

JOURNAL OF AVIAN BIOLOGY

Research article

Sex, landscape diversity and primary productivity shape the seasonal space use of a migratory European raptor

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Journal of Avian Biology

2022: e02925

doi: 10.1111/jav.02925

Subject Editor:

Judy Shamoun-Baranes

Editor-in-Chief: Jan-Åke Nilsson

Accepted 25 July 2022



Intrinsic and extrinsic drivers shape the space use of wide-ranging raptors. A large proportion of raptors are migrants that shift their activity ranges between summer and winter habitats, where they encounter different environmental conditions. Analysing the effects of intrinsic and extrinsic drivers on the space use in summer and winter habitats provides crucial insights into the ecology of migratory raptors. Here, we investigated the seasonal space use by 43 red kites *Milvus milvus* tracked by GPS-transmitters across central and south-western Europe over seven consecutive years. We compared space use patterns, i.e. activity range sizes and mean daily distances of the birds between summer and winter, and analysed the influence of extrinsic (landscape diversity, primary productivity) and intrinsic factors (sex). Within summer, we investigated the influence of breeding success and sex on activity range sizes. We further analysed differences in habitat availability and habitat selection between seasons. We found that space use was smaller in summers than in winters. When compared to those of males, activity ranges of female red kites were larger in summers and smaller in winters, with shorter mean daily distances in both seasons. Within summer, successfully breeding red kites had smaller activity range sizes in both sexes, but this effect was stronger in females than in males. Regardless of the season, landscape diversity was positively correlated with space use, whereas primary productivity was negatively correlated with it. The habitat use differed between seasons, with agricultural landscapes being less proportionally used in summers than in winters. Overall, we showed that both intrinsic and extrinsic drivers shaped space use in both seasons, leading to differences in space use patterns and habitat use in migratory raptors between their summer and winter habitats. Our findings underline the importance of consideration of the entire annual cycle of migratory species for conservation management.

Keywords: activity ranges, habitat use, migration, movement ecology, summer habitat, winter habitat



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Introduction

Through their ability to fly, birds are highly mobile animals. Their space use is influenced by several extrinsic drivers, such as the availability and distribution of resources, and intrinsic drivers, such as sex or reproductive status (Nathan et al. 2008, La Sorte et al. 2014, Tucker et al. 2019). By understanding these drivers and their influence on space use, we can derive important information on mortality or reproduction, for example, and thus ultimately draw conclusions about the population dynamics of these mobile animals (Nathan et al. 2008, Morales et al. 2010).

About 19% of all bird species are migrants that shift their activity ranges (ARs) between summer and winter habitats to live in an environment that promotes survival (Kirby et al. 2008). By intersecting movement data of migrants with satellite-derived land cover data or vegetation indices, extrinsic drivers of space use across large spatial scales can be assessed (Trierweiler et al. 2013, La Sorte et al. 2014, Tucker et al. 2019, Mirski et al. 2021). Migrating birds follow resources, which they can explore over large spatial scales (Klaassen et al. 2010, La Sorte et al. 2014). The extent of space use further depends on landscape diversity, as more diverse landscapes provide more resources within smaller ranges (Tews et al. 2004, Tucker et al. 2019, Mirski et al. 2021). Likewise, the availability of key habitats (e.g. grasslands used for hunting) has been directly linked to space use in birds, as increasing proportions of key habitats lead to decreasing AR sizes (Mirski et al. 2021).

In addition to these extrinsic drivers, intrinsic drivers such as territoriality and reproduction also influence space use (Brodin et al. 2003, Hernández-Pliego et al. 2017, Mirski et al. 2021). During the breeding season many bird species, especially raptors, show a reproductive role specialization between sexes, with females incubating the eggs and males providing food, which often results in smaller ARs of females compared with those of males (Wesolowski 1994, Brodin et al. 2003, Pfeiffer and Meyburg 2015, Hernández-Pliego et al. 2017, Spatz et al. 2019, Mirski et al. 2021). Breeding success is also known to be correlated with the AR size in birds, especially that of the male parent (Pfeiffer and Meyburg 2015). Sex-specific differences in space use may disappear at the end of the breeding season, e.g. when both sexes are engaged in chick rearing; or at the end of the summer, shortly before autumn migration begins (Brodin et al. 2003, Hernández-Pliego et al. 2017, Spatz et al. 2019).

Beside such variations in space use within seasons, there are also variations between seasons. For example, the wood thrush *Hylocichla mustelina* prefers smaller forest patches during the breeding season (summer), but larger forest patches during winter (Stanley et al. 2021). Male Montagu's harriers *Circus pygargus* fly shorter distances during winter than during summer, while females show the opposite space use pattern (Schlaich et al. 2017). Similarly, Spanish imperial eagle *Aquila adalberti* ARs during the non-breeding season (winter) are smaller than during the breeding season (summer) (Fernández et al. 2009). By intersecting seasonal movement

data with extrinsic and intrinsic drivers, we expect to gain a better understanding of the ecology of migratory birds.

Approximately 25% of the raptors in Africa and Eurasia are migratory (Goriup and Tucker 2007). As they have comparably large body sizes and are often top predators, raptors have extensive space requirements and are frequently used as flagship species in conservation, which makes them a suitable study group for seasonal movement (Peery 2000, Sergio et al. 2006). We used the red kite *Milvus milvus*, a short-distance migratory raptor and a generalist forager, as the model species to compare the space use patterns of both sexes during summer and winter. Like many raptors, red kites show a strong breeding-site fidelity during summer and site fidelity during winter (Jenkins and Jackman 1993, Shiu et al. 2006, Aebischer 2009, Trierweiler et al. 2013, Pfeiffer and Meyburg 2015; own observation). They are central-place foragers that show reproductive role specialization between the sexes, which is reflected in their movement during the breeding season in summer (Heuck et al. 2013, Pfeiffer and Meyburg 2015, Mirski et al. 2021). Furthermore, although red kites are territorial during the breeding season, they show communal roosting in the late post-breeding period during summer and during winter, as well as communal foraging in highly attractive foraging grounds (Aebischer 2009). Using GPS-data of 43 adult red kites (16 females, 27 males), collected over five summers and six winters, we calculated ARs and mean daily distances (MDs), and related these to landscape parameters, namely landscape diversity and primary productivity, of summer and winter habitats. We further compared the habitat availability within the ARs and the habitat selection between seasons.

