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On the wintering ecology of Montagu's Harriers in West Africa: itinerancy in relation to varying annual environmental conditions

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Palearctic migrants wintering in Africa commonly use several sites throughout the winter, a strategy known as 'itinerancy'. In this way, migrants track spatio-temporal variation in resources. Despite the importance of this strategy for migratory landbirds, we still lack detailed understanding of how variation in environmental conditions affects site use and the timing of movements between sites. We tracked 125 adult Montagu's Harriers *Circus pygargus* from Western European breeding populations between 2005 and 2018 using satellite transmitters and GPS trackers. In total, data on 129 complete wintering seasons were obtained, including 33 individuals that were followed in two or more winters. Montagu's Harriers were itinerant, using on average 3.3 wintering sites, to which they showed high site fidelity between years. The first sites harriers used after arriving in their wintering range were situated in the northern Sahel and were dominated by natural and sparse vegetation. Subsequent sites, situated further south in the Sahel, were mainly dominated by agricultural and natural habitats. Sites used by harriers had higher habitat diversity compared to random sites. Home range size and activity (time flying per day, daily distance) peaked at the last sites harriers used (i.e. the site from which they commenced spring migration). For individuals tracked in multiple seasons, we showed that home range size did not depend on vegetation greenness. However, the birds covered longer daily distances at the same site in drier years compared to greener (wetter) years. Importantly, the timing of the movements between wintering sites was affected by local environmental conditions, with individuals staying for shorter durations and departing earlier from first sites in drier years and arriving earlier at last sites in greener years. We conclude that within the context of a strategy of itinerancy, Montagu's Harriers are faithful to the sites they use between years (spatial component), but flexible in the timing of use of these sites (temporal component), which they adjust to annual variation in environmental conditions.

Key words: winter ecology, site fidelity, Sahel, NDVI, long-distance migrants, *Circus pygargus*

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Most long-distance migrants spend more than half of their annual cycle outside their breeding areas (Newton 2008). In recent years, migration patterns of many species have been mapped thanks to advances in tracking technologies (Bridge *et al.* 2011, López-López 2016). Although we consequently have a much better idea about where birds spend the winter, this does not mean that we have achieved a better understanding of their ecology and how they are impacted by (varying) environmental conditions during winter. This is a serious omission, since many long-distance migrants are in decline (Sanderson *et al.* 2006, Vickery *et al.* 2014), and these declines have been associated with changes in environmental conditions (e.g. variation in rainfall; Baillie & Peach 1992, Szép 1995, Zwarts *et al.* 2009), including human-induced changes in land use (e.g. overuse of natural habitats; Zwarts *et al.* 2015).

Palearctic migrants wintering in Africa commonly use several sites throughout the winter, a strategy known as 'itinerancy' by Moreau (1972). The alternative strategy of residency is notably rare, especially among terrestrial species (landbirds), where species that appear resident (e.g. Pied Flycatcher *Ficedula hypoleuca*) might still perform small-scale seasonal movements within their winter home ranges (Salewski *et al.* 2002, Bil *et al.* 2023). The strategy of itinerancy is believed to be a way to track spatiotemporal variation in resources throughout the winter (Moreau 1972, Thorup *et al.* 2017). This does not mean that the birds are continuously on the move. Instead they use multiple distinct non-breeding residency sites (hereafter wintering sites). Intra-tropical movements between wintering sites can occur at relatively small scales of some hundred kilometres, as for example found in the Turtle Dove *Streptopelia turtur* moving between the Sahel and the Sudanian savannah (Eraud *et al.* 2013). But more commonly, these movements occur over thousands of kilometres, such as in the Redbacked Shrike *Lanius collurio* which moves from the Sahel to the Kalahari south of the equator (Tøttrup *et al.* 2012).

Although it is well-established that a strategy of itinerancy allows migrants to profit from ephemeral resources, we still lack a more detailed understanding of how individual wintering sites are used within and between years and the factors steering the timing of movements between sites. This was also acknowledged by Moreau who posed the question "The great problem is to know the extent to which an individual's movements in Africa, before settling into identically the same wintering site each year, are replicated during the lifetime of the migrant." (Moreau 1972, page 266). One possible way to answer this question is by tracking individual migrants in multiple winters.

