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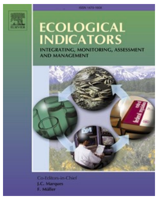

Original Articles

Multi-scale habitat selection throughout the annual cycle of a long-distance avian migrant

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ABSTRACT

Long-distance migrants are constrained by widely separated hospitable habitats in geographically isolated locations, making them vulnerable to environmental change, both through natural and anthropogenic causes. Knowledge about their resource selection decisions is imperative to understand the drivers of their declines. The distinct periods within an annual cycle, when individuals experience different environmental circumstances, are inextricably linked through carry-over effects which can have important consequences for the individual, and consequently the population. In this study, we employ precise archival GPS-tracking data of European Nightjars (*Caprimulgus europaeus*) and high-resolution global land cover data to examine habitat selection during the sedentary wintering and breeding periods, as well as during autumn and spring migration, using a correlational approach. We demonstrate how nightjars use general habitat characteristics, such as landscape diversity, for high-order habitat selection, while resource selection at a finer spatial scale is reliant on fine-scale variables related to a habitat's suitability, such as surface area of grassland and shrubland. We show that nightjars favour spatially diverse landscapes, which allows them to minimize time spent searching for optimal habitats. The considerable variation in the drivers of habitat selection between and within seasons shows how anthropogenic land-use change can have an array of different impacts on migrants by influencing large- and fine-scale habitat selection. This study shows the advantages of an individual based GPS-tracking approach, combined with high spatial resolution remote sensing data, and highlights the need for full annual-cycle research on scale dependent habitat selection of long-distance avian migrants.

1. Introduction

During the annual cycle of long-distance migratory birds, spatio-temporal variation in resource availability drives dynamic processes of settlement decisions (Börger et al., 2008; Viana et al., 2018). These settlement decisions inherently link distinct locations through carry-over effects (Norris, 2005; Marra et al., 2015) and inflict important individual- and population level fitness consequences (Mayor et al., 2009). Habitat selection is expected to be an adaptive, hierarchical decision-making process (Simons et al., 2000; Charnov and Orians, 2006) wherein both habitat suitability and mechanisms for assessing habitat suitability may change for each individual over space and time (Stanley et al., 2021).

At a coarse spatial scale, a combination of geographic factors, such as longitude, latitude, altitude or climatic parameters are expected to attract individuals to certain regions as an initial step towards habitat

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selection (Hutto, 1985; Moore and Aborn, 2000). At an intermediate scale, costs and benefits associated with specific habitats will play an important role in habitat selection (Hutto, 1985). It is expected that an interplay of both intrinsic (e.g. fuel load or immune functions) and extrinsic (e.g. wind, precipitation, availability of land during sea crossing and daylight/darkness) factors will likely influence a migrant's decision to land (Buler and Moore, 2011; Rüppel et al., 2023), while environmental characteristics (e.g. habitat type) serve as indicators of habitat quality (Cohen et al., 2014; McCabe and Olsen, 2015; Lafleur et al., 2016). Once individuals decide to terminate migratory flight bouts, they are expected to select (micro)habitats through exploratory behaviour, ranking available habitats according to their suitability. Here, ultimate factors such as food availability or resting opportunities will most likely determine habitat selection (Hutto, 1985).

Habitat requirements for individuals may also change over time and determine selection processes (Orians and Wittenberger, 1991). Long-distance migrants often require different habitat types during the breeding- and wintering season and at stopovers during migration (Zurell et al., 2018b; Cunningham et al., 2022). The flexibility to select different habitats between seasons suggests that individuals attempt to maximize their fitness across seasons (Stanley et al., 2021). Within specific seasons, habitat selection may also change in response to an individual's condition and behavioural state (Tietz and Johnson, 2007; Allen et al., 2020). For example, when energy reserves of migrating individuals deplete, their habitat requirements become less strict, and they may select any habitat that offers foraging possibilities (Wang and Moore, 2005). In contrast, individuals with larger fuel stores might invest more time in searching for habitat that provides safe resting opportunities rather than high levels of food availability as these individuals do not aim to refuel but may only be waiting for optimal departure conditions (Chernetsov, 2006).

Investigating spatio-temporal variation in habitat selection of small-sized long-distance migrants has long been challenging due to the difficulty to track individuals across large spatial and temporal scales, and at a sufficiently fine spatial resolution. To date, most studies described year-long habitat selection of larger species, able to carry large tracking devices (Zurell et al., 2018a; Cunningham et al., 2022), or fragmented habitat selection of smaller species during the breeding season, the wintering season (Askren et al., 2022; Bakermans et al., 2022) or single stopovers sites along the annual migration route (Allen et al., 2020; Wright et al., 2020; Wang et al., 2022). It is, however, necessary to move beyond the "single-season approach" and adopt a full-annual cycle perspective (Marra et al., 2015).

Here, we investigate habitat selection of a small-sized, long-distance migrant, the European Nightjar (*Caprimulgus europeaus*; hereafter nightjar), through a multi-scale approach and across the full annual cycle. Nightjars migrate from their Eurasian breeding areas across the palearctic region to winter in sub-Saharan Africa (Evens et al., 2017b; Jacobsen et al., 2017; Norevik et al., 2017; Lathouwers et al., 2022b). They breed in open semi-natural and other habitats containing bare ground and often with sparse trees (Cramp, 1985) and use complementary habitats, such as extensively-cultivated grasslands and wet grasslands, to forage for aerial insects (Evens et al., 2017a). Foraging sites may be located at a considerable distance from for nesting/roosting sites, which indicates that nightjars evaluate the habitat in the landscape for up to a ca 5 km radius in the breeding season (Evens et al., 2018). We combine fine-scale GPS-tracking data with detailed global land-cover data to evaluate habitat selection during stationary periods (i.e. stopover sites, breeding- and wintering period) and during migration. First, we describe the landcover association niches of our study population throughout the annual cycle. Second,we examine intra-annual variation in habitat selection patterns, testing whether nightjars exhibit a higher degree of selectivity in their habitat use on the breeding grounds compared to their non-breeding grounds. Finally, we investigate the variation in habitat selection across spatial scales. We hypothesize that selection of stationary sites from the landscape during migration is largely driven by general indicators of habitat quality such as forest cover (Cohen et al., 2014), while habitat selection within stationary sites is closely linked with optimal foraging conditions determined by proximity and configuration of suitable foraging habitats such as grasslands (Evens et al., 2018).

2. Methods

2.1. Field methods and GPS telemetry

We conducted fieldwork in Belgium (51.1° N, 5.5° E; 2015–2021) and the UK (52.5° N, 0.7° E; 2015–2018, 53.1° N, −3.5° E; 2018–2019) where we captured nightjars in breeding areas using ultra-fine mist nets (Ecotone, 15 × 3 m) and tape lures. We marked each individual with a unique alphanumeric ring and fitted a data logger dorsally between the wings using a full body harness with a 1 mm wide flat braided cord to avoid abrasion (Lathouwers et al., 2022a), or 2 mm Teflon ribbon. In total, we tagged 91 adult male individuals, with 1.8 g Pathtrack Ltd. nanoFix or Biotrack Ltd. PinPoint-40 archival GPS-loggers (for deployments see Table S1). GPS-loggers were programmed to record longitude, latitude to a high degree of accuracy (within 10 m), when nightjars were active (Lathouwers et al., 2022a; Lathouwers et al., 2022b), and loggers were deployed for year-round recording.

2.2. GPS data annotation

For each individual, we calculated the distance (km) travelled between subsequent GPS-locations. To obtain an empirical distribution of step distances between subsequent GPS-locations and to account for temporal autocorrelation, we excluded observation intervals < 24 h apart. Next, we fitted a Gaussian fixed kernel density estimator to the natural log-transformed step distances. Based on the density curve (Fig. 1), we visually identified a break in the distribution at a log step distance of 2.32, corresponding to an actual step distance of 10.14 km. This value was used as a threshold to classify each GPS-location into one of two categories *sensu* Beatty et al. (2014). GPS-locations with a step distance < 10.14 km were interpreted as "local-scale" movements corresponding to movements between locations within a selected stationary site. GPS-locations with a step distance of > 10.14 km were categorized as "relocation-scale" movements, i.e. movements outside of the confines of a stationary site (Fig. 2).

This distinction between local- and relocation-scale movements was used to divide the annual cycle of each individual into four distinct periods: the breeding period, autumn migration, the wintering period and spring migration. The start of migratory periods (autumn and spring migration) was based on the first relocation-scale movement (movement larger than 10.14 km) recorded after the stationary breeding and wintering periods. Stationary sites were defined as areas containing GPS-locations which were categorized as local-scale movements. These areas therefore correspond to a site where an individual remained for $>$ 24 h.

Habitat selection analyses that include multiple spatial scales can improve understanding of wildlife-habitat relationships. For each period of the annual cycle, we therefore examined habitat selection separately, both at the relocation- and the local-scale. To investigate selection of stationary sites during migration, we identified each first GPS-location that was categorized as a local-scale movement after relocation movement and defined these used locations as settlement points. These settlement points were then paired with the previous GPS-location (i-1; i.e. the last relocation movement), after which we constructed a 45° wedge-shaped buffer for each pair of relocation- and settlement GPS-locations. This buffer started from the relocation-scale GPS-location (i-1) and extended twice the length of the step distance from the relocation-scale location to the settlement location. The length of the buffer was chosen to represent the possible activity window of minimum 1/2 night and maximum a full night and to reflect the available area to choose a

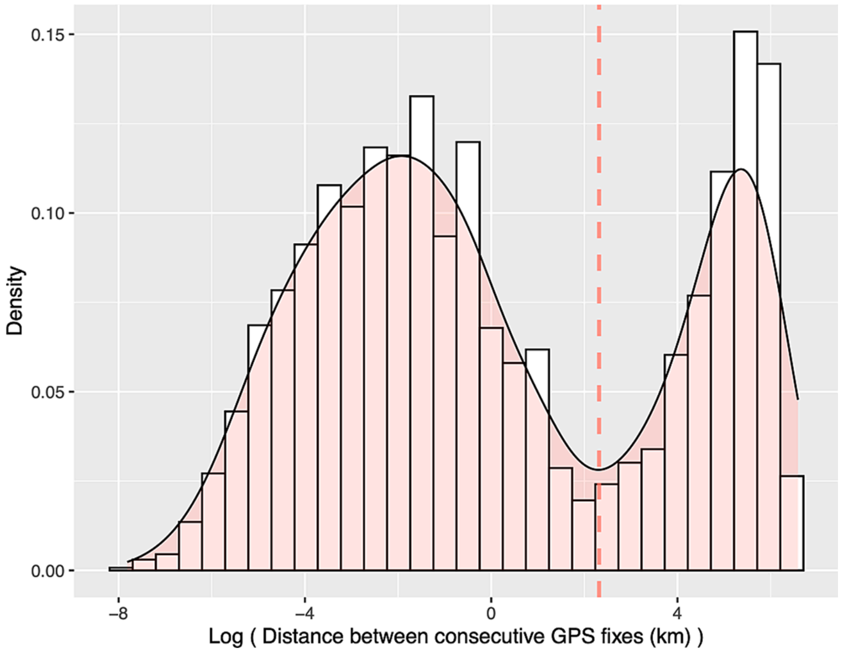

Fig. 1. Density curve of logarithmic distances between consecutive gps-locations. the dotted red line indicates the breakpoint in the distribution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

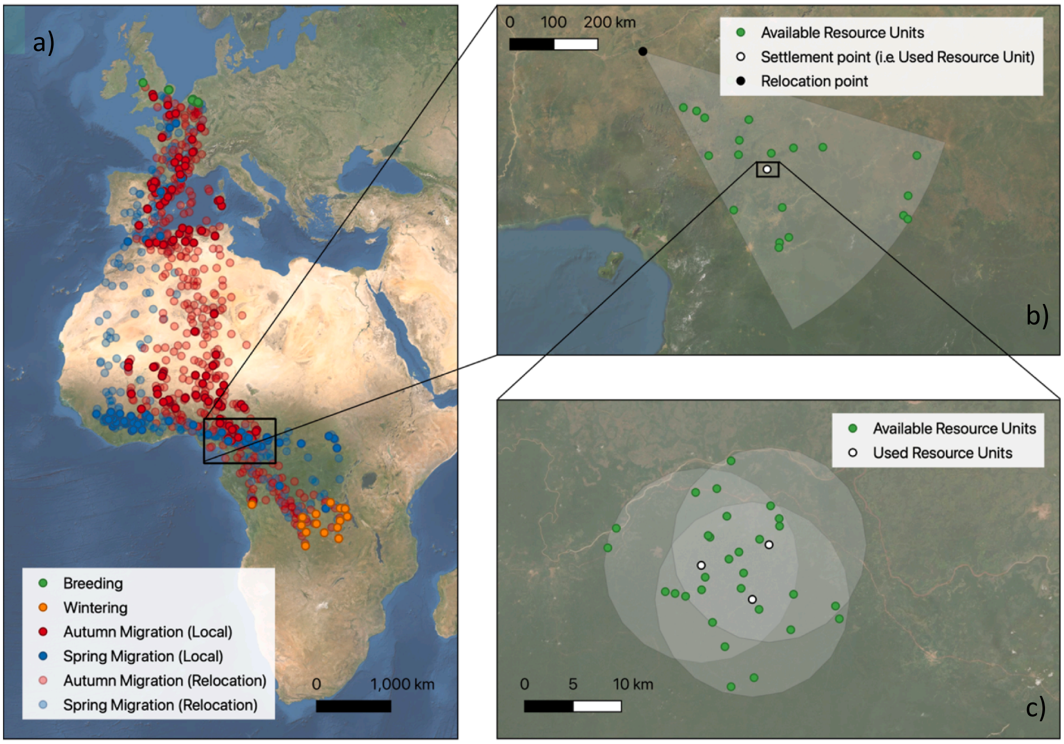

Fig. 2. Workflow of a) dividing GPS data in local- and relocation-scale movement according to the step distance of 10.14 km b) defining the settlement point (white), i.e. the first point associated with local scale movement immediately after relocation scale movement (black), as the used resource unit. The wedge-shaped buffer, constructed between the relocation point and the settlement point, is then used to define 20 available resource units (yellow) c) defining used (white) and available (yellow) resource units on the local-scale using a 10.14 km buffer delineating local scale movement points. For each used and available resource unit environmental characteristics were point sampled and sampled within a 1236 m buffer corresponding to the relevant landscape in the context of foraging (see Table 1). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stationary site. Within this wedge-shaped buffer we plotted a set of 20 randomly chosen alternative locations. Environmental covariates were subsequently compared between the used and the alternative locations in order to determine individuals' selection of stationary sites at the relocation-scale (Fig. 2).

To investigate habitat selection within stationary sites, we considered all local-scale GPS-locations as resource units used by the individual for e.g. foraging. Around each used GPS-location we plotted a set of

Table 1

Overview of environmental covariates used in binomial glmm's to evaluate observed versus alternative resource units at the local- and relocation-scale. Variables are grouped categorized into habitat composition and habitat configuration. Variables indicated in bold are those quantifying habitat within the 1236 m landscape buffer surrounding each point location. Variables in plain text describe habitat through point sampling.

Variable	Description
Habitat composition	
Non-Vegetated Cover	Fraction of non-vegetated cover in ground vegetation cover (%)
Non-Tree Cover	Fraction of non-tree cover in ground vegetation cover (%)
Tree Cover	Fraction of tree cover in ground vegetation cover (%)
EVI	Vegetation greenness of habitat feature
Tree Area	**Surface area of Tree land cover class within landscape buffer (km^2)**
Built Area	**Surface area of Built Area land cover class within landscape buffer (km^2)**
Crops Area	**Surface area of Crops land cover class within landscape buffer (km^2)**
Rangeland Area	**Surface area of Rangeland land cover class within landscape buffer (km^2)**
Diversity	**Shannon-Wiener Diversity Index of land cover classes within landscape buffer**
Habitat configuration	
Tree Distance	Distance to nearest pixel of Tree land cover class (km)
Built Distance	Distance to nearest pixel of Built Area land cover class (km)
Crops Distance	Distance to nearest pixel of Crops land cover class (km)
Rangeland Distance	Distance to nearest pixel of Rangeland land cover class (km)
Patch Size	Surface area of habitat feature in which resource unit is located (km^2)
Mean Patch Size	**Mean area of habitat features within landscape buffer (km^2)**
Tree Patch Size	**Mean area of Tree habitat features within landscape buffer (km^2)**
Built Patch Size	**Mean area of Built habitat features within landscape buffer (km^2)**
Crops Patch Size	**Mean area of Crops habitat features within landscape buffer (km^2)**
Rangeland Patch Size	**Mean area of Rangeland habitat features within landscape buffer (km^2)**
Tree Cohesion	**Connectedness of patches of Tree land cover class within landscape buffer**
Built Cohesion	**Connectedness of patches of Built Area land cover class within landscape buffer**
Crops Cohesion	**Connectedness of patches of Crops land cover class within landscape buffer**
Rangeland Cohesion	**Connectedness of patches of Rangeland land cover class within landscape buffer**

10 randomly chosen alternative locations within a 10.14 km buffer. Environmental covariates were subsequently compared between the used and the alternative locations (Fig. 2).

We estimated home range size using the "*KernelUD*" function in the R-package "*adehabitatHR*" (Calenge, 2022) for a subset of stationary sites. Due to limitations of this approach, we were only able to use stationary sites where individuals remained for > 5 days.

2.3. Environmental parameters

We quantified various measures of both habitat composition and configuration for each used and available location (Table 1), using high accuracy geospatial environmental remote sensing data. We used Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1), generated every 16 days at a spatial resolution of 250 m, to extract Enhanced Vegetation Index (EVI) values at each point location as a habitat composition variable. These data are archived at the Land Processes Distributed Active Archive Center (LP DAAC) managed by the NASA Earth Science Data and Information System (ESDIS). EVI is a metric similar to the Normalized Difference Vegetation Index (NDVI) and is used to quantify vegetation greenness. However, EVI corrects for some atmospheric conditions and canopy background noise and is more sensitive in areas with dense vegetation (Huete et al., 2002).

We also used the MODIS MOD44B Vegetation Continuous Fields (VCF) product to extract vegetation cover as habitat composition

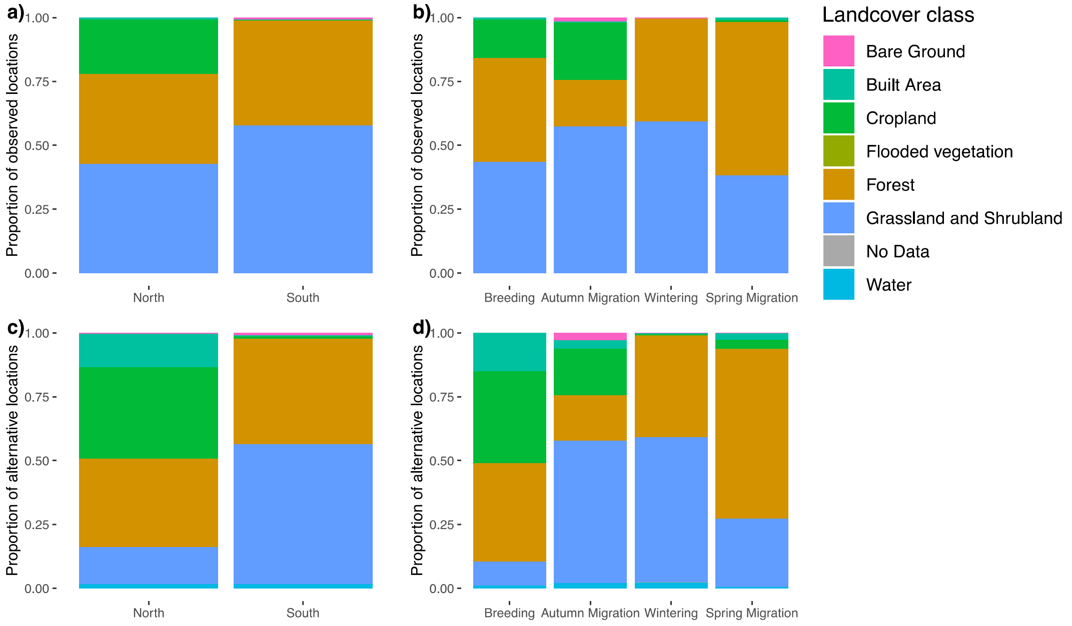

Fig. 3. Proportion of observed (a,b) and alternative (c,d) gps-locations in each sentinel-2 land cover class by region (a,c) and by period (b,d).

variables. The product provides a yearly global representation of surface vegetation cover as gradations of three ground cover components: percent tree cover, percent non-tree cover, and percent non-vegetated (bare), with a resolution of 250 m (Table 1).

Subsequently, we used the Sentinel-2 Land Use/Land Cover Timeseries which displays a global map of land use/land cover (LULC) derived from ESA Sentinel-2 imagery at 10 m resolution and with ten distinct land cover classes (Karra et al., 2021). The full dataset was used to report land cover associations of used locations throughout the annual cycle. In further analyses of habitat selection we only considered four out of ten land cover classes (Trees, Crops, Built Area and Rangeland; hereafter referred to as forest, cropland, built area and grassland and shrubland respectively) based on previous studies investigating nightjars' habitat selection during the breeding period (Evens et al., 2017a; Evens et al., 2018; Polakowski et al., 2020). To quantify habitat configuration, we measured the distance (m) to the nearest feature for the four aforementioned land cover classes. If the GPS-location was observed in the specified land cover class itself this value was equal to zero. We specifically used proximity metrics instead of point sampling of the land cover classes to characterize habitat near each location to account for any spatial error associated with the land cover data (Conner et al., et al., 2003). Additionally, we calculated the surface area (m^2), or patch size, of the habitat feature in which each available and used resource unit was located as a habitat configuration variable.

Next, we calculated a series of covariates that quantified the composition and configuration of the landscape surrounding each used and available resource unit using the "*Landscapemetrics*" R-package (Hesselbarth et al., 2019). To calculate landscape metrics at the local scale, we placed a 1263 m buffer centered on each point location. This distance corresponds to the mean foraging distance observed for nightjars at the breeding site (Evens et al., 2017a) and is similar to the peak in density of local-scale step distances across seasons (log(distance) = -1.9068 km; distance = 1485 m; see Fig. 1), thus corresponding to the landscape surrounding individuals at a relevant distance in the context of foraging ecology.

Within these 1236 m buffers surrounding each point location we estimated the surface area (m^2) of the four selected Sentinel-2 land cover classes as a habitat composition variable. Subsequently, to quantify habitat configuration we calculated the cohesion metric for each land cover class within these buffers. The cohesion metric characterizes the connectedness of patches belonging to a certain land cover class. It can be used to assess if patches of the same class are located aggregated or rather isolated and thereby giving information about the configuration of the landscape (Hesselbarth et al., 2019). We also calculated the Shannon-Wiener diversity metric of land cover classes within the buffers around each resource unit. The Shannon-Wiener diversity index is a widely used metric in biodiversity and ecology, in this case reflecting both the number of classes and the abundance of each class in the buffer constructed around resource units (Hesselbarth et al., 2019). As a final habitat composition variable, we calculated the average patch size for each land cover class in the landscape buffers surrounding the point locations, as well as the average patch size irrespective of land cover class.

2.4. Statistical analyses

We modeled the choice of observed versus alternative locations in R (R-core-team, 2022) using binomial generalized linear mixed models. All candidate variables were tested for independence using a Spearman correlation matrix ($r < 0.6$ indicating independence; Dormann et al., 2013). To avoid collinearity between explanatory variables within the same model we constructed two separate models, one including the habitat composition and proximity variables as predictor, and another with the habitat configuration variables as predictors. These two models were constructed separately for each spatial scale, i.e. local- and relocation-scale. We included the ID of each habitat selection event, nested within bird individual identity as a random effect term. These models were constructed separately for the four different annual cycle periods. In order to examine regional differences, models for spring and autumn migration were subsequently split up according to geographic location, north or south of the Sahara Desert (30°N). As the Sahara is well established as the major ecological barrier for palearctic migrants (Bairlein, 1988), its crossing represents a shift in a migrants' behavioural strategy likely to be represented in the habitat selection process. We used the R-Package "*buildmer*" (Voeten, 2023) to simplify models by removing uninformative variables and interaction terms through automatic stepwise elimination based on likelihood ratio tests.

3. Results

3.1. Tracking-data information

Out of 91 deployed GPS loggers, we recaptured 28, constituting a recapture rate of 30.1 % (for details, see Table S1). Five GPS loggers did not contain usable data. In total, we obtained 2767 24 h interval GPS-locations, 631 during the breeding season ($n = 22$), 919 during autumn migration ($n = 22$), 607 during the wintering period ($n = 16$) and 610 during spring migration ($n = 13$). The analysis of step distances between subsequent GPS-locations allowed us to categorize these into two distinct categories according to a break in the distribution of step distances at 10.14 km: 1854 GPS-locations were associated with local-scale movements and 913 with relocation-scale movements. The median step distance of local-scale movements was 1.14 km and 174.75 km for relocation-scale movements. With the exception of one individual making a single relocation-scale movement of 40.05 km during the wintering period in 2019, no relocation-scale movements take place during the breeding and wintering periods.

Individuals interrupted their migration for longer than 24 h nine times (median; range 1–20) during autumn migration and nine times during spring migration (median; range: 1–20). These stopovers lasted three days (median; range: 1–24 days) during autumn and three days during spring migration (range: 1 – 27 days). Median home ranges (95 % kernels) of stationary sites where individuals remained for > 5 days were estimated at 130.77 ha (range: 8.75 – 2088.65 ha) during the breeding period, 17.83 ha (range: 3.01 – 114.33 ha) during the wintering period, 13.16 ha (range: 0.15 – 795.69 ha) during autumn migration and 18.53 ha (range: 0.01 – 391.39 ha) during spring migration.

Of all used resource units ($n = 1854$), 0.44 % were located in bare ground and built area land cover classes, 9.77 % in cropland, 38.43 % in forest and 50.91 % in grass- and shrublands (Fig. 3). The distribution of used resource units among the different land cover classes was variable between seasons ($\chi^2 = 161.2$, df = 12, $p < 0.001$) and regions ($\chi^2 = 237.13$, df = 4, $p < 0.001$), which was also true for alternative resource units (region: $\chi^2 = 6518$, df = 7, $p < 0.001$; season: $\chi^2 = 7395.7$, df = 21, $p < 0.001$; Fig. 3). For example, a significant proportion of used resource units was observed in croplands during the breeding period and autumn migration (Fig. 3). This proportion exceeded the one we found in croplands for alternative locations during autumn migration, while the reverse was true during the breeding season (Fig. 3). Additionally, the proportional use of grasslands and shrublands, built area and forests varied between seasons and regions, and differed between observed and alternative locations (Fig. 3).

3.2. Relocation-scale habitat selection

Our data show that nightjars select specific habitats during each phase of the annual cycle. During the autumn migration, nightjars avoid dense tree cover ($Z = -2.059$, $P = 0.040$) and croplands ($Z = 2.264$, $P = 0.024$), while selecting locations with diverse land cover in the surrounding landscape ($Z = 2.326$, P 0.020; Table S2). We observed no clear habitat selection during spring migration (Table S2). The separate

Table 2
Binomial GLMM model results comparing habitat composition and configuration between observed and alternative resource units on the “relocation” scale for the different seasons and regions.

Habitat composition				
	Estimate	**Std. Error**	**z value**	**P value**
Breeding				
Area Built Landscape	0.051	0.011	4.450	<0.001
Area Crops Landscape	0.064	0.011	5.673	<0.001
Area Rangeland Landscape	0.069	0.011	6.092	<0.001
Area Tree Landscape	0.073	0.011	6.400	<0.001
Cover NonTree	−0.024	0.009	−2.794	0.005
Cover Tree	−0.029	0.008	−3.513	<0.001
Diversity Landscape	2.559	0.281	9.107	<0.001
Rangeland Distance	−0.002	0.000	−6.553	<0.001
Tree Distance	0.002	0.000	6.007	<0.001
Wintering				
Area Crops Landscape	−0.979	0.258	−3.793	<0.001
Area Rangeland Landscape	0.045	0.008	5.536	<0.001
Area Tree Landscape	0.048	0.008	5.866	<0.001
Built Distance	0.000	0.000	−3.823	<0.001
Cover NonTree	−0.082	0.009	−9.690	<0.001
Cover Tree	−0.072	0.009	−8.463	<0.001
Crops Distance	0.000	0.000	−10.541	<0.001
Diversity Landscape	1.602	0.307	5.214	<0.001
EVI	1.623	0.714	2.274	0.023
Rangeland Distance	0.001	0.000	7.067	<0.001
Autumn				
Area Built Landscape	0.010	0.005	2.085	0.037
Area Crops Landscape	0.014	0.005	2.914	0.004
Area Rangeland Landscape	0.014	0.005	2.915	0.004
Area Tree Landscape	0.014	0.005	2.989	0.003
Autumn - North				
Area Crops Landscape	0.007	0.002	3.786	<0.001
Area Rangeland Landscape	0.008	0.002	4.375	<0.001
Area Tree Landscape	0.005	0.002	2.960	0.003
Cover NonVegetated	−0.015	0.005	−3.178	0.001
Autumn - South				
Area Tree Landscape	0.004	0.002	2.171	0.030
Spring				
Area Crops Landscape	−0.006	0.002	−2.652	0.008
Cover NonTree	−0.028	0.011	−2.476	0.013
Cover Tree	−0.023	0.011	−2.076	0.038
Diversity Landscape	1.140	0.334	3.414	0.001
Spring - North				
Area Built Landscape	0.010	0.004	2.613	0.009
Cover Tree	−0.079	0.030	−2.665	0.008
Diversity Landscape	−2.626	1.183	−2.221	0.026
EVI	15.862	4.377	3.624	<0.001
Rangeland Distance	−0.012	0.004	−3.004	0.003
Spring - South				
Diversity Landscape	1.721	0.400	4.304	<0.001
Tree Distance	−0.003	0.001	−2.445	0.014
Habitat configuration				
	Estimate	**Std. Error**	**z value**	**P value**
Breeding				
Cohesion Built Landscape	0.004	0.001	2.855	0.004
Cohesion Crops Landscape	0.004	0.002	2.015	0.044
Cohesion Rangeland Landscape	0.217	0.022	9.782	<0.001
Cohesion Tree Landscape	0.176	0.055	3.185	0.001
Mean Patch Size Landscape	0.010	0.004	2.566	0.010
Patch Size	0.000	0.000	−6.254	<0.001
Patch Size Built Landscape	−0.085	0.010	−8.110	<0.001
Patch Size Crops Landscape	0.006	0.001	7.846	<0.001
Patch Size Rangeland Landscape	0.007	0.002	3.537	<0.001
Patch Size Tree Landscape	0.002	0.000	4.614	<0.001
Wintering				
Cohesion Tree Landscape	0.666	0.064	10.399	<0.001
Mean Patch Size Landscape	0.002	0.001	3.950	<0.001
Patch Size Crops Landscape	−2.301	0.843	−2.731	0.006
Patch Size Tree Landscape	−0.002	0.000	−4.602	<0.001
Autumn				
Patch Size Built Landscape	−0.038	0.012	−3.068	0.002
Autumn - North				
Cohesion Rangeland Landscape	−0.005	0.002	−2.338	0.019
Cohesion Tree Landscape	0.009	0.003	3.111	0.002
Patch Size Built Landscape	−0.044	0.016	−2.799	0.005
Patch Size Rangeland Landscape	0.002	0.001	3.393	0.001

(*continued on next page*)

Table 2 (*continued*)

Habitat composition	Estimate	Std. Error	z value	P value
Autumn - South				
Patch Size	0.000	0.000	−3.182	0.001
Patch Size Crops Landscape	−0.197	0.091	−2.166	0.030
Spring				
Patch Size Tree Landscape	−0.002	0.001	−3.588	<0.001
Spring - North				
Cohesion Crops Landscape	0.020	0.009	2.114	0.034
Patch Size Rangeland Landscape	0.005	0.002	2.168	0.030
Spring - South				
Patch Size Tree Landscape	−0.002	0.001	−3.363	0.001

models for each region during the migration periods show further support towards selection for locations with diverse land cover north of the Sahara during spring (Z = 2.061, P = 0.039), as well as avoidance of large croplands during autumn south of the Sahara (Z = -2.121, P = 0.034; Table S2).

3.3. Local-scale habitat selection

Compared to the relocation-scale, habitat selection at the local-scale is more pronounced (Table 2). During the breeding period nightjars prefer a diverse landscape, selecting high land cover diversity and the presence of all four Sentinel-2 land cover classes (Table 2). Our results also indicate a preference for the proximity to grasslands and shrublands, while forests are avoided (Table 2). Additionally, we observe that nightjars avoid tree cover and non-forest vegetation cover, based on MODIS VCF variables. The habitat configuration model shows a preference for cohesion of all four land cover classes and larger patch sizes of forest, grassland and cropland while large patches of built area are avoided (Table 2).

During the wintering period, nightjars select higher surface area of grassland and shrubland and forest in the surrounding landscape, while they avoid croplands (Table 2). Contrastingly, we observe a preference for croplands and built area through the proximity variables, while proximity to grasslands and shrublands is avoided (Table 2). Additionally, nightjars prefer diverse land cover and higher vegetation productivity (Table S3). In accordance with our findings on the breeding period, wintering nightjars avoided tree cover and non-forest vegetation cover. These results, based on MODIS VCF variables with a spatial resolution of 250 m, seemingly contrast with the preference for forest, grassland and shrubland reported from the variables based on 10-m resolution Sentinel-2 data. The habitat composition model indicates a preference for cohesion of forest and larger average patch sizes, irrespective of land cover class, in the surrounding landscape. In contrast, we observe avoidance of large croplands and forest (Table 2).

During autumn migration, nightjars once again prefer a higher surface area of all four land cover classes in the surrounding landscape (Table 2). Our results also show a preference for a higher surface area of forest in both regions, with an additional preference for higher area of cropland and grassland and shrubland, as well as avoidance of barren land north of the Sahara (Table 2). Results on habitat configuration indicate that nightjars avoid large patches of built area (Table 2). North of the Sahara we observe a preference for large and disaggregated patches of grassland and shrubland, as well as high cohesion of forest, while individuals avoid large patches of built area (Table 2). In the south nightjars prefer to use small patches of habitat and avoid large croplands (Table 2).

During spring migration, nightjars avoid tree cover and non-forest vegetation cover as well as surface area of cropland and large forest patches (Table 2). Additionally, we observe a preference for higher diversity of land cover. In the region north of the Sahara, nightjars prefer higher vegetation productivity and surface of built area in the surrounding landscape as well as high cohesion of cropland and larger patches of grassland and shrubland (Table 2). In contrast, we observe avoidance of grasslands and shrublands and dense tree cover as well as diversity of land cover (Table 2). In the southern region nightjars prefer locations with diverse land cover while they avoid forests, both in terms of proximity and patch size (Table 2).

4. Discussion

In our study, nightjars change habitat requirements in response to varying resource availability during different periods of the annual cycle. During autumn and spring migration, nightjars choose stopover sites containing a high diversity of land cover types. At breeding and wintering sites, nightjars prefer, among other factors, the proximity of grasslands and shrublands in a diverse landscape while they avoid croplands. Local-scale habitat selection is strongly influenced by each period of the annual cycle.

4.1. Landcover association niches

GPS-data show that habitat associations of nightjars differ between seasons and regions. For example, during the breeding period and autumn migration, nightjars select cropland, while cropland is avoided during the wintering period and during spring migration. Despite travelling thousands of kilometers, avian migrants are considered to track environmental conditions across the year to a greater extent than resident bird species (Gomez et al., 2016; Zurell et al., 2018a) in order to counteract seasonal fluctuation in the ecological niche they occupy (Somveille et al., 2018). However, our results suggest that nightjars are not “niche-trackers”, which apply conservative habitat selection across seasons, for example, for foraging and roosting (Zurell et al., 2018a). Instead, similar to 80 % of 335 other migratory bird species in the Eurasian–African flyways (Ponti et al., 2019), nightjars appear to be “niche-switchers” which vary certain aspects of their niche, partitioning niche space over the course of the year in order to adjust habitat use to accommodate seasonal life history requirements (Ponti et al., 2019; John and Post, 2021). The niche management strategy employed by migrants, and the ability to use alternative approaches during migration, will likely determine their ability to persist under future global change as it allows them to maximize their fitness throughout variable environments (John and Post, 2021). If seasonal ranges undergo inconsistent environmental change, past strategies of niche tracking and niche switching may fail to accommodate novel conditions. A better understanding of the factors that constrain seasonal niches is critical for predicting how migration patterns could respond to future environmental changes.

4.2. Scale-dependent habitat selection

At the relocation scale, a landscape with a high diversity in habitat types is important for migratory nightjars. Likely, diverse landscapes increase the potential for nightjars to find high-quality foraging habitat, even if suitable habitat will be interspersed with other habitat types, minimizing time spent searching for suitable habitat. Though a further investigation of stopover duration in relation to environmental parameters and refueling rates is needed, these first findings coincide with the time minimizing strategy observed for nightjars through opportunistic foraging in hospitable areas during the movement phases of their migration (Lathouwers et al., 2022a). Because the most important aspect of an individual's migration is not the time spent travelling, but rather the time spent on stopovers to replenish fuel reserves (Hedenström and Alerstam, 1997), maximising fuel deposition rate is one of the main drivers in resource selection processes (Chernetsov, 2006). When a migrant interrupts its active flight, a rapid selection of high-quality habitat makes it possible to start refueling quickly while avoiding the costs of prolonged habitat sampling in terms of time, energy and security (Chernetsov, 2006). Migrants that arrive in higher-quality habitat types have been shown to acquire more fuel reserves. It is clear that quickly locating habitat with sufficient food resources at each stopover may be the most important determinant to a successful migration (Moore and Aborn, 2000). Within this decision-making process, initial habitat selection is thought to involve broad geographic or anthropogenic factors (Schekler et al., 2022) or general habitat features such as e.g., forest cover (Cohen et al., 2014; Guo et al., 2023; Moore, 2018).

After the initial habitat selection, associated with the arrival at a stationary site, migrants select appropriate habitats based on their innate preferences and functional morphology (Chernetsov, 2006), foraging strategies, the food resource distribution (Zuckerberg et al., 2016) and habitat carrying capacity (Liu et al., 2022). Habitat selection of nightjars within stationary sites during the migration periods show how composition and configuration of habitat play an important role at the local scale. Although results vary markedly between seasons and regions, nightjars generally selected mosaic landscapes composed of forest, grassland, shrubland and cropland cover, with a preference for smaller patches and lower levels of habitat aggregation. Previous studies demonstrate how the abundance and behaviour of nightjars and related species during the breeding season is influenced by landscape configuration, showing they prefer landscapes consisting of semi-open and closed habitats (Sierro et al., 2001; Camacho et al., 2014; Evens et al., 2017a; Evens et al., 2018; Polakowski et al., 2020). These mosaic landscapes provide ecotones between habitat types which provides the species with foraging opportunities through sallying/hawking for flying insects (Cleere and Nurney, 1998). This supports the theory that the general characteristics associated with the initial choice of a habitat at stopover sites reflect characteristics of previously chosen habitat (Moore and Aborn, 2000). While landscape composition is known to have a primary and constraining effect on ecological processes, landscape configuration has been proposed to be less influential in habitat selection (Beatty et al., 2014). Therefore, landscape configuration has often been excluded from large-scale habitat selection studies due to the limitation of spatial inaccuracy of remote sensing data (Beatty et al., 2014).

4.3. *Spatio-temporal variation in habitat selection*

Nightjars, in our study, select different habitat characteristics during each distinct period of the annual cycle. This suggests that nightjars' resource selection may be strongly influenced by both intrinsic and/or extrinsic factors. As migrants anticipate heightened energy demand, and increased uncertainty that these demands can be met, energetic condition in accordance with progression throughout the migration period play a large role in shaping behavioural- and resource selection decisions (Wang and Moore, 2005; Cohen et al., 2012). These decisions are additionally impacted by the quality and quantity of resources encountered *en route* (Börger et al., 2008; Bastille-Rousseau et al., 2015), and may therefore vary between regions within a single season. This variation may potentially compromise conservation and management decisions when they are based on data of limited sample size or limited regional coverage. We thus highlight the need for a full annual-cycle approach and sampling designs that cover diverse regional landscapes and ensure robust estimates of habitat suitability to conserve avian migrants.

In comparison with the sedentary wintering and breeding period, we observe less evidence for consistent habitat selection during the autumn and spring migration periods. Recent studies have demonstrated how species with specific habitat requirements during the breeding period will relax these requirements during migration (Lack, 1968; Stanley et al., 2021; Cunningham et al., 2022). This shift towards a more generalist lifestyle may be favored to minimize time spent on migration (Hutto, 1985; Alerstam and Lindström, 1990). We observed the least evidence for habitat selection during spring, when migrants likely experience intense selective pressure for early arrival on breeding grounds to secure a territory and begin reproduction (Kokko, 1999). Nightjars migrating from the eastern edge of the breeding distribution in Mongolia have been shown to adapt their migration schedules to ensure optimal arrival dates on breeding grounds through faster migration speed (Lathouwers et al., 2022b), while this has not been observed for European populations (Norevik et al., 2017). Lowering the threshold of acceptable habitat during spring migration to reduce search time for high-quality stopover sites may therefore serve as an alternative for maintaining an optimal migration schedule (Nilsson et al., 2013). Additionally, the high concentration of individuals at sub-Saharan stopover sites in spring, as well as the fact that the locations of stopover sites differ significantly between seasons (Fig. 2), may suggest that in spring food availability plays a larger role in dictating site use than habitat characteristics (Van der Graaf et al., 2006; Thorup et al., 2017).

As migrants transition from a migration period to a sedentary period, the circumstances for habitat selection become vastly different. Variation in available time for the resource selection decision, consequences of a sub-optimal decision and ability to change the decision (Orians and Wittenberger, 1991) all cause individuals to perceive their surroundings in a fundamentally different way when they are sedentary versus when they migrate (Allen et al., 2020). Sedentary breeding and wintering nightjars were more selective in their habitat settlement decisions at the local scale. We found that nightjars selected for higher surface area of grassland, shrubland and forest habitats with higher EVI values, which are indicative of habitat quality in the context of foraging. However, in contrast to the non-breeding period, we observe a significant selection for landscapes with higher levels of aggregation of grassland, shrubland, cropland, and forest during the breeding period. This, together with observed larger home-ranges during the breeding period, may indicate that breeding nightjars are under more pressure to select high-quality habitat, likely due to the energetic demands and spatial constraints during breeding and chick-rearing (O'Hanlon et al., 2022). Temperate migrants wintering in the tropics have been known to select approximately the same (micro)habitat types as they do during the breeding seasons (Leisler, 1990). However, similar to our findings, other species show shifts in their selected habitats, showing a higher degree of flexibility during the winter period (O'Hanlon et al., 2022).

4.4. *Conservation implications*

Notably, we observed no clear pattern in the role of anthropogenic infrastructure on nightjars' habitat selection. Agricultural land may provide open spaces for aerial insectivores, such as nightjars, to forage more efficiently, although agricultural intensification and pesticide use have been identified as drivers of insect population declines (Spiller and Dettmers, 2019) and aerial insectivore population declines (English et al., 2018). Additionally, nightjars, known for their sensitivity to subtle changes in ambient light (Evens et al., 2020), are believed to be influenced by artificial night lighting. This influence may have a negative impact (Korpach et al., 2022), but it is more likely that artificial light at night enhances foraging conditions by simulating moonlit nights (Evens et al., 2020; Evens et al., 2023). The precise role of this phenomenon in the results of the current study remains uncertain. However, this could be an explanation for e.g. contrasting results between the wintering period, where nightjars selected against proximity to urban areas and preferred lower surface area of cropland, and the breeding season, where we observed positive selection for surface area of cropland and urban area in the surrounding landscape.

We provide first insights into the drivers of habitat selection throughout the annual cycle of this long-distance migrant. Nevertheless, we believe the study may have limitations. Our data are gathered from experienced adult individuals which have previously migrated and bred successfully, and who have already explored and selected their habitats at each stage of their annual cycles. Therefore they may be biased towards selecting these same, or similar, locations (Moore and Aborn, 2000). We also observe possible contradicting results between the 250 m and 10 m resolution habitat variables, showing that spatial accuracies of several 100–1000 m limit the possibility of analyzing full annual-cycle habitat selection at a fine-scale. This makes it difficult to gain detailed ecological insight from these analyses. Therefore, our study shows the necessity of incorporating sufficient spatial detail and range when investigating habitat selection. Additionally, the high spatial resolution data we worked with is limited in thematic resolution, obscuring further insights into the role of e.g. extensive vs. intensive agriculture in nightjars' habitat selection. Our study also highlights the need to consider season specific effects to determine how anthropogenic alterations to the environment may impact migrants. However, the environmental data that currently are available at this large global range do not provide information on land use and management, which limits our understanding of the heterogeneity within land cover types. An increase in thematic resolution of global land cover data coupled with information on land management, would help to refine the results of this study (Marshall et al., 2020) and allow us to determine the potential impacts of anthropogenic alterations to the environment on long-distance avian migrants.

CRediT authorship contribution statement

Michiel Lathouwers: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization. **Nicolas Dendoncker:** Conceptualization, Writing – review & editing, Supervision. **Tom Artois:** Conceptualization, Supervision. **Natalie Beenaerts:** Conceptualization, Writing – review & editing, Supervision. **Greg Conway:** Resources, Writing – review & editing. **Ian Henderson:** Resources. **Mike Shewring:** Resources. **Tony Cross:** Resources. **Eddy Ulenaers:** Resources. **Ruben Evens:** Conceptualization, Investigation, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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