Effect of landscape diversity, primary productivity and season on activity range (AR) and daily distance

Owing to the communal roosting in winter and the territoriality of red kites during summer, we expected (1a) larger ARs and daily distances during winter than during summer, but (1b) the ARs and daily distances to decrease with increasing landscape diversity and increasing primary productivity, regardless of the season. Owing to the reproductive role specialization of red kites during the breeding season, we expected (1c) no differences between sexes during winter, but smaller ARs and daily distances for females than for males during summer. Within summer, we expected (1d) the ARs of non-breeders or unsuccessfully breeding red kites to be larger than those of successfully breeding individuals; however, within successfully breeding red kites, the AR of females should be smaller than that of males.

Differences in habitat availability and habitat use between seasons

As winter and summer habitats of red kites are located in distinct areas with different landscape features, we expected (2a) differences in the availability of various land-use types within the ARs between summer and winter habitats, and checked for individual preferences in the habitat availability that persisted over seasons (e.g. high amounts of grassland within the AR of

an individual in winter and summer habitats). In the second step, we analysed the habitat use of certain land-use types by red kites and compared them between seasons. We expected (2b) land-use types significant for foraging (agricultural landscapes and grasslands) to be used with similar intensity during summer and winter, while the land-use types significant for nesting (forests) to be used more in summer than in winter.

Material and methods

Study species

The red kite is a diurnal raptor, and endemic to Europe. Its population is estimated to consist of 32 200–37 700 breeding pairs (BirdLife International 2020). Of these, 14 000–16 000 pairs breed within Germany, which corresponds to 37–50% of the world population (Grüneberg and Karthäuser 2019). The red kite forages mainly in agricultural landscapes and grasslands as well as in smaller settlement areas (Aebischer 2009, BirdLife International 2020). It feeds opportunistically on small mammals, smaller birds, fish, insects and carrion (Aebischer 2009, Bischofberger et al. 2019, BirdLife International 2020). The red kite nests in trees near forest edges or in rows of single trees and shows a high breeding-site fidelity (Aebischer 2009, Gelpke and Hormann 2010). The red kite shows reproductive role specialization: the female incubates the clutch and broods the nestlings, and only when they are about two to three weeks old does it help with the search for food. Meanwhile, the male provides most of the food for the female during incubation, and for nestlings during chick rearing period (Aebischer 2009, Pfeiffer and Meyburg 2015). Territoriality weakens shortly before the start of migration, when red kites often spend the night at communal roosts (Aebischer 2009, Spatz et al. 2019). Such communal roosts are also used, but often changed irregularly in the wintering habitats, where at least some red kites show site fidelity over several years (Pfeiffer 2009; own observations).

Data collection

The summer habitats of all animals studied were in the German federal states of Hesse, Thuringia, Saxony and Lower Saxony. These states are reported to represent 30% of the German red kite population (Grüneberg and Karthäuser 2019). The winter habitats were in different regions of Spain ($n = 60$), France ($n = 17$) and Portugal ($n = 5$; Fig. 1).

During the breeding seasons of 2014–2019 we fitted GPS-transmitters to 43 adult red kites (16 female, 27 male). All birds were caught during chick rearing in proximity to their nests using the dho-gaza method with a stuffed eagle owl *Bubo bubo* as a lure (Bloom et al. 2007). We measured the wing length and mass of the captured birds and banded them with individual rings from the respective bird ringing centre. Sex was determined by the measures and the presence of a brood patch.

The GPS-transmitters were fitted to the backs of the birds with a backpack harness made of Teflon ribbon. We used two

different GPS-transmitter types: e-obs SOLAR-GPS-ACC and Ornitela E-20-B or OT-E25B. All transmitters were equipped with an integrated battery and a solar panel for power supply. The frequency of GPS-fixes by the transmitters depended on the battery level and varied from five minutes to eight-hour intervals during daytime. Each individual provided data for one to eight seasons from winter 2014 to summer 2020.

Additionally, we recorded the individual annual breeding success, defined as at least one successful juvenile fledging from the nest. The assessment of the breeding success depended on the local conditions. Wherever possible, and only if the necessary permits were available, trained tree climbers accessed the nests of the red kites to measure the chicks and band them with rings from the respective bird ringing centre. On inaccessible nests we determined their breeding success with suitable optical aids. Breeding success data were available for 53 of the 59 summer datasets and consisted of 19 female summers (12 individuals) and 34 male summers (22 individuals), with 30 successful (12 females, 18 males) and 23 unsuccessful (7 females, 16 males) breeding attempts. The latter included 4 different individuals (1 females, 3 males) that each did not breed in one year.

Processing of movement data

The initial step of data processing comprised the clean-up and standardisation of the movement data. All duplicates (same timestamp and same position), zero coordinates (no GPS signal received), as well as positions with speeds above 30 m s^{-1} (faulty GPS acquisition; outliers) were excluded. As the frequency of data acquisition depended on the battery level, we aligned the minimum time interval between two coordinates to $60 \pm 15 \text{ min}$ to equalise the data density between individuals, resulting in an average of 16 ± 2 fixes per individual per day during summer and 9 ± 2 fixes per individual per day during winter. These number of fixes per individual per day hardly varied between the years (Supporting information). In total we used 270 781 data points, distributed over 141 individual-season combinations (82 winter and 59 summer) collected by 43 individuals over eleven year-season combinations (winter 2014/2015 to winter 2019/2020).

Delimitation of winter/summer habitats

We defined the stay in their winter or summer habitats as the timespan between the first day after the end of migration and the last day before the start of the consecutive migration, for each individual separately. Most red kites left their summer habitats mid/end of September, while some individuals left not before November or December in single years. The same could be applied to spring migration as most red kites left their winter habitats mid/end of February, but some individuals had already started spring migration in January, while others not before March. Due to this high individuality, we used the data from August to January and December to April to determine the individual start and end dates of migration.

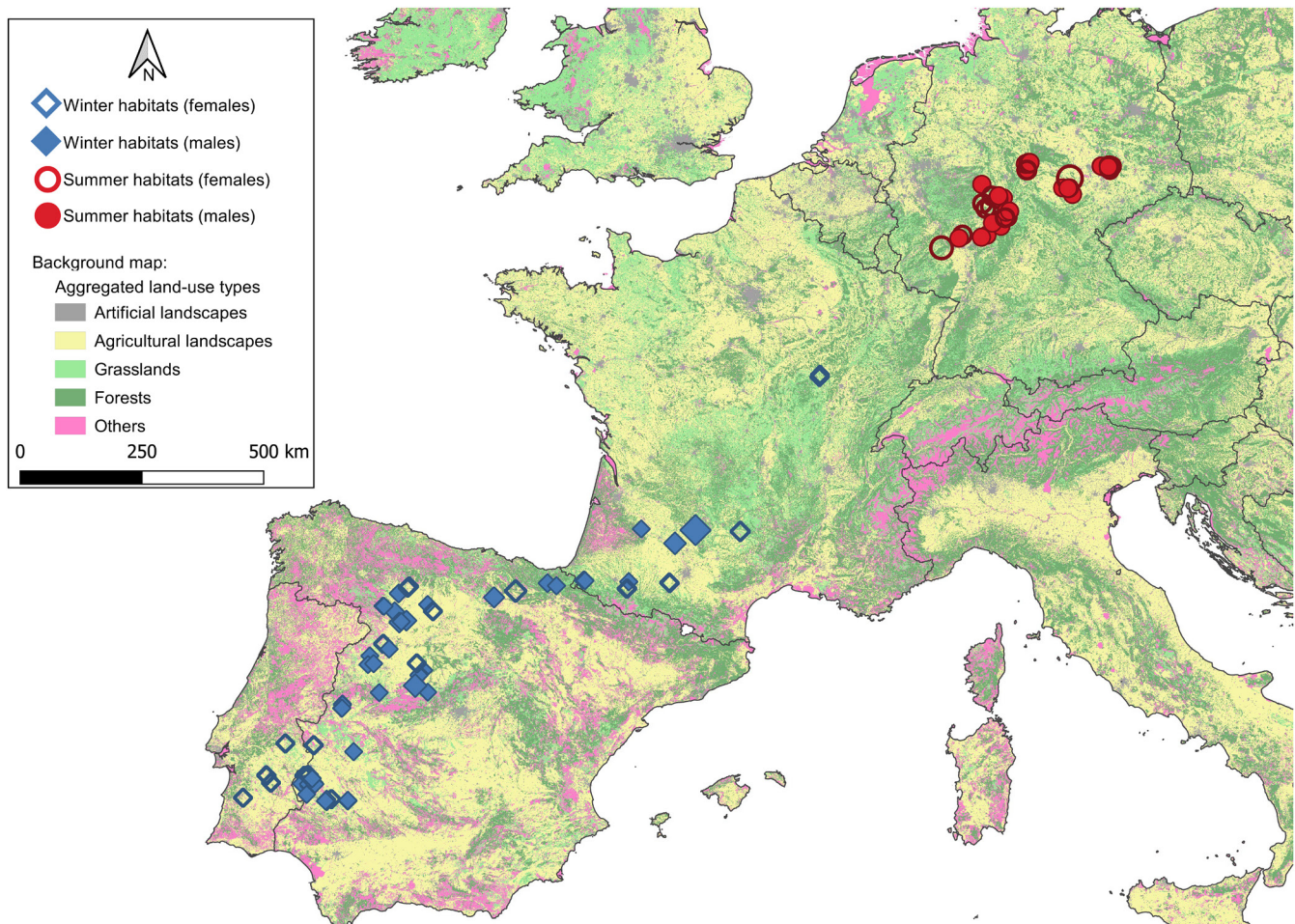


Figure 1. Distribution of the summer and winter habitats of 43 red kites over 141 individual-year-season combinations within seven years (winter 2014/2015 to winter 2019/2020). Given are the centroids of the respective activity ranges (ARs). Red points and blue diamonds refer to summer and winter habitats, respectively. Unfilled points/diamonds correspond to females, and filled points/diamonds to males. The size of points/diamonds corresponds to the respective AR size. The background map shows the aggregated land-use types, based on CORINE Land Cover 2018 data (<<https://land.copernicus.eu/pan-europe/corine-land-cover/clc2018>>).

To determine these dates, we conducted broken stick regressions, a data-driven approach that is related to change point analysis, which has already been successfully used for other migratory bird species (Limíñana et al. 2008, Soriano-Redondo et al. 2020). For each individual we calculated the straight-line distance between all consecutive locations within one day to determine the daily distance covered by the individual and summed it cumulatively over time. When plotting the cumulative daily distance over time, abrupt behavioural changes became visible as breaks in the curve. For example, the curve showed a steeper slope during migration as the individual daily distance was higher. We identified the breaks that referred to start and end of the individual migration by using the *segmented* package in R (Muggeo 2008).

The method had its limitations when the movement data showed gaps due to low battery level; no reception of GPS signal; or if an individual changed its whereabouts irregularly, a behaviour that was shown by some individuals, especially in winter habitats. In such cases we determined the beginning and end of migration using a combination of visual inspection

of the data and daily displacement of an individual, calculated as straight-line distance between the first and last location of a day. If the daily displacement was more than 50 km, we declared the day as a migration day. To ensure that we do not falsely define a stop-over as a stay in the winter habitat, especially when individuals changed their whereabouts irregularly, we only used the longest timespan without migratory movements as a stay in the individual winter habitat. On average, the stay in the summer habitats lasted for 221 ± 19 days (mean \pm standard deviation (SD); range: 157–270 days) and that in the winter habitat lasted for 94 ± 25 days (mean \pm SD; range: 26–136 days).

Calculation of the activity ranges (ARs) and mean daily distances (MDs)

We determined the AR for each individual-year-season combination with the *akde*-function in *ctmm* R (Calabrese et al. 2016). This method provides three different movement models that can be used to calculate an AR: the

Ornstein-Uhlenbeck Foraging (OUF) model, the Ornstein-Uhlenbeck (OU) model and the independent identically distributed (IID) model. Like other models, there are pre-assumptions on the data to use the respective model. In the OUF model the positions and the velocity of the data need to be autocorrelated. In the OU model only the positions, but not the velocity, need to be autocorrelated; and in the IID model neither positions nor velocity should be autocorrelated (Calabrese et al. 2016). Due to the subsampling of our data to 60 ± 15 min, the spatiotemporal autocorrelation in our data was weak. Furthermore, as some adult red kites constantly shifted between roost sites during winter on a relatively large scale, the use of OU or OUF models led to an overestimation of the used area in these individuals. To be able to compare the ARs of all individuals over seasons we needed to choose a model that fits to all of them and has no restrictive pre-assumptions some of the individuals' data might not meet. We therefore used an independent identically distributed model to calculate autocorrelated kernel density estimations (AKDEs), which determined the ARs closest to the respective data points, and therefore suited the data best. However, it does not account for autocorrelation and is therefore equivalent to the calculation of utilization distributions with Kernel density estimation (KDE; Calabrese et al. 2016). All further analyses were based on the core 95% of the ARs to exclude single explorative flights.

For each individual and all days with more than three fixes, we calculated the straight-line distances between all consecutive locations within a day and summed them to determine the daily distances. These daily distances were averaged to an MD for each individual-year-season combination.

Environmental data

Our analyses regarding landscape diversity, habitat availability and habitat use were based on CORINE Land Cover 2018 (CLC), funded by the European Union. This dataset divides the European surface into 100×100 m grid cells and classifies them into 44 different land-use types (Büttner et al. 2017). Our study area had 38 of the 44 land-use types. As we aimed to compare the habitat availability within the ARs and the use of land-use types between seasons, we merged the observed land-use types into five aggregated land-use types of higher order to achieve comparability between the summer and winter habitats of red kites. We chose the following five aggregated land-use types as they reflect very distinct habitats that are relevant for red kites. Agricultural landscapes and grasslands are the main foraging habitats of red kites (Aebischer 2009). Forests, especially the forest edges, are at least partly used by red kites as breeding habitats (Aebischer 2009). Artificial surfaces are mainly areas with high amounts of sealed grounds and high human population densities, which red kites usually avoid (Hessische Gesellschaft für Ornithologie und Naturschutz 2010, Heuck et al. 2013). All other occurring less common land-use types were combined in the land-use type others (see Supporting information for detailed description of the aggregated land-use types). In the

following, we determined the proportions of each of the five aggregated land-use types within the ARs of all individual-year-season combinations.

Landscape diversity has already been linked successfully to the ARs of generalist raptors (Navarro-López and Fargallo 2015, Mirski et al. 2021). Hence, we used the proportions of the aggregated land-use types within the ARs to calculate the Shannon diversity index for the ARs of all individual-year-season combinations. However, as landscape diversity is likely to increase with increasing range or distance covered, we ran linear models investigating the relationship between Shannon diversity as dependent variable and ARs and MDs, respectively, as explanatory variable. The residuals of these models mirror the variance in landscape diversity that is not explained by AR or MD, respectively. We used these residuals in our final models (below) and refer to them as landscape diversity in the following. All values were centred and scaled.

To assess the primary productivity within the ARs of the red kites, we used normalized difference vegetation index (NDVI) data. NDVI is the most common proxy for primary productivity (Fernández-Tizón et al. 2020). NDVI has already been linked successfully to the abundance of arthropods or small mammals, as primary and secondary productivity are positively correlated (Trierweiler et al. 2013, Smith et al. 2016, Fernández-Tizón et al. 2020). We therefore assume NDVI to be a good proxy for food availability for a generalist like the red kite. NDVI data were derived from PROBA-V NDVI collection 300 m, generated by the land service of Copernicus, the Earth Observation program of the European Commission. It is 10-days composite raster data with a grid cell size of 300×300 m, available for the entire study period. We extracted the NDVI values that occurred within the ARs at the time of use and calculated a mean NDVI for each individual-year-season combination. All values were centred and scaled before fitting the models.

Effect of landscape diversity, primary productivity and season on activity range (AR) and daily distances

(1a–c) Based on the data of 141 individual-year-season combinations provided by 43 adult red kites, we compared the AR sizes and MDs between winter and summer, and assessed the impact of landscape diversity and primary productivity on them, while taking sex-specific differences into account. Therefore, we used generalized linear mixed effect models (*glmmTMB* R package, Brooks et al. 2017), with individual as a random factor and Gaussian distribution in the log-transformed response variables. As fixed effects, we integrated season, sex, landscape diversity and mean primary productivity within the ARs, as well as their interactions with season. In the MD model, we further integrated the number of data points per day as offset, as the calculation of the daily distance is sensitive to the number of points used for the calculation. For each model we performed backwards model selection based on effect sizes/z-values.

(1d) Based on a subset of the data (53 summers) for which information about the breeding success was available, we tested the effect of breeding success on the summer ARs of adult red kites, taking sex-specific differences into account. For this, we used a linear mixed effect model (*lme4* R package; Bates et al. 2014) with the log-transformed summer AR sizes as response variable. The explanatory variables sex and breeding success were used as binary variables (1: breeding success, 0: no breeding success). The individual was added as random factor.

Differences in habitat availability and habitat use between seasons

For all individuals with data of at least one summer and one winter ($n=33$ individuals), we determined habitat availability and habitat use based on the five aggregated land-use types. As red kites show site fidelity in winter and summer habitats, and the number of seasons per individual ranged from one to eight, the availability and use of certain land-use types could have been over- or underestimated. Therefore, we determined the mean habitat availability within the ARs as well as the mean habitat use for each individual separately for summer and winter, as described hereafter. We determined the individual-specific habitat availability as proportions of the five aggregated land-use types present within the individual ARs and used them to calculate the individual mean habitat availability during winter and summer. To evaluate the individual-specific habitat use, we determined the proportions of the five aggregated land-use types present at the 270 781 GPS locations and used them to calculate the individual mean habitat use during winter and summer.

(2a) To determine differences in the availability of the different land-use types within the ARs between summer and winter, we used non-metric multidimensional scaling (NMDS). We calculated the Bray–Curtis distances, a dissimilarity measure to detect ecological gradients, based on the individual mean habitat availability within the respective winter and summer ARs (Faith et al. 1987). We Hellinger-transformed these distances and arranged them in a three-dimensional space (*metaMDS*-function in *vegan* package, Oksanen et al. 2020). With a subsequently performed ANOSIM (*vegan* package, Oksanen et al. 2020) we checked for significant differences in the habitat availability between winter and summer.

(2b) To assess if individual preferences in habitat availability persist over seasons (e.g. individuals with high amounts of grassland available in summer habitats prefer high amounts of grassland available also in winter habitat), we used the function *protest* of the *vegan* package, to perform a subsequent Procrustes analysis (Oksanen et al. 2020). The Procrustes analysis rotates the habitat availability of the two seasons based on the data score matrices gained by the NMDS performed earlier, and tries to maximize similarity between them. The *protest*-function does this repeatedly and estimates the significance (Oksanen et al. 2020). A match between the two matrices in our case would mean that there are individual

preferences in the availability of certain habitats that persist over seasons.

(2c) To compare the habitat use of red kites between their winter and summer habitats, we compared the individual mean habitat availability with the individual mean habitat use in both winter and summer. Therefore, we calculated Manly's selectivity index (ω_i) for each of the five aggregated land-use types by dividing the individual mean use of a land-use type by the individual mean availability of the respective land-use type in winter and summer. If $\omega_i=1$, the use corresponds to the availability of the land-use type. If $\omega_i > 1$, the use is over-proportional to the availability; hence, there is a preference of an individual for this land-use type. If $\omega_i < 1$, the usage is under-proportional; hence, there is an avoidance of an individual for this land-use type. To test if within seasons a land-use type was used significantly more or less than expected from its availability, we compared the distribution of ω_i -values of each land-use type against 1, using a Wilcoxon test for non-normally distributed data. With additional Wilcoxon tests we compared the ω_i -values of each land-use type between seasons to identify differences in the use of the five aggregated land-use types between summer and winter habitats.

Results

We compared the space use and habitat selection of migratory red kites between summer and winter habitats. The AR size ranged from 2.6 km² to 13 504.0 km² during summer and from 7.9 km² to 33 337.1 km² during winter (see Supporting information for a distribution plot of the AR data 3). The MD flown by adult red kites ranged from 5.0–34.3 km to 5.4–49.9 km in summer and winter, respectively (Table 1).

Effect of landscape diversity, primary productivity and season on activity ranges (ARs) and daily distances

Our models were able to explain a considerable proportion of the variability in space use of red kites using the intrinsic and extrinsic factors (38–54%; Table 2).

(1a) AR sizes and MDs of red kites were smaller during summer than during winter (Table 2).

(1b) AR sizes and MDs rose with increasing landscape diversity, but decreased with increasing primary productivity (Table 2).

(1c) In both seasons, the MDs of females were shorter than those of males. The ARs of females in winter were smaller than those of males, but larger than those of males during summer (Table 2, Fig. 2).

(1d) In summer the ARs of successfully breeding red kites were smaller than those of non-breeders or unsuccessfully breeding individuals. Within the successfully breeding red kites, the AR sizes hardly differed between sexes, whereas unsuccessfully breeding red kite females showed larger ARs than males (Fig. 3, Table 3 and 4). The model explained 67.7% of the variance in the data.

Table 1. Activity range (AR) sizes [km²] and mean daily distances (MDs) [km] of 141 individual-year-season combinations provided by 43 adult red kites during winter and summer. Range (min, max, quantiles), median and mean with SD are given for both sexes [♀♀ = females, ♂♂ = males], separately.

	Activity range sizes [km ²]						Mean daily distances [km]					
	Min	Qu ^{0.25}	Median	Qu ^{0.75}	Max	Mean ± SD	Min	Qu ^{0.25}	Median	Qu ^{0.75}	Max	Mean ± SD
Winter												
♀	7.9	55.9	101.1	196.1	8880.6	115.7 ± 4.9	5.4	10.4	14.8	17.5	42.9	13.6 ± 0.002
n=28												
♂	13.2	72.5	280.5	655.3	33 337.7	288.9 ± 6.3	7.6	13.2	19.3	27.7	49.9	18.8 ± 0.002
n=54												
Summer												
♀	2.6	8.8	16.7	66.0	13 504.0	36.0 ± 10.8	5.0	7.5	8.8	11.0	31.7	9.4 ± 0.002
n=19												
♂	3.1	8.5	13.2	23.3	649.5	15.9 ± 2.8	7.3	11.3	14.3	15.6	34.3	13.9 ± 0.001
n=40												

Differences in habitat availability and habitat use between seasons

(2a) The habitat availability of the various land-use types within the ARs differed between winter and summer (NMDS: $k=3$, stress = 0.08; ANOSIM: $R=0.22$, $p=0.001$, permutations = 999; Supporting information). There were no individual preferences in habitat availability that persisted over seasons (Procrustes analysis: $r=0.13$, $p=0.77$, permutations = 999). The dominating land-use type within the ARs in both seasons were agricultural landscapes, followed by grasslands and forests in different order (Fig. 4).

(2b) In summer habitats, red kites used artificial landscapes and others significantly less than expected from availability (Wilcoxon tests: $p_{\text{artificial}} = 0.001$, $p_{\text{others}} = 0.003$). In winter habitats, red kites used artificial landscapes, forests and others significantly less, but agricultural landscapes significantly more than expected from availability (Wilcoxon test: $p_{\text{artificial}} < 0.001$, $p_{\text{agricultural}} = 0.005$, $p_{\text{forest}} < 0.001$, $p_{\text{other}} < 0.001$; Fig. 4; Supporting information).

While red kites used grasslands and forests in similar intensity in both seasons, agricultural landscapes were used significantly less during summer than during winter (Wilcoxon tests: $p_{\text{grassland}} = 0.49$, $p_{\text{forest}} = 0.07$, $p_{\text{agricultural}} = 0.03$). There were no differences between seasons in the use of the remaining land-use types.

Discussion

Our findings show that ARs and the MDs of red kites were larger in winter than in summer, were associated with both landscape diversity and primary productivity, and differed between sexes. While ARs and MDs increased with increasing landscape diversity, they decreased with increasing primary productivity. Females had shorter MDs than males, regardless of the season. Female red kites used smaller ARs than males during winter, while the opposite was the case during summer. During summer, the ARs of successfully breeding red kites were smaller than those of unsuccessful ones or non-breeders. The habitat availability within the ARs and the use of agricultural landscapes differed between seasons.

Effect of landscape diversity, primary productivity and season on activity ranges (ARs) and daily distances

As expected, and in line with other birds of prey such as the golden eagle *Aquila chrysaetos* and the Spanish imperial eagle *A. adalberti*, the sizes of ARs and MDs of migratory red kites were smaller during summer than during winter (Marzluff et al. 1997, Fernández et al. 2009). It is likely that these patterns are driven at least partly by their territoriality

Table 2. Model output for the generalized linear mixed models (GLMM) relating the log(AR sizes [km²]) and the log(MDs [km]) of 141 individual-year-season combinations provided by 43 adult red kites to season, sex, landscape diversity (Shannon diversity) and primary production (NDVI, normalized difference vegetation index). Shown are the estimates of the resulting coefficients, their standard errors (SE) and test statistics. AR, activity range; MD, mean daily distances.

	log(activity range sizes [km ²])				log(mean daily distances [km])			
	Estimate	SE	z-value	p-value	Estimate	SE	z-value	p-value
(Intercept)	3.86	0.43	9.01	< 0.001***	6.60	0.10	67.10	< 0.001***
Season (winter)	0.99	0.41	2.41	0.016*	0.74	0.05	13.49	< 0.001***
Sex (♂)	-1.05	0.52	-2.02	0.044*	0.23	0.12	1.97	0.049*
Shannon diversity	0.51	0.15	3.46	< 0.001***	0.13	0.03	4.25	< 0.001***
NDVI	-0.34	0.15	-2.22	0.026*	-0.13	0.03	-3.89	< 0.001***
Season (winter): Sex (♂)	1.73	0.47	3.67	< 0.001***				
Random effect (individual)		Variance		SD		Variance		SD
		1.18		1.09		0.10		0.32
		R ² marginal: 38.2%				R ² marginal: 53.7%		
		R ² conditional: 64.4%				R ² conditional: 81.8%		

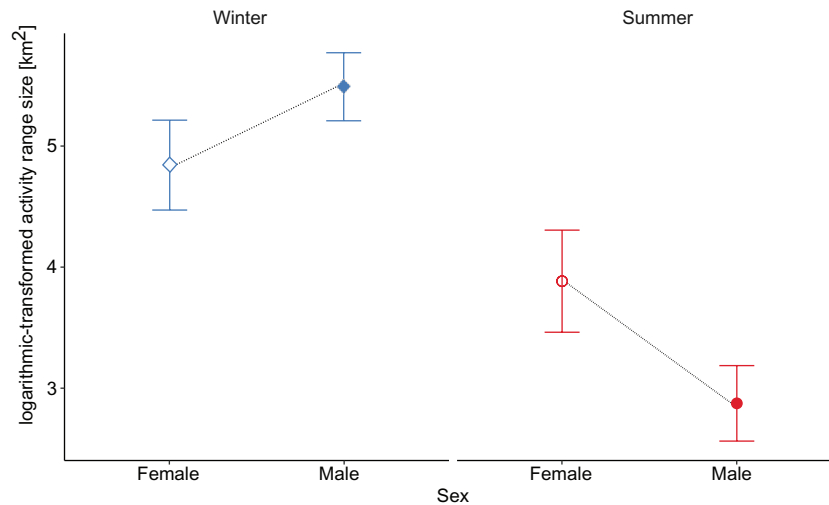


Figure 2. Effect plot of the generalized linear mixed model used to compare the sizes of the activity ranges (ARs) between seasons: red points (summer) and blue diamonds (winter) mark the estimates, bars show the standard error given by the model. During summer, the ARs of female red kites (unfilled) were larger than those of males (filled). Conversely, during winter, females showed smaller ARs compared to male red kites.

during summer. Although territories are blurred after fledging, the distance of red kites to their nest hardly changes throughout summer (Spatz et al. 2019). Hence, territoriality of red kites persists during the entire summer, and lessens only shortly before the start of migration when the red kites still spend some nights in their territories but also start using communal roosts. Given the duration of time at the summer habitats, these comparatively few night outs at communal roosts do not carry any weight in the calculation of the AR sizes. Wintering red kites, however, tend to change communal roosts irregularly, leading to larger ARs (Heredia et al. 1991, Aebischer 2009). Moreover, as residential and wintering red kites co-occur in winter habitats, there is a high intra- and interspecific competition for food, which affects space use (Powell 2000, Bildstein 2004). The larger ARs of red kites

in winter could, therefore, also be driven by the competition for food sources, as wintering red kites use different habitats from residents (Heredia et al. 1991). Similar to the residential red kites, in which males made higher use of ecotones and cultivated fields while showing larger ARs and daily distances than females, the use of different food sources could also be a possible explanation for the larger ARs of males compared to females in winter (Heredia et al. 1991). However, in contrast to our expectations, in summer, female red kites used larger ARs than males. Larger ARs of females than those of males in summer were also reported for lesser spotted eagles *Clanga pomarina* (Mirski et al. 2021). The authors explained this with a lower territoriality of females and a higher number of explorative visits in other territories and nests, potentially to find territories of better quality. Male red kites, however,

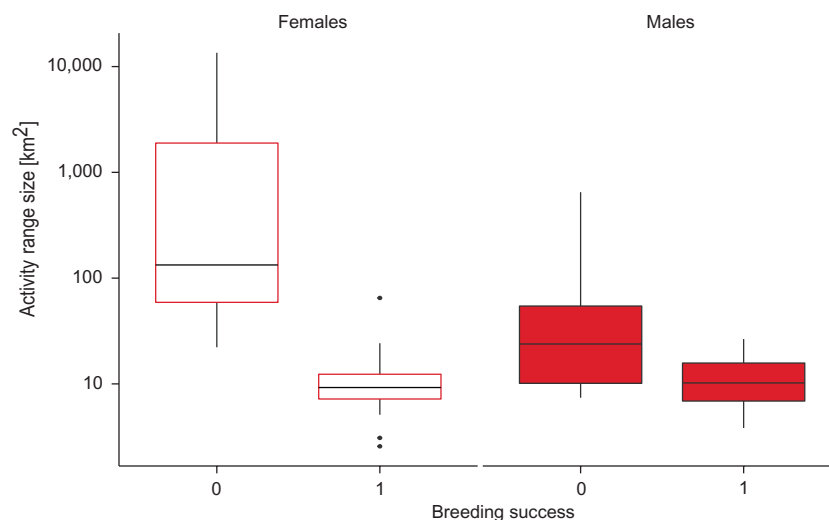


Figure 3. Variation in activity range (AR) sizes of 34 adult red kites in summer: red kites with breeding success showed smaller ARs than those without breeding success. The AR size of females that were unsuccessful in breeding increased more than that of unsuccessfully breeding males (Table 3). Note the logarithmic scale of the y-axis.

Table 3. Activity range (AR) sizes of successfully and unsuccessfully breeding red kites during summer, based on breeding success data of 53 summers provided by 12 female and 22 male red kites. Range (min, max and quantiles), median and mean with SD are given for both sexes [♀ = females, ♂ = males].

	Activity range sizes [km ²]					
	Min	Qu ^{0.25}	Median	Qu ^{0.75}	Max	Mean ± SD
Successfully breeding						
♀	2.6	7.2	9.2	12.3	64.9	9.7 ± 2.4
n = 12						
♂	3.8	6.9	10.2	15.7	26.5	10.6 ± 1.8
n = 18						
Unsuccessfully breeding						
♀	22.2	59.0	133.2	1892.3	13 504.0	337.4 ± 12.4
n = 7						
♂	7.4	10.1	23.8	54.5	649.5	29.9 ± 3.4
n = 16						

are probably more territorial than females. Considering that our study was conducted in one of the distribution centres of the red kite, where relatively high population densities occur, we can assume high numbers of neighbouring red kite territories, which most likely led to a more restricted space use of male red kites in summer. However, for red kites, our finding of larger ARs of females than those of males, contrasts with a previous study by Pfeiffer and Meyburg (2015), which used a slightly different methodological approach.

Taking a closer look at the ARs in summer revealed that their size is strongly affected by the breeding success of the individual: the ARs of successfully breeding red kites were significantly smaller and did not differ between sexes, in contrast to individuals that had lost their brood or were non-breeders in a respective year. Within the latter, the ARs of females increased more than those of males (Fig. 3). In fact, we observed four female individuals that left their territory for a few days or even weeks after they lost their brood. However, since success and failure of broods are natural and regularly occurring events in summer and were present for both sexes in our dataset, we included both of them in our comparative analyses between summer and winter space use. Successfully reproducing red kites showed no difference in the AR size between the sexes in summer. It is known that, during the breeding and nestling period, female red kites partially have a very restricted space use, as they incubate the eggs and start helping with providing food only when the nestlings

are about two to three weeks old (Aebischer 2009, Pfeiffer and Meyburg 2015). However, such a temporally restricted space use of successfully breeding females implies that they also have periods with increased space use demands, resulting in similar ARs for females and males over the whole summer. Telemetry studies on juvenile red kites in Switzerland showed that females typically show more extensive prospecting behaviour than males, during which they visit areas potentially suitable for dispersal (Scherler 2020, Ponchon et al. 2021). This could also apply to older individuals.

Our findings show that there are sex-specific differences in AR sizes and MDs between summer and winter habitats. It remains a challenge for future studies to disentangle to what extent intra- and interspecific competition influences the space use of female and male red kites in summer and winter habitats.

In line with our expectations, AR sizes and MDs decreased with increasing primary productivity (normalized difference vegetation index, NDVI). NDVI has been used as proxy for food availability in many other raptor species, as it can be linked to the abundance of prey species such as arthropods or small mammals (Schaub et al. 2005, Trierweiler et al. 2013, Klaassen et al. 2014, La Sorte et al. 2014, Smith et al. 2016). Hence, the result supports our assumption that NDVI is also a good proxy for resource availability for a generalist like the red kite. Here we chose to aggregate the NDVI to a mean value for the respective individual-year-season combination to compare the conditions in winter and summer habitats on a rather coarse scale, and to evaluate if the red kites respond to it in similar way in both seasons. However, as NDVI is available as 10-day composite data, further studies could focus on linking the variation in space use of red kites to the variability in environment on a higher temporal and spatial scale.

Contrary to our expectations, the AR sizes and the MDs increased with increasing landscape diversity. This finding is counterintuitive for a food opportunist like the red kite, as a diverse landscape should provide various and sufficient resources at a small spatial scale (Tucker et al. 2019, Mirski et al. 2021). However, besides small mammals and birds, large parts of the diet of red kites consists of carrion (Heredia et al. 1991, Bischofberger et al. 2019). Carrion is

Table 4. Model output for the linear mixed effect models relating the log(AR size in km²) of 34 red kites in summer to their breeding success. Shown are the estimates of the resulting coefficients, their standard errors (SE) and test statistics. AR, activity range.

	Estimate	SE	t-value	p-value
(Intercept)	5.83	0.51	11.54	< 0.001***
Sex (♂♂)	−2.47	0.64	−4.02	< 0.001***
Breeding success	−3.58	0.65	−5.54	< 0.001***
Sex (♂♂): Breeding success	2.70	0.79	3.41	0.001**
Random effect (individual)	Variance		SD	
	0.71		0.85	
	R ² marginal: 43.9%			
	R ² conditional: 67.7%			

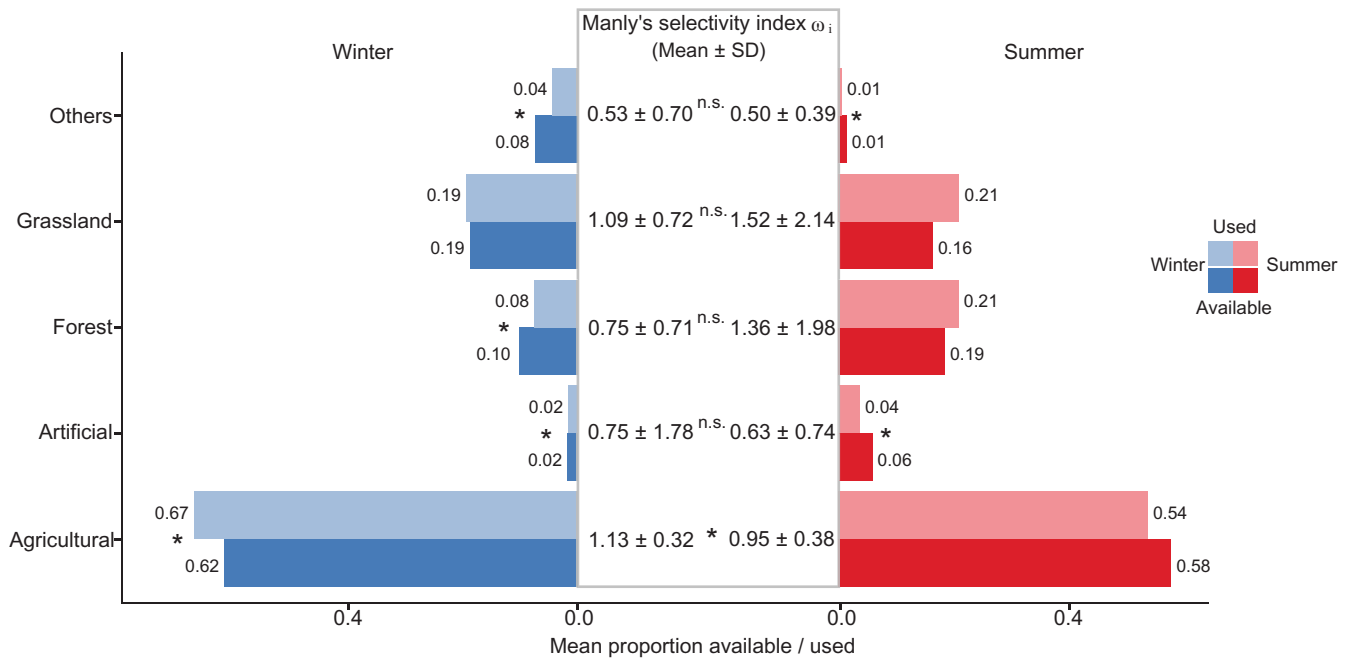


Figure 4. Mean proportion of available (dark) and used (light) land-use types within the activity ranges (ARs) of 33 adult red kites in winter (left/blue) and summer (right/red). We compared the use of the various land-use types within seasons based on Manly's selectivity indices (ω_i) for each land-use type, given as mean \pm SD. We tested for a significantly different use of land-use types than that expected from its availability during the seasons with a Wilcoxon test against 1. Significant differences in use and availability within seasons are marked with * at the bar ends. ω_i were compared between seasons using Wilcoxon tests to identify significant differences in the use of the various land-use types between summer and winter habitats. Significant differences in use and availability between seasons are marked with * in the figure centre. Only agricultural landscapes were used significantly more in winter than in summer (Wilcoxon test: $p=0.03$; Supporting information).

a less predictable and often widely distributed food source and leads to increasing AR sizes in raptors foraging on it (Griffin and Baskett 1985, Rolando 2002). Another explanation for this counterintuitive pattern may be the coarse temporal and spatial resolution of our land-use data. The land-use data used gave the status of habitat availability in 2018; hence, potential variations in land-use types within the seven years of data collection were not considered. Moreover, land-use data comprised only five aggregated land-use types. Hence, higher amounts of relatively unattractive foraging grounds, like forests, led to an increased landscape diversity. Therefore, we might arrive at a different result if the landscape diversity was analysed with focus on the main foraging habitats of red kites: agricultural landscapes, grasslands and smaller settlements. However, this would require more finely resolved spatial and temporal land-use data, which unfortunately were not available over the entire study area and period. As red kites are soaring raptors that hunt visually, preferably over very low vegetation (Wakeley 1978, Aebischer 2009, Mebs and Schmidt-Rothmund 2014, Karthäuser et al. 2019), different growth rates of crops and different harvesting times, as well as the prevalence of interspersed fallows or freshly mown meadows would most likely lead to smaller ARs and shorter distances. Furthermore, artificial food provisioning like dump sites or livestock carcass disposal sites are known to be important

food sources for red kites, especially in their winter habitats (Serrano 1999). Hence, further research with higher resolution land-use data and the inclusion of artificial food sources could help to identify the key landscape elements that shape the space use of red kites in winter and summer habitats.

Differences in habitat availability and habitat use between seasons

The habitat availability within the ARs differed significantly between seasons. In the summer habitats, the five aggregated land-use types occurred more balanced compared to winter habitats. We found no individual preferences in the habitat availability that persisted across seasons (e.g. high proportion of grasslands within the AR of an individual in both seasons). Hence, predictions on favoured land-use types cannot be made across seasons. Common to all ARs was a high proportion of agricultural landscapes, which were also used most intensively in both seasons. This underlines the importance of this land-use type as foraging habitat for red kites (Aebischer 2009). However, agricultural landscapes were used more intensively in winter than in summer, which might be due to agricultural fields being mostly fallow or with sparse vegetation during winter and therefore prey may be more easily accessible for the visually hunting red kites (Aebischer 2009). Considering

this, further knowledge about the effects of different crops and structural richness on the suitability of hunting ground would be of advantage. As expected, grasslands were used in both seasons with similar intensity, as they are valuable foraging grounds for red kites (Aebischer 2009). Forests were the second most common land-use type in summer and the third most common land-use type in winter. The intensity of forest use did not differ significantly between seasons, but there was a tendency for more intense use in summer habitats than in winter habitats. In winter habitats, resident red kites are territorial throughout the year, leading to a more intense use of forests (and shrub lands) by resident red kites than by wintering individuals (Heredia et al. 1991). Forest edges (and lines of single trees) are especially important breeding habitats of red kites (Aebischer 2009). Breeding site is a key element that decisively influences habitat use of central-place foragers like red kites (Carrete and Donazar 2005, Heuck et al. 2013). However, there is a high variance in the preferred nesting sites of red kites from single trees to forest edges. Despite their role as breeding habitat, closed forests are not very attractive for scavenging or hunting red kites, as the vegetation is too dense to forage visually (Aebischer 2009). In summer, this limited attractiveness, paired with the use as breeding habitat by some individuals, led to a wide span of selectivity of forests, and therefore no difference in use between the seasons.

Habitat availability depends on the range considered available. In our study, we calculated the ARs as AKDE with an IID model. This model does not account for the autocorrelation inherent in movement data and hugs quite closely to the data points used for calculation (Calabrese et al. 2016). It was chosen because autocorrelation in our data was weak, and to reach comparability between our study individuals. By using a different model (e.g. the OU model, which accounts for spatial but not velocity autocorrelation, Calabrese et al. 2016) or a different home range estimator the ARs calculated and consequently the habitat considered available to our study individuals might have been slightly different. However, this would not affect comparability of, for example, MDs among individuals or seasons. Moreover, as our analysis of habitat use was based on a relatively coarse resolution of the land-use data, we do not expect that choosing different movement models or home range estimators would significantly change the overall results. As this field of research is constantly evolving, further studies might combine improved movement models with more fine-scaled land-use data to broaden our knowledge about the habitat use of red kites or other birds of prey.

Conclusion

Our study revealed that space use of migratory red kites differed between seasons and was associated with both landscape diversity and primary productivity. In summer, breeding success in particular has a decisive impact on space use. Extrinsic drivers, such as key habitats, and intrinsic drivers, such as sex, influenced space use in both seasons, although often in

different ways from those anticipated. Accordingly, knowledge about the space use of red kites is not directly transferable from one season to the other. As both seasons contribute to a vital population, these findings underline the importance of considering the entire annual cycle of migratory species in conservation practices and future studies. Conservation success for migratory species strongly benefits from a good networking and exchange of expert knowledge between local research groups and conservationists on an international level to sustainably protect and support populations year-round. Further studies should focus on the interplay of extrinsic and intrinsic drivers and how they shape space-use patterns of migratory raptors.

Acknowledgements – We gratefully acknowledge the support of C. Grüneberg, J. Karthäuser, M. Korn, P. Solluntsch, W. Nachtigall and S. Johanning in organizing and collecting the telemetry data from project Rotmilan-Land zum Leben. We are also grateful to C. Exner, W. Kürschner, K. Bettinger and R. Lösekrug for supporting our work with their experience and skills. Thanks to HessenForst for supporting field work with a road use permit. We also thank all other partners and students involved in the projects for their good cooperation. Further, we greatly appreciated the helpful comments of the handling editor and two anonymous reviewers that improved the manuscript. We thank Arsha Liz for proofreading the manuscript as a native English speaker.

Funding – The research leading to the current version of the PROBA-V NDVI Collection used in this study has received funding from various European Commission Research and Technical Development programs and is based on PROBA-V 333m data ((c) ESA and distributed by VITO). This study is a cooperative research project between the Philipps-University of Marburg, Department of Biology, Nature Conservation Group and the Rotmilan – Land zum Leben project represented by the Dachverband Deutscher Avifaunisten e.V.. The work is funded by a PhD scholarship from German Federal Environmental Foundation (DBU) for T. Spatz. The project Rotmilan-Land zum Leben was financially supported from the Federal Agency for Nature Conservation (BfN), with funds from the Ministry for the Environment, Nature Conservation and Nuclear Safety (FKZ grant no. 3511685C10) and we gratefully acknowledge this support. We also thank Stiftung Naturschutz Thüringen for financial support, as well as all private donors, for individual Red Kite sponsorships.

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Transparent peer review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02925>>.

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.jh9w0vtf7>> (Spatz et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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