The subject of this study is the Montagu's Harrier *Circus pygargus*, a long-distance migratory raptor (Ferguson-Lees & Christie 2001). European breeding birds winter in the western part of the Sahel (Limiñana *et al.* 2012c, Trierweiler *et al.* 2014), a relatively narrow zone with open savannah vegetation sandwiched between the Sahara in the north and wooded savannah in the south (Moreau 1972, Zwarts *et al.* 2009). On the basis of satellite tracking telemetry Trierweiler *et al.* (2013) described the strategy of itinerancy adopted by Montagu's Harriers, in which individuals use on average four distinct sites during the winter. Montagu's Harriers arrive in the Sahel at the end of the wet season, and wintering conditions progressively get drier during their stay (Schlaich *et al.* 2016). By moving between different sites during the winter, harriers track a shifting 'green belt' of vegetation (Normalized Difference Vegetation Index: NDVI) indicative of higher grasshopper abundance, their main prey in Africa (Mullié 2009, Mullié & Guèye 2010, Trierweiler *et al.* 2013). Only at their final wintering site, often located in the southern Sahel just at the southern edge of open savannah vegetation, do they face deteriorating environmental conditions. Harriers respond to declining grasshopper numbers at their last wintering sites by increasing their daily foraging time (Schlaich *et al.* 2016).

Since Trierweiler *et al.* (2013), we accumulated additional tracking data. Moreover, since 2009 we have also been tracking Montagu's Harriers with more accurate GPS trackers (Bouten *et al.* 2013). This allows for detailed analyses of site use, including many individual harriers that were tracked in several consecutive years. Specifically, with this dataset we are able to analyse within-individual differences in timing and site use between years in order to answer Moreau's longstanding question of how variation in environmental conditions affects site use and the timing of movements between sites.

METHODS

Overview

Since this study comprises several analyses, we provide here a short overview of the following sections. First, the two datasets we used, satellite-tracking data and GPS-tracking data, are described. This is followed by a description of site use, including the number of sites used, distance and direction between sites, arrival and

departure date, and duration of stay. The following definition of site categories is used throughout the paper: first site, i.e. wintering site used after arrival from autumn migration, last site, i.e. wintering site used before departure on spring migration, and intermediate site, i.e. all wintering sites used in-between, which could be more than one depending on how many sites an individual used. The next section describes the habitat composition at wintering sites and how this compares to random sites regarding habitat categories, habitat diversity and vegetation greenness. This is followed by a section on home range size and activity measures where daily home range size, daily time flying and daily distance covered are compared between site categories and total home range size is related to environmental variables (habitat and vegetation greenness). The next section describes site fidelity using a subset of birds that were tracked in at least three winters. In the last section, we investigated, for sites used in several years, the relation between site use (number of sites used, home range size, time spent flying and mean daily distance) to environmental conditions (vegetation greenness). Furthermore, within-individual differences in the timing of movements between sites in different years were analysed in relation to vegetation greenness.

All data selection procedures and analyses were performed in R v. 3.5.1 (R Core Team 2018). The specific R-packages and R-functions used are stated in the respective sections below.

Satellite-tracking data

We tracked 60 adult Montagu's Harriers (24 males and 36 females) using solar-powered satellite transmitters (PTT-100 series, Microwave Telemetry Inc., Columbia, MD, USA) between 2005 and 2018. Birds were captured in breeding areas in Germany ($n = 15$), The Netherlands ($n = 13$), the United Kingdom ($n = 12$), Belarus ($n = 8$), Denmark ($n = 8$) and Poland ($n = 4$). Of those, 49 individuals (23 males and 26 females) produced tracks including wintering movements. Due to birds being tracked in consecutive years, we recorded a total of 99 wintering tracks (year×individual combinations). After removal of incomplete tracks (start or end missing, gaps), the final satellite-tracking dataset comprised of 78 tracks of 38 individuals (16 males and 22 females; Table S1).

Satellite-transmitters were programmed either to a longer duty cycle of 10:48 h on:off (9.5-g and part of the 12-g tags) or a shorter duty cycle of 6:16 h on:off (12-g tags only) to recharge their batteries. Data were received via the ARGOS system (CLS, Toulouse,

France). Raw data were filtered using R-function 'sdafilter' from package 'argosfilter' v. 0.63 (Freitas 2012). This function filters location data obtained from Argos, using the Freitas *et al.* (2008) algorithm. Filtered data were checked visually and remaining outliers were removed by hand.

GPS-tracking data

We tracked 65 adult Montagu's Harriers (45 males and 20 females) using UvA-BiTS GPS trackers (Bouten *et al.* 2013; www.uva-bits.nl) between 2009 and 2018. Birds were captured in breeding areas in The Netherlands ($n = 39$), France ($n = 12$) and Denmark ($n = 9$), plus five at a wintering site in the area of Khelcom near the village of Diabel, Senegal. Of those, 39 individuals (28 males and 11 females) returned to the study areas and tracks including wintering movements could be downloaded via the local UvA-BiTS antenna system. A Danish male that over-summered in Africa (Sørensen *et al.* 2017) was removed from the dataset. Due to birds being tracked in consecutive years, we recorded a total of 63 wintering tracks (year×individual combinations). After removal of incomplete tracks (start or end missing, gaps), the final GPS-tracking dataset comprised of 51 tracks of 34 individuals (24 males and 10 females; Table S1).

GPS trackers were programmed to collect GPS positions at an interval of 5 min ($n = 15$ tracks), 10 min (10), 15 min (20) or 30 min (6) during the day and at maximum once per hour during the night. Intervals differed because memory storage increased with newer trackers. Positions with instantaneous speeds or trajectory speeds higher than 25 m/s were removed from the dataset. In addition, data were visually checked for outliers.

General description of the strategy of itinerancy

Each point, in the satellite-tracking data, or each day, for GPS-tracking data, was annotated as 'wintering site' (clustered movements within a site south of the Sahara), 'trip' (explorative movement outside a wintering site that could last one or several days but returned to the same site) or 'movement between sites' (movement between consecutive wintering sites). For examples see Figure S1. A stay at a wintering site was defined as lasting at least three days. Within a site, several night roosts could be used, but distances between consecutive roosts at a site were generally small (Figure S1D and E). Consecutive wintering sites were defined as being at least 10 km apart with no overlapping tracks (see Figure S1B). These annotations were done manually, since automated annotation using

a threshold of distance between consecutive roosts did not define all wintering sites correctly. This was due to birds with large home ranges occasionally having inter-roost distances of more than 10 km. A geographical wintering site could be revisited during the same winter. For each site, we calculated a centroid using mean latitude and longitude of all positions at this site. Sites were grouped into the categories first, intermediate and last (definition see above). In case only a single site was used, this was classified as last site.

Distance between consecutive sites was calculated using the R-function 'distMeeus', which calculates the shortest distance between two points on an ellipsoid, from the package 'geosphere' v. 1.5-7 (Hijmans 2017). To test whether the distance of movements between sites changed over time (e.g. shorter distances between consecutive sites earlier in the winter) we used Linear Mixed-Effects Models (LMM) with 'track' as random effect by means of R-function 'lme' from package 'nlme' v. 3.1-137 (Pinheiro *et al.* 2018).

Direction between sites was calculated using the R-function 'bearing', which calculates the initial bearing between two positions following the shortest path on an ellipsoid, from the package 'geosphere'. Change of direction of movements between sites during the course of the winter was modelled using LMM with 'track' as random effect. The difference in direction of movements between sites during the first and second half of the winter (before and after 15 December) was compared using a Pearson's Chi-squared test.

Arrival date at and departure date from the wintering grounds were defined as the first and last day at a stationary wintering site, as derived from the annotated dataset. Differences in mean arrival and departure date between the sexes were investigated using LMM with 'track' as random effect.

The length of stay at a site was the number of days spent at that site during a visit. The difference in length of stay at last sites compared to preceding sites was investigated using LMM with 'track' as random effect and the R-function 'testInteractions', which calculates and tests contrasts for factor interactions, from package 'phia' v. 0.2-1 (De Rosario-Martinez 2015).

Habitat composition at wintering sites and site selection
We used the GlobCover 2009 V2.3 land use map (ESA GlobCover 2009 Project: http://due.esrin.esa.int/page_globcover.php) with a 300-m resolution to investigate habitat composition at Montagu's Harriers' wintering sites. The whole wintering zone of our tracked birds was defined as the 100% MCP (maximum

convex polygon) around all wintering sites ($n = 449$, except for one site that was beyond the natural wintering range at the southern coast of Ghana; Figure S2). Sixteen of the 23 GlobCover land use categories occurred in the MCP (Figure S3, Table S2), with only seven categories covering more than 5% of the surface area. Habitat types ranged from bare and sparsely vegetated to grassland and shrubland savannahs and mosaic or agriculture dominated habitats. These subsequent habitat types were spatially correlated and approximately form a gradient from north to south with increasing vegetation cover and agricultural productivity. Habitat types may overlap except when at either end of the gradient (e.g. 'bare' and 'crops' seldom occur at the same site; Figure S4). The habitat composition at Montagu's Harriers' wintering sites was determined by extracting habitat information from all GlobCover map cells within a radius of 3.53 km around a site's centroid. Each such circle consisted of about 430 pixels of 300×300 m (c. 39 km²) which is similar to the average wintering home range size (median: 35 km², 193 sites; see Results). To illustrate variation in habitat composition across sites, we gave each habitat type a value (from 1 for sparsely vegetated habitats up to 13 for agricultural habitats; see Table S2) and subsequently calculated a habitat score for each site which is the average habitat value weighted by the habitats' surface areas. To determine which habitat types were dominant at each site, we combined similar categories into three main habitat groups: agricultural, natural and bare (see Table S2). Colours in graphs match these main groups: blues for bare and sparsely vegetated zones, greens for natural habitat types and reddish colours for agricultural habitats. A site was considered being dominated by one of these groups if the sum of all habitat types in one of the groups covered more than 50% of the surface area. If none of them did, the site was categorised into a fourth group called 'other'. Frequencies were compared using Pearson's Chi-squared tests.

The selection of wintering sites within the whole wintering zone (MCP) was analysed by compositional analysis (Aebischer *et al.* 1993) with the R-function 'compana' from package 'adehabitatHS' (Calenge 2006). This analysis was conducted for all wintering sites together and for the three subsets of sites (first, intermediate, last) separately. The habitat composition at harrier sites was compared to the habitat composition at random sites. For this, 4500 (ten times the number of harrier wintering sites) random points were created within the maximum and minimum latitude and longitude of harrier sites using R-function 'runif-

point' from package 'spatstat' v. 1.56-0 (Baddeley *et al.* 2015). As for the harrier wintering sites, habitat information from all GlobCover map cells within a radius of 3.53 km around each random point was extracted. Subsets of random sites were created for all, first, intermediate and last sites based on their respective MCPs (MCP-all see red polygon Figure S2, MCP-first, MCP-intermediate and MCP-last see Figure 4A). Sample sizes for random sites were 3295 for all, 1585 for first, 2408 for intermediate and 2490 for last sites. The average habitat composition at the random sites was compared to the habitat composition at sites used by harriers. Habitat categories that occurred less than 1% were excluded (nine habitat categories remained in the compositional analyses).

To investigate habitat diversity we compared Shannon's diversity indexes calculated using R-function 'diversity' from package 'vegan' v. 2.5-2 (Oksanen *et al.* 2018). Habitat diversity was compared between random sites and those used by the harriers. Frequency distributions of indexes were compared using *t*-tests.

In addition to habitat types, we used vegetation greenness at wintering and random sites as another environmental variable. It has been shown previously that vegetation greenness can be used as proxy for food availability (grasshoppers being the main prey in the winter diet of Montagu's Harriers (Szép & Møller 2005, Trierweiler & Koks 2009, Trierweiler *et al.* 2013, Schlaich *et al.* 2016). Therefore, we used NASA's MODerate resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) remotely sensed data (product MOD13Q1: data provided every 16 days at 250-m spatial resolution) downloaded from The Land Processes Distributed Active Archive Center (LP DAAC; https://lpdaac.usgs.gov) using R-package 'MODISTools' (Tuck *et al.* 2014). Around each harrier wintering site centroid, $25 \times 25 = 625$ pixels of 250×250 m (c. 39 km^2, which is similar to the average wintering home range size (median = 35 km^2, n = 193 sites; see Results)) were downloaded for the winters 2006/2007 till 2017/2018. The average of the 625 pixels was calculated for each 16-day period after removal of fill values (−3000) and then multiplied by the scaling factor of 0.0001 to get NDVI values between −0.2 and 1 (Zhu *et al.* 2013). The same was done for 750 of the random points within the MCP-all. Of those, 346 lay within MCP-first, 550 within MCP-int and 567 within MCP-last. To compare vegetation greenness between harrier sites and random sites, we used the closest NDVI values to three dates: the peak of harrier presence at first, intermediate and last sites (derived from Figure 1B).

These were NDVI measures on 30 September, 1 November and 6 March, respectively (in the leap years 2008, 2012 and 2016 these dates were 29 September, 31 October and 5 March, respectively). We selected the values on those dates of all 12 winters for harrier sites (5400 NDVI measures, first: 1500, intermediate: 2352, last: 1548) as well as random sites (n = 17,556, first: 4152, intermediate: 6600, last: 6804) and compared the frequency distributions using *t*-tests. To determine how dry or wet a year was in general, we calculated a 'yearNDVI' value for each year. This was done by using the mean NDVI values of the three dates for the 750 random points and calculating a median NDVI over these 750 values per year.

Home range size and activity measures

For this part, we only used data of the GPS-tracked Montagu's Harriers since these were more precise and denser (on average 92 positions per day for GPS-tracks compared to on average four positions per day for satellite tracks). Days with fewer than 75% of expected positions (<108 for 5-min, <54 for 10-min, <36 for 15-min, <27 for 20-min and <18 for 30-min interval tracks) were removed from this dataset. Two tracks had too many days with insufficient data and were removed, thus 49 tracks remained. For this analysis, days of movements between sites and trip days were excluded.

Daily home ranges were calculated as 90% kernel density estimation using R-function 'rhrKDE' from package 'rhr' v. 1.2.909 (Signer & Balkenhol 2015) with bandwidth parameter *h* determined by reference bandwidth estimation using R-function 'rhrHref'. Surface area of daily home ranges was retrieved using R-function 'rhrArea'. For the calculation of daily activity measures, only positions during daylight were used (daylight defined as being between nautical dawn and nautical dusk). Time spent flying and distance covered were calculated for each day. We determined for each GPS-position if the bird was sitting or flying using instantaneous speed and a threshold of 1.2 m/s (local minimum of a two-peaked frