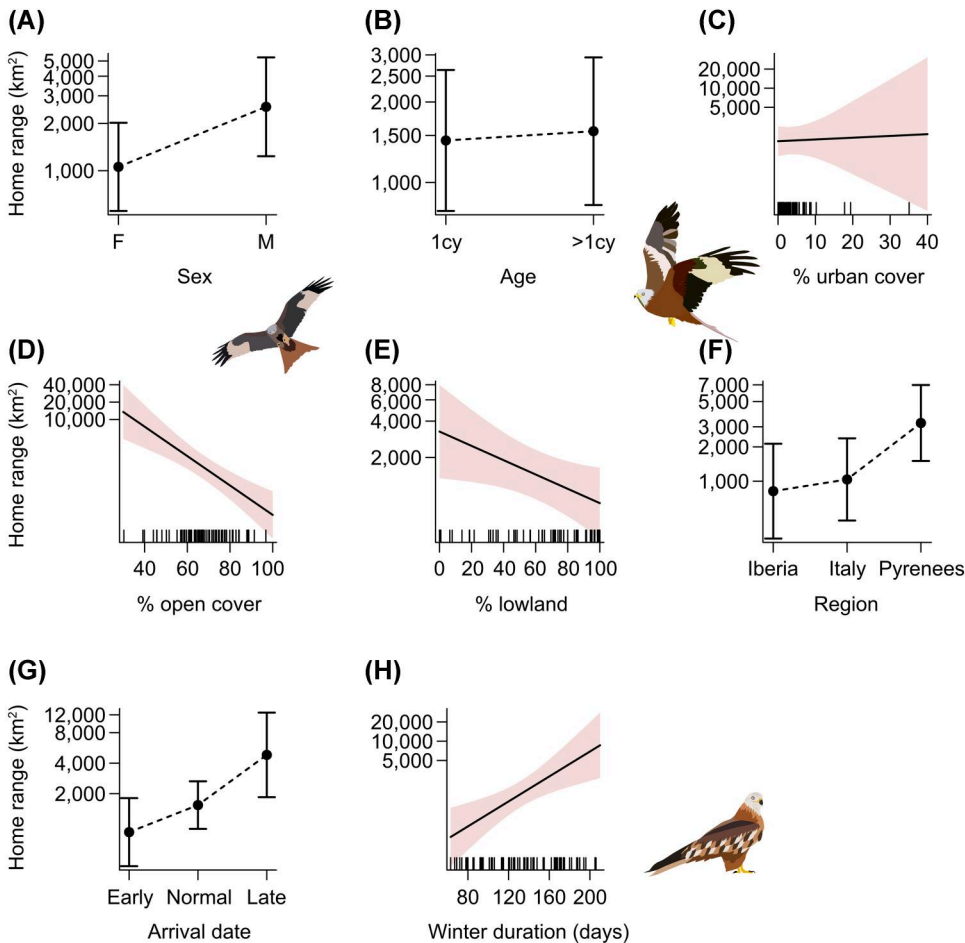[a]Age is a categorical variable of first calendar year versus after first calendar year (>1 cy).

FIGURE 3 Predicted effects with 95% confidence intervals for home range (km^2; 95% kernel density estimators [KDE]) model variables: (A) sex, (B) age, (C) percent urban land cover, (D) percent open land cover, (E) percent lowland, (F) winter region, (G) winter arrival date, and (H) winter duration (days; F = female, M = male, 1 cy = first calendar year individuals, >1 cy = individuals in their second calendar year or older) for 36 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020

Over the study period, 20 kites (56% of tagged kites) died or the transmitter malfunctioned. Mean survival of kites since the date of tagging was 654 ± 273 days (±SD; Table 3). We documented 6 anthropogenic causes of mortality from 13 deaths (5 poisoned, 1 shot). Anthropogenic causes of mortality were higher in Italy and the Pyrenees compared to natural causes; however, this difference was non-significant (Fisher's exact test; $P > 0.05$; Figure 4) and we did not document differences between males and females dying because of anthropogenic causes (Fisher's exact test; $P > 0.05$). No anthropogenic causes of mortality were attributed to juveniles.

DISCUSSION

We explored spatio-temporal, landscape, and demographic factors determining space use by migratory kites during winter. Our results were partially consistent with H1 (the Pyrenees and Iberian Peninsula would be associated with reduced ranging), in that kites over-wintering in Italy and the Iberian Peninsula moved approximately 1.5 and 1.79

TABLE 3 Number of days survived, causes of anthropogenic mortality, and percentage of anthropogenic mortality for 20 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. Data are split by demographic and geographic variables (<1 cy = first calendar year individuals, >1 cy = individuals in their second calendar year and older). Sample sizes include anthropogenic, natural, and unknown causes of death for the 20 kites that either died or for which the transmitter malfunctioned

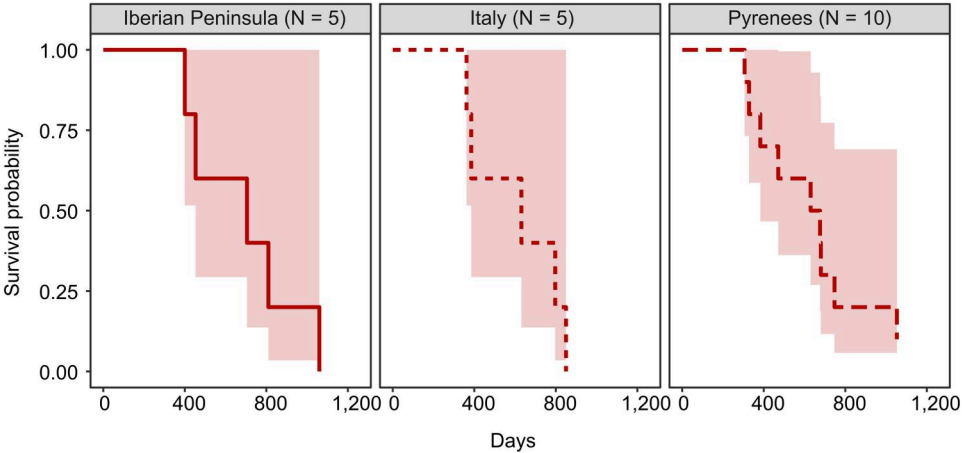| Variable		n	$\bar{x}$ number of days since tagging	SD	Cause Poisoned (n)	Shot (n)	Percentage of anthropogenic-related mortalities
Sex	Male	10	668	284	3	1	40
	Female	10	639	262	2	0	20
Age	<1 cy	3	332	23	0	0	0
	>1 cy	17	710	258	5	1	35
Region	Iberia	5	686	242	0	1	20
	Italy	5	605	203	2	0	40
	Pyrenees	10	662	313	3	0	60

FIGURE 4 Kaplan-Meier survival probability plots for 20 red kites wintering in Italy, the Iberian Peninsula, and the Pyrenees, 2015–2020. Plots are fitted with 95% confidence intervals. Data include kites that stopped transmitting data whereby the cause could not be ascertained (Italy n = 2, Iberian Peninsula = 1, Pyrenees = 5)

times farther than those wintering in the Pyrenees. We detected contrasting effects for range size; kites occupied larger home ranges and core areas in Pyrenean wintering areas relative to both other regions. In support of H2 (kite ranges would be reduced following earlier arrival dates where open, lowland, and urban land cover types predominate), proportional lowland and open land cover were important negative predictors of home range and core area size, and kites arriving earlier had smaller ranges than late birds. The effect of arrival date was only the case for older kites, and proportional urban land cover did not affect ranging for any of the parameters investigated. Evidence for H3 (younger kites would range more widely) was also mixed because although 1 cy kites occupied larger core areas than their older conspecifics, we did not detect age-related effects for either distance traveled or home range size.

The apparently high rate of anthropogenic causes of mortality in male kites in our study, including poisoning by carbofuran, warrants further investigation. Cholinesterase inhibitors, such as carbofuran and other carbamates, are

common substances contributing to the secondary poisoning of wildlife including kites (Berny & Gaillet, 2008; BirdLife International, 2004; Literák et al., 2018; Molenaar et al., 2017; Villafuerte et al., 1998). They are often used as pesticides to control rodent populations; however, in some cases they are directly applied to meat baits to persecute raptors (Berny & Gaillet, 2008). Smart et al. (2010) reported that illegal killing by means of direct poisoning slowed kite population growth in Scotland. Despite the species' recent down-listing from near threatened to least concern on the International Union for the Conservation of Nature's Red List of Threatened Species (BirdLife International, 2020), our data suggest that poisoning is still a conservation issue across some parts of the species' winter range.

The increased range sizes of kites over-wintering in the Pyrenees was unexpected given the apparent availability of carrion from supplementary feeding programs in the region (Margalida et al., 2011). It may reflect a lack of human modification in this mountainous landscape, compared to other study regions, with a corresponding paucity of open land cover favored by kites. Further, topographic features such as mountain valleys and ridges may obstruct kites during foraging, making mountainous areas less optimal and requiring kites to expand their range extent to obtain necessary resources, as seen in Bonelli's eagles (*Aquila fasciata*; Pérez-García et al., 2013).

Our data indicate that the association between arrival date and range size in our study is due to a combination of variation in resource richness and dispersion in kite winter ranges, and competition for the most resource-rich areas. Food is the predominant limiting resource for over-wintering raptors, with concentrated, high-quality food resources during winter well-documented to negatively predict raptor home range size (Kenward, 1982; Linkhart et al., 1998; López-López et al., 2014; Rolando, 2002; Tornberg & Colpaert, 2001). Although over-wintering kites are not strictly territorial, as evidenced by communal roosting (Literák et al., 2019a; Panter et al., 2020), threshold group sizes at roosts may mediate acceptance of incomers, and earlier arrivals are more likely to secure areas with rich, concentrated resources, potentially defending these against intruders while foraging. Late arrivals, conversely, will have less choice about where to over-winter and will consequently be more likely to inhabit less optimal habitats with sparser and more widely distributed resources, resulting in greater ranges. The negative association between proportion of open land cover and range size in our study is likely to be partially mediated by carrion spatial distribution, as carrion is more readily detectable and accessible in open areas (Barton et al., 2013; Carter, 2007; García et al., 1998; Newton et al., 1982).

Our finding that kites moved more and occupied larger home ranges within areas where they wintered for longer may relate to increased variation in the spatial distribution of resources over time. It is likely that winter duration is at least in part a function of food availability given that previous studies have linked the 2 variables. Tjernberg (1977) reported positive associations between livestock carrion provision for golden eagles (*Aquila chrysaetos*) and winter duration. Kites that move more within their wintering areas may potentially also over-winter for longer in accordance with optimal foraging theory (Pyke, 1984) assuming adequate food resources are available (i.e., the calorific expenditure of traveling farther is compensated for by staying longer and foraging more). The use of IAA to determine winter duration, as determined by eye in our study could be considered subjective; however, this method is arguably more robust and repeatable than more traditional approaches such as field observations and radio-telemetry, which frequently miss rare rapid movements along the migratory journey (Hebblewhite & Haydon, 2010; Kie et al., 2010).

Despite the well-documented use of urban areas by kites (Knott et al., 2009; Literák et al., 2017, 2019a; Panter et al., 2020), urban land cover was not a predictor of kite winter space use in our study. This may be an artefact of the large-scale approach of our study because urban land cover constituted a very small proportion of the landscape relative to more open and closed cover types. Therefore, it may be more suitable to examine the effects of urbanized areas on kite space use at smaller geographic scales or at different periods of the year, for example, during the summer when kites occupy reduced breeding season ranges (Pfeiffer & Meyburg, 2015). We also recommend further investigation of peri-urban or rural sites such as municipal refuse facilities (garbage dumps), that would not have been classed within urban layers in our data set but which nevertheless are anthropogenic in origin and attractive to kites (Heredia et al., 1991; Panter et al., 2020). One kite (AUKI189 2019–2020) within our study

occupied a small winter home range extending 1.7 km^2 with a core area of 0.4 km^2. This bird wintered within proximity to a wastewater treatment plant and disused garbage dump with the surrounding area used for quarrying and mining activities. The contractor pattern evident in this bird's winter range is indicative of high food resource availability within the local area, either from the disposal of human food waste or disturbance to wild prey populations from quarrying and mining activities.

The limited evidence of sex-related biases in winter ranging behavior reported in our study likely relates to kites displaying relatively little sexual dimorphism owing to their scavenging dietary preferences, unlike bird-eating raptors such as the Eurasian sparrowhawk (*Accipiter nisus*; Panter & Amar, 2021). Previous literature on this topic is mixed; in the breeding season, Pfeiffer and Meyburg (2015) reported larger home ranges in male kites, whereas Baucks (2018) reported female ranges to be larger, as putatively explained by differential susceptibility to food availability and meteorological conditions. There was large individual variation in space use in our study, which is consistent with Pfeiffer and Meyburg (2015), Baucks (2018), and Maciorowski et al. (2019). Differential selection pressures are likely to operate on kite ranging behavior at different times of year, explaining our large winter home range estimates relative to breeding season estimates in Germany (Pfeiffer & Meyburg, 2015) and Switzerland (Baucks, 2018). We suggest this relates to scarcity of or dispersed food resources during winter (Blanco et al., 1990; García et al., 1998; Nachtigall et al., 2003; Peery, 2000; Pfeiffer & Meyburg, 2009). Our core area results support the general patterns of age-related differences identified by previous researchers (Kenward et al., 1981; Marquiss & Newton, 1981; Rolando, 2002), where 1 cy bird core areas were larger than those of older conspecifics. This likely reflects winter site fidelity around areas of high resource availability or communal roosting opportunities (Literák et al., 2019a; Skyrpan et al., 2020).

We decided to use KDE over other methods such as adaptive local convex hulls (Getz et al., 2007), which have been interpreted to be more biologically meaningful (Getz & Saltz, 2008; Miller et al., 2017), to maximize the comparability of our results with other studies focusing on the movements of kites. Consequently, comparisons with those that adopted different methods (e.g., minimum convex polygons) are not possible and our inability to exclude areas not used by kites may overestimate true winter space use values. Furthermore, ranges derived from GPS data tend towards overestimation (Trierweiler et al., 2012). Our approach, however, likely outperforms very high frequency radio-telemetry when estimating home range because of increased precision and accuracy, and a reduction in sampling bias (Hebblewhite & Haydon, 2010). Our winter home range estimates (1.7–32,942 km^2) were much larger than those derived using very high frequency radio-telemetry in Spain (Heredia et al., 1991; 6.6–53.5 km^2), England (Carter & Grice, 2000; 19–32 km^2), and Germany (Nachtigall et al., 2003; 6.2–8 km^2). This may be due to differences in tracking methodologies whereby visual observations and radio-telemetry underestimate range size (Kenward, 2001; López-López et al., 2014). Previous winter studies have also only included data for resident kites, which have smaller winter home ranges than their migratory conspecifics (Heredia et al., 1991). Random, lengthy mid-winter movements are common for many migratory bird species because of the unpredictability of temporary food concentrations. The largest estimated home range and core area values in our results may be due to individual cases of itinerancy (Trierweiler et al., 2012). Our home range results are also larger than those from studies of wintering kites in southeast Europe. Literák et al. (2019a) reported mean home range sizes for kites in Greece ranging from 21–1,268 km^2 using identical GPS-GSM satellite telemetry and KDE analysis techniques as ours. Differences between our estimates may relate to variation in topography (i.e., central Iberia is flat compared to the Greek archipelago), differences in extent of land cover, and the relatively recent occurrence of kites overwintering in southeastern Europe (Literák et al., 2019a), resulting in lower rates of intraspecific competition.

Of the 36 kites in this study, 6 wintered in or partially within the Portuguese border. According to the European Commission Regulation (EU) No 142-2011, Article 14 1(a) competent authorities may supply entire bodies or parts of dead animals for feeding "in feeding stations, to endangered or protected species of necrophagous birds and other species living in their natural habitat, for the promotion of biodiversity" (https://eur-lex.europa.eu/eli/reg/2011/142/oj; L 54/10; accessed 11 Aug 2021). With the exception of Portugal, all countries in our study area include red kites on the list of necrophagous birds eligible for supplementary feeding. Further, Portuguese farmers

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are required to remove livestock carcasses from the field under Decreto-lei 38-2012 in response to an outbreak of bovine spongiform encephalopathy. Our data suggest that kites from a central European population are more inclined to winter in the Pyrenees, Italy, or the Spanish areas of the Iberian Peninsula than in Portugal. This may be due to reduced food availability as a combined result of Decreto-lei n° 38-2012 and the absence of the species on Commission Regulation (EU) number 142-2011. Arrondo et al. (2018) reported similar findings, with the Spain-Portugal border acting as a quasi-impermeable barrier restricting Spanish griffon vultures (*Gyps fulvus*) and cinereous vultures (*Aegypius monachus*) in their migratory movements. Included within the 2009 Species Action Plan, the removal of carcasses throughout Portugal poses a high-effect threat towards local kite populations alongside poisoning and the illegal shooting and trapping of individuals, despite legal protection of this species (Decreto-lei number 140-99, modified by Decreto-lei number 49-2005; Knott et al., 2009). A survey among rural Portuguese communities revealed a high prevalence of trapping birds for consumption (47 ± 15% [SE]) and shooting raptors (14 ± 11; Fairbrass et al., 2016). To ensure continued population growth and stabilization across the species' range, we recommend that the red kite is included on the list of necrophagous birds targeted for conservation-led supplementary feeding in Portugal.

Like all avian facultative scavengers, kites provide key ecosystem services via the stabilization of food webs, disease transfer mitigation, and waste-disposal services (Cereghetti et al., 2019; DeVault et al., 2016; O'Bryan et al., 2018). Despite being recently down-listed to least concern on the International Union for the Conservation of Nature's Red List of Threatened Species, kites are still experiencing population declines in southern Spain, Portugal, and locally in Germany and France (BirdLife International, 2020). A recent study estimated that juvenile kite survival has experienced a long-term decline of >40% since the 1970s mostly due to collisions, poisoning, and predation (Katzenberger et al., 2019); however, we were unable to attribute any cases of juvenile mortality to anthropogenic factors, likely a consequence of our small sample sizes. Subsequently, our data are of particular importance in southern Spain where the species has been declining for several years (Blanco et al., 2017; Mougeot et al., 2011; Viñuela et al., 1999). Findings by Crespo-Luengo et al. (2020) revealed that the most suitable areas for kites in Spain were also those at most risk of electrocution via collisions with powerlines, which pose a considerable threat (Bayle, 1999). Population declines have also been attributed to the loss of suitable breeding and wintering habitats (Maciorowski et al., 2019, 2021; Moreau, 2009). Compliance with wildlife laws is low in some parts of our study areas such as Portugal (Fairbrass et al., 2016). Spain, Italy, and Portugal have been identified as countries with the largest estimated number of illegally killed kites per year (Brochet et al., 2016). Despite advancements in the enforcement of wildlife poisoning in Europe (Badia-Boher et al., 2019), more than a decade on, our mortality data suggests that poisoning is still occurring in kite wintering areas (14% [5 birds] of tagged kites died because of suspected poisoning).

MANAGEMENT IMPLICATIONS

Our data showed that kites range across large areas during winter; therefore, appropriate management of habitats with abundant natural food resources at a landscape scale is required for kite persistence during this period. More broadly, low-elevation open land cover is important for over-winter site selection for migratory kites and in line with optimal foraging theory, winter space use is likely to be associated with food availability. Supplementary feeding programs are encouraged, to ensure continued kite population growth, especially in open lowland landscapes throughout the species' winter range. This is particularly important in Portugal where kites have yet to be included as a necrophagous species for supplementary feeding and in Italy where the sudden closure of existing supplementary feeding stations poses a significant threat. The continued use of poison baits throughout the species' winter range is alarming and our data on kite survival may be of interest to conservation practitioners and policy-makers within our study regions. Therefore, to prevent future up-listing of the species on the International Union for the Conservation of Nature's Red List of Threatened Species, increased enforcement and education surrounding the use of illegal poison baits and shooting is required throughout the species' winter range.

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ETHICS STATEMENT

Ethical approval for tagging and handling activities was granted by the local authorities for nature protection in Austria (MIL2-J-0812/012, GFL2-J-107/014, BHBRN-2019-314986/5-PS), the Czech Republic (permissions S-JMK 188552/2014 OŽP/Kuč, S-JMK 32177/2015 OŽP/Kuč, S-JMK 545 30634/2016 OŽP/Ško, S-JMK 177265/2017/OŽP/Ško), and by The Ministry of Environment of the Slovak Republic (permissions MŽP SK 664/297/05-5.1pil and MŽP SK 2944/2017-547 6.3).

DATA AVAILABILITY STATEMENT

All data and code featured in this study is provided using the following link https://github.com/ConnorPanter/Panter_et_al_JWM.

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REFERENCES

Alarcón, P. A. E., and S. A. Lambertucci. 2018. A three-decade review of telemetry studies on vultures and condors. Movement Ecology 6:13.

Alerstam, T. 2011. Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Allen, A. M., and N. J. Singh. 2016. Linking movement ecology with wildlife management and conservation. Frontiers in Ecology and Evolution 3:155.

Amat, J. A. 1986. Some aspects of the foraging ecology of a wintering greylag goose *Anser anser* population. Bird Study 33:74–80.

Arrondo, E., M. Moleón, A. Cortés-Avizanda, J. Jiménez, P. Beja, J. A. Sánchez-Zapata, and J. A. Donázar. 2018. Invisible barriers: differential sanitary regulations constrain vulture movements across country borders. Biological Conservation 219:46–52.

Badia-Boher, J. A., A. Sanz-Aguilar, M. de la Riva, L. Gangoso, T. van Overveld, M. García-Alfonso, O. P. Luzardo, A. Suarez-Pérez, and J. A. Donázar. 2019. Evaluating European LIFE conservation projects: improvements in survival of an endangered vulture. Journal of Applied Ecology 56:1210–1219.

Barton, K. 2020. MuMIn: multi-model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn. Accessed 16 Nov 2020.

Barton, P. S., S. A. Cunnigham, D. B. Lindenmayer, and A. D. Manning. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–772.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Baucks, C. 2018. The effect of food supplementation on range use of red kites (*Milvus milvus*) in Switzerland. Thesis, University of Natural Resources and Life Sciences, Vienna (BOKU), Department for Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management (IWJ), Vienna Austria.

Bayle, P. 1999. Preventing birds of prey problems at transmission lines in western Europe. Journal of Raptor Research 33:43–48.

Bellebaum, J., F. Korner-Nievergelt, T. Dürr, and U. Mammen. 2013. Wind turbine fatalities approach a level of concern in a raptor population. Journal for Nature Conservation 21:394–400.

Berny, P., and J. R. Gaillet. 2008. Acute poisoning of red kites (*Milvus milvus*) in France: data from the sagir network. Journal of Wildlife Diseases 44:417–426.

Bevanger, K. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biological Conservation 86:67–76.

BirdLife International. 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge, United Kingdom.

BirdLife International. 2020. Species factsheet: *Milvus milvus*. http://www.birdlife.org. Accessed 10 Aug 2020.

Blanco, G. 2014. Can livestock carrion availability influence diet of wintering red kites? Implications of sanitary policies in ecosystem services and conservation. Population Ecology 56:569–604.

Blanco, G., J. Cardells, and M. M. Garijo-Toledo. 2017. Supplementary feeding and endoparasites in threatened avian scavengers: coprologic evidence from red kites in their wintering stronghold. Environmental Research 155:22–30.

Blanco, J. C., F. Hiraldo, and B. Heredia. 1990. Variations in the diet and foraging behaviour of a wintering red kite (*Milvus milvus*) population in response to changes in food availability. Ardeola 37:267–278.

Brochet, A. L., W. Van Den Bossche, S. Jbour, P. K. Ndang'ang'a, V. R. Jones, W. A. L. I. Abdou, A. R. Al-Hmoud, N. G. Asswad, J. C. Atienza, I. Atrash, et al. 2016. Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. Bird Conservation International 26:1–28.

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

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York, New York, USA.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemety: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B 365:2157–2162.

Carter, I. 2007. The red kite. Arlequin Press, Shrewsbury, England.

Carter, I., and P. Grice. 2000. Studies of re-established red kites in England. British Birds 93:304–322.

Cereghetti, E., P. Scherler, J. Fattebert, and M. U. Grüebler. 2019. Quantification of anthropogenic food subsidies to an avian facultative scavenger in urban and rural habitats. Landscape and Urban Planning 190:103606.

Choi, C.-Y., H.-B. Peng, P. He, X.-T. Ren, S. Zhang, M. V. Jackson, X. Gan, Y. Chen, Y. Jia, M. Christie, et al. 2019. Where to draw the line? Using movement data to inform protected area design and conserve mobile species. Biological Conservation 234:64–71.

Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott, and P. J. Butler. 2004. Biotelemetry: a mechanistic approach to ecology. Trends in Ecology & Evolution 19:334–343.

Costantini, E. A. C., and C. Dazzi. 2013. The soils of Italy, world soils book series. Springer, New York, New York, USA.

Cramp, S., and K. E. Simmons. 1980. The birds of the Western Palearctic, volume II. Oxford University Press, Oxford, England.

Crespo-Luengo, G., R. E. Hernández-Lambraño, I. Barbero-Bermejo, and J. A. Sánchez-Agudo. 2020. Analysis of spatio-temporal patterns of red kite *Milvus milvus* electrocution. Ardeola 67:247–268.

DeVault, T. L., J. C. Beasley, Z. H. Olsen, M. Moleón, M. Carrete, A. Margalida, and J. A. Sánchez-Zapata. 2016. Ecosystem services provided by avian scavengers. Pages 235–270 in C. H. Şekercioğlu, D. G. Wenny, and C. J. Whelan, editors. Why birds matter: avian ecological function and ecosystem services. University of Chicago Press, Chicago, Illinois, USA.

Duijns, S., L. J. Niles. A. Dey, Y. Aubry, C. Friis, S. Koch, A. M. Anderson, and P. A. Smith. 2017. Body condition explains migratory performance of a long-distance migrant. Proceedings of the Royal Society B 284:20171374.

Dürr, T. 2009. Zur gefährdung des rotmilans *Milvus milvus* durch windenergieanlagen in Deutschland. Informationdienst Naturschutz Niederachsen 29:185–191 [in German].

Etienne, M., J. Aronson, and E. Le Floch. 1998. Abandoned lands and land use conflicts in southern France. Pages 127–140 in P. W. Rundel, G. Montenegro, and F. M. Jaksic, editors. Landscape disturbance and biodiversity in Mediterranean type ecosystems. Springer, Berlin, Germany.

Evans, I. M., and M. W. Pienkowski. 1991. World status of the red kite. A background to the experimental reintroduction to England and Scotland. British Birds 84:171–187.

Fairbrass, A., A. Nuno, N. Bunnefeld, and E. J. Milner-Gulland. 2016. Investigating determinants of compliance with wildlife protection laws: bird persecution in Portugal. European Journal of Wildlife Research 62:93–101.

Ferández-Nogueira, D., and E. Corbelle-Rico. 2018. Land use changes in Iberian peninsula 1990–2012. Land 7:99.

Ferreira, R., H. Zina, A. T. Marques, A. Delgado, D. Venade, and H. Costa. 2015. Wintering population of red kite *Milvus milvus* in the Castro Verde SPA (Portugal). Airo 23:55–60.

Fischer, T. 1920. The Iberian Peninsula: Spain. Pages 368–377 in H. R. Mill, editor. The international geography. Appleton and Company, New York, New York, USA.

Fratianni, S., and F. Acquaotta. 2017. The climate of Italy. Pages 29–39 in M. Soldati and M. Marchetti, editors. Landscapes and landforms of Italy. Springer, Cham, Switzerland.

García, J. T., J. Viñuela, and C. Sunyer. 1998. Geographic variation of the winter diet of the red kite *Milvus milvus* in the Iberian Peninsula. Ibis 140:302–309.

Génsbøl, B., and W. Thiede. 2008. Collins birds of prey. HarperCollins publishers, London, England.

Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS ONE 2:e207.

Getz, W. M., and D. Saltz. 2008. A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences USA 105:19066–19071.

Gómara, B., M. J. Gonzáles, R. Baos, F. Hiraldo, E. Abad, J. Rivera, and B. Jiménez. 2008. Unexpected high PCB and total DDT levels in the breeding population of red kite (*Milvus milvus*) from Doñana National Park, south-western Spain. Environment International 34:73–78.

Harrell, F. E., Jr. 2020. Hmisc: Harrell miscellaneous. R package version 4.4-0. https://CRAN.R-project.org/package=Hmisc. Accessed 4 Jul 2020.

Hebbali, A. 2020. olsrr: tools for building OLS regression models. R package version 0.5.3. https://CRAN.R-project.org/package=olsrr. Accessed 4 Jul 2020.

Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B 365:2303–2312.

Heredia, B., J. C. Alonso, and F. Hiraldo. 1991. Space and habitat use by red kites *Milvus milvus* during winter in the Guadalquivir marshes: a comparison between resident and wintering populations. Ibis 133:374–381.

Horne, J. S., and E. O. Garton. 2010. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641–648.

Hötker, H., U. Mammen, and L. Rasran. 2017. Red kites and wind farms—telemetry data from the core breeding range. Pages 3–18 *in* J. Köppel, editor. Wind energy and wildlife interactions. Springer, Cambridge, England.

Janns, G. F. E. 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biological Conservation 95:353–359.

Katzenberger, J., E. Gottschalk, N. Balkenhol, and M. Waltert. 2019. Long-term decline of juvenile survival in German red kites. Journal of Ornithology 160:337–349.

Kenward, R. E. 1982. Goshawk hunting behaviour, and range size as a function of food and habitat availability. Journal of Animal Ecology 51:69–80.

Kenward, R. E. 2001. A manual for wildlife radio tagging. Academic Press, London, England.

Kenward, R. E., N. M. Casey, S. S. Walls, and A. B. South. 2014. Ranges9: for the analysis of tracking and location data. Online manual. Anatrack, Wareham, England.

Kenward, R. E., V. Marcström, and M. Karlbom. 1981. Goshawk winter ecology in Swedish pheasant habitats. Journal of Wildlife Management 45:397–408.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations, Academic Press, San Diego, California, USA.

Kie, J. G., J. Matthiopoulos, K. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J. M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B 365:2221–2231.

Knott, J., P. Newbury, and B. Barov. 2009. Action plan for the red kite *Milvus milvus* in the European Union. BirdLife International for the European Union, Cambridge, United Kingdom.

Kolnegari, M., G. J. Conway, A. A. Basiri, C. T. Panter, M. Hazrati, M. S. Rafiee, M. Ferrer, and J. F. Dwyer. 2020. Electrical components involved in avian-caused outages in Iran. Bird Conservation International 1–15. https://doi.org/10.1017/S0959270920000507

Krüger, S., T. Reid, and A. Amar. 2014. Differential range use between age classes of southern African bearded vultures *Gypaetus barbatus*. PLoS One 9:e114920.

Kumar, N., U. Gupta, Y. V. Jhala, Q. Qureshi, A. G. Gosler, and F. Sergio. 2020. GPS-telemetry unveils the regular high-elevation crossing of the Himalayas by a migratory raptor: implications for definition of a "Central Asian Flyway". Scientific Reports 10:15988.

Lenth, R. V. 2016. Least-squares means: the R package lsmeans. Journal of Statistical Software 69:1–33.

Limiñana, R., B. Arroyo, J. Terraube, M. McGrady, and F. Mougeot. 2014. Using satellite telemetry and environmental niche modelling to inform conservation targets for a long-distance migratory raptor in its wintering grounds. Oryx 49:329–337.

Linkhart, B. D., R. T. Reynolds, and R. A. Ryder. 1998. Home range and habitat of breeding flammulated owls in Colorado. Wilson Journal of Ornithology 110:342–351.

Literák, I., D. Horal, H. Alivizatos, and H. Matušík. 2017. Common wintering of black kites (*Milvus migrans migrans*) in Greece, and new data on their wintering elsewhere in Europe. Slovak Raptor Journal 11:91–102.

Literák, I., D. Horal, R. Raab, H. Matušík, S. Vyhnal, D. Rymešová, P. Spakovszky, T. Skartsi, K. Poirzidis, S. Zakkak, A. Tomik, and M. Skyrpan. 2019*a*. Sympatric wintering of red kites and black kites in south-east Europe. Acta Zoologica Academiae Scientiarum Hungaricae 65:381–398.

Literák, I., R. Raab, M. Petretto, J. Škrábal, P. Spakovszky, and J. Steindl. 2019b. Diverse natal dispersal in four sibling red kites originating from Austria, including wintering in Tunisia. Biologia 75:1399–1407.

Literák, I., R. Raab, S. Vyhnal, P. Spakovsky, and J. Steindl. 2018. Occurrence of red kites Milvus milvus in Serbia based on birds tracked by telemetry devices. Acrocephalus 39:27–32.

Literák, I., M. Skyrpan, and N. G. Andreyenkova. 2019c. A mixed pair of black and red kites in Ukraine, including DNA analysis of hybrid offspring. Biologia 75:115–120.

Loidi, J. 2017. The vegetation of the Iberian Peninsula 1–2. Springer, Cham, Switzerland.

López-López, P., C. García-Ripollés, and V. Urios. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. Ecological Applications 24:938–949.

Lorenzo-Lacruz, J., S. M. Vincente-Serrano, J. I. López-Moreno, J. C. González-Hidalgo, and E. Morán-Tejeda. 2011. The response of Iberian rivers to the north Atlantic oscillation. Hydrology and Earth System Sciences 15:2581–2597.

Macdonald, D. W., and D. D. P. Johnson. 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. Journal of Zoology 295:75–107.

Maciorowski, G., J. Kosicki, M. Polakowski, M. Urbańska, P. Zduniak, and P. Tryjanowski. 2019. Autumn migration of immature red kites Milvus milvus from a central European population. Acta Ornithologica 54:45–50.

Maciorowski, G., P. Zduniak, M. Bocheński, M. Urbańska, P. Król, and M. Polakowski. 2021. Breeding habitats and long-term population numbers of two sympatric raptors–red kite Milvus milvus and black kite M. migrans–in the mosaic-like landscape of western Poland. Journal of Ornithology 162:125–134.

Margalida, A., M. Carrete, D. Hegglin, D. Serrano, D. Arenas, and J. A. Donázar. 2013. Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. PLoS ONE 8:e65857.

Margalida, A., D. Oro, A. Cortés-Avizanda, R. Heredia, and J. A. Donázar. 2011. Misleading population estimates: biases and consistency of visual surveys and matrix modelling in the endangered bearded vulture. PLoS ONE 6:e26784.

Marquiss, M., and I. Newton. 1981. A radio-tracking study of the ranging behaviour and dispersion of European sparrowhawks Accipiter nisus. Journal of Animal Ecology 51:111–133.

Mateo-Tomás, P., P. P. Olea, E. Mínguez, R. Mateo, and J. Viñuela. 2020. Direct evidence of poison-driven widespread population decline in a wild vertebrate. Proceedings of the National Academy of Sciences of the United States of America 117:16418–16423.

May, R., T. Nygård, E. L. Dahl, O. Reitan, and K. Bevanger. 2011. Collision risk in white-tailed eagles. Modelling kernel-based collision risk using satellite telemetry data in Smøla wind power plant. NINA Report 692, Trondheim, Norway. [in Norwegian].

McClure, C. J. W., J. R. S. Westrip, J. A. Johnson, S. E. Schulwitz, M. Z. Virani, R. Davies, A. Symes, H. Wheatley, R. Thorstrom, A. Amar, et al. 2018. State of the world's raptors: distributions, threats and conservation recommendations. Biological Conservation 227:390–402.

McGowan, J., M. Beger, R. L. Lewison, R. Harcourt, H. Campbell, M. Priest, R. G. Dwyer, H.-Y. Lin, P. Lentini, C. Dudgeon, et al. 2016. Integrating research using animal-borne telemetry with the needs of conservation management. Journal of Applied Ecology 54:423–429.

McKinley, J. O., and B. Mattox. 2010. Winter site fidelity of migratory raptors in southwestern Idaho. Journal of Raptor Research 44:240–243.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97:133–140.

Miller, T. A., R. P. Brooks, M. J. Lanzone, J. Cooper, K. O'Malley, D. Brandes, A. Duerr, and T. E. Katzner. 2017. Summer and winter space use and home range characteristics of golden eagles (Aquila chrysaetos) in eastern North America. Condor: Ornithological Applications 119:697–719.

Molenaar, F. M., J. E. Jaffe, I. Carter, E. A. Barnett, R. F. Shore, J. M. Rowcliffe, and A. W. Sainsbury. 2017. Poisoning of reintroduced red kites (Milvus milvus) in England. European Journal of Wildlife Research 63:94.

Morant, J., J. M. Abad-Gómez, T. Álvarez, Á. Sánchez, I. Zuberogoitia, and P. López-López. 2020. Winter movement patterns of a globally endangered avian scavenger in south-western Europe. Scientific Reports 10:17690.

Moreau, R. E. 2009. Changes in Africa as a wintering area for Palaearctic birds. Bird Study 17:95–103.

Mougeot, F., J. T. García, and J. Viñuela. 2011. Breeding biology, behaviour, diet and conservation of the red kite (Milvus milvus), with particular emphasis on Mediterranean populations. Pages 190–204 in I. Zuberogoitia and J. E. Martínez, editors. Ecology and conservation of European dwelling forest raptors and owls. Departamento de Agricultura de la Diputación Foral de Bizkaia, Bilbao, Spain.

Nachtigall, W., M. Stubbe, and S. Herrmann. 2003. Aktionsraum und habitatnutzung des rotmilans (Milvus milvus) im winter-eine telemetrische studie im Nordharzvorland. Journal of Ornithology 144:284–294 [in German].

Newton, I. 2004. Population limitation in migrants. Ibis 146:197–226.

Newton, I., P. E. Davis, and J. E. Davis. 1982. Ravens and buzzards in relation to sheep-farming and forestry in Wales. Journal of Applied Ecology 19:681–706.

O'Bryan, C. J., A. R. Braczkowski, H. L. Beyer, N. H. Carter, J. E. M. Watson, and E. McDonald-Madden. 2018. The contribution of predators and scavengers to human well-being. Nature Ecology & Evolution 2:229–236.

O'Donnell, K., and J. del Barco Trillo. 2020. Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis. Journal of Urban Ecology 6:juaa014.

Oro, D., A. Margalida, M. Carrete, R. Heredia, and J. A. Donázar. 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. PLoS ONE 3:e4084.

Orros, M. E., and M. D. E. Fellowes. 2014. Supplementary feeding of the reintroduced red kite Milvus milvus in UK gardens. Bird Study 61:260–263.

Orros, M. E., and M. D. E. Fellowes. 2015. Widespread supplementary feeding in domestic gardens explains the return of reintroduced red kites Milvus milvus to an urban area. Ibis 157:239–249.

Pain, D. J., I. Carter, A. W. Sainsbury, R. F. Shore, P. Eden, M. A. Taggart, S. Konstantinos, L. A. Walker, A. A. Mehard, and A. Raab. 2007. Lead contamination and associated disease in captive and reintroduced red kites Milvus milvus in England. Science of the Total Environment 376:116–127.

Panter, C. T., and A. Amar. 2021. Sex and age differences in the diet of the Eurasian sparrowhawk (Accipiter nisus) using web-sourced photographs: exploring the feasibility of a new citizen science approach. Ibis 163:928–947.

Panter, C. T., S. Xirouchakis, Š. Danko, H. Matušík, P. Podzemný, S. Ovčiariková, and I. Literák. 2020. Kites (Milvus spp.) wintering on Crete. The European Zoological Journal 87:591–596.

Peery, Z. M. 2000. Factors affecting interspecies variation in home-range size of raptors. Auk 117:511–517.

Pérez-García, J. M., A. Margalida, I. Afonso, E. Ferreiro, A. Gardiazábal, F. Botella, and J. A. Sánchez-Zapata. 2013. Interannual home range variation, territoriality and overlap in breeding Bonelli's eagles (Aquila fasciata) tracked by GPS satellite telemetry. Journal of Ornithology 154:63–71.

Pfeiffer, T., and B.-U. Meyburg. 2009. Satellitentelemetrische untersuchungen zum zug- und Überwinterungsverhalten thüringischer rotmilane Milvus milvus. Vogelwarte 47:171–187 [in German].

Pfeiffer, T., and B.-U. Meyburg. 2015. GPS tracking of red kites (Milvus milvus) reveals fledgling number is negatively correlated with home range size. Journal of Ornithology 156:963–975.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15:523–575.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raab, R., I. Literák, C. Schütz, P. Spakovszky, J. Steindl, N. Schönemann, G. Szilvia, G. Tarjányi, L. Peške, K. Makoň, et al. 2017. GPS basierte telemetriestudien an mitteleuropäischen Rotmilanen Milvus milvus—methodische schwierigkeiten und analytische möglichkeitenbasierend auf ersten ergebnissen. Ornithologische Mitteilungen 69:245–260 [in German].

Radi, M., J. J. Iglesias, R. El Khalimchi, J. Martín, K. Rousselon, F. Lorcher, M. Belamine, C. Torralvo, B. Fajardo, I. Farjardo, and J. R. Garrido. 2020. New roosting site of red kite Milvus milvus in the province of Ifrane (Morocco). Go-South Bulletin 17:4–7.

Rolando, A. 2002. On the ecology of home range in birds. Revue D'Ecologie-la Terre et la Vie 57:53–73.

Sambucini, V., I. Marinosci, and N. Bonora. 2010. Analisi dei cambiamenti della copertura ed uso del suolo in Italia nel periodo 2000–2006. Istituto Superiore per la Protezione e la Ricerca Ambientale—ISPRA, Rome, Italy [In Italian].

Schaub, M. 2012. Spatial distribution of wind turbines is crucial for the survival of red kite populations. Biological Conservation 155:111–118.

Schwitter, P. 2020. Determinants of stopover sites of migrating Swiss red kites (Milvus milvus). Thesis, University of Zurich, Department of Geography, Zurich, Switzerland.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Seoane, J., J. Viñuela, R. Díaz-Delgado, and J. Bustamente. 2003. The effects of land use and climate on red kite distribution in the Iberian Peninsula. Biological Conservation 111:401–414.

Sergio, F., J. Blas, M. Feroro, N. Fernández, J. A. Donázar, and F. Hiraldo. 2005. Preservation of wide-ranging top predators by site-protection: black and red kites in Doñana National Park. Biological Conservation 125:11–21.

Sergio, F., A. Tanferna, J. Chicano, J. Blas, G. Tavecchia, and F. Hiraldo. 2019. Protected areas under pressure: decline, redistribution, local eradication and projected extinction of a threatened predator, the red kite, in Doñana National Park, Spain. Endangered Species Research 38:189–204.

Shiu, H.-J., K.-I. Tokita, E. Morishita, E. Hiraoka, Y. Wu, H. Nakamura, and H. Higuchi. 2006. Route and site fidelity of two migratory raptors: grey-faced buzzards Butastur indicus and honey-buzzards Pernis apivorus. Ornithological Science 5:151–156.

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Skyrpan, M., C. T. Panter, W. Nachtigall, R. Riols, G. Rystad, J. Škrábal, and I. Literák. 2020. Kites *Milvus migrans lineatus* (*Milvus migrans migrans/lineatus*) are spreading west across Europe. Journal of Ornithology 162:317–323.

Smart, J., A. Amar, I. M. W. Sim, B. Etheridge, D. Cameron, G. Christie, and J. D. Wilson. 2010. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern–the red kite *Milvus milvus*. Biological Conservation 143:1278–1286.

Suh, A., J. O. Kriegs, J. Brosius, and J. Schmitz. 2011. Retroposon insertions and the chronology of avian sex chromosome evolution. Molecular Biology and Evolution 28:2993–2997.

Swihart, B., and J. Lindsey. 2019. gnlm: generalized nonlinear regression models. R package version 1.1.1. https://CRAN.R-project.org/package=gnlm. Accessed 6 Jul 2020.

Tjernberg, M. 1977. Individual recognition of golden eagles *Aquila chrysaetos* in the field, and results of winter censuses in southwest Uppland, central Sweden. Vår Fågelvårld 36:21–32.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B 365:2163–2176.

Tornberg, R., and A. Colpaert. 2001. Survival, ranging, habitat choice and diet of the northern goshawk *Accipiter gentilis* during winter in Northern Finland. Ibis 143:41–50.

Trierweiler, C., W. C. Mullié, R. H. Drent, K.-M. Exo, J. Komdeur, F. Bairlein, A. Harouna, M. de Bakker, and B. J. Koks. 2012. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. Journal of Animal Ecology 82:107–120.

van Eeden, R., D. P. Whitefield, A. Botha, and A. Amar. 2017. Ranging behaviour and habitat preferences of the martial eagle: implications for the conservation of a declining apex predator. PLoS One 12:e0173956.

van Winkle, W. 1975. Comparison of several probabilistic home range models. Journal of Wildlife Management 39:118–123.

Vasilakis, D. P., D. P. Whitefield, S. Schindler, K. S. Poirazidis, and V. Kati. 2016. Reconciling endangered species conservation with wind farm development: cinereous vultures (*Aegypius monachus*) in south-eastern Europe. Biological Conservation 196:10–17.

Villafuerte, R., J. Vinuela, and J. C. Blanco. 1998. Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain. Biological Conservation 84:181–188.

Viñuela, J. 1997. Road transect as a large-scale census method for raptors: the case of the red kite *Milvus milvus* in Spain. Bird Study 44:155–165.

Viñuela, J., R. Martí, and A. Ruiz. 1999. El milano real en España. SEO/BirdLife, Madrid, Spain. [in Spanish].

Watson, J. W., A. A. Duff, and R. W. Davies. 2014. Home range and resource selection by GPS-monitored adult golden eagles in the Columbia Plateau Ecoregion: implications for wind power development. Journal of Wildlife Management 78:1012–1021.

World Bank. 2021. World Development Indicators: France. https://databank.worldbank.org. Accessed 20 Jul 2021.

Zduniak, P., M. Bocheński, and G. Maciorowski. 2021. How littered are birds' of prey nests? Study of two sympatric species. Science of the Total Environment 790:148079.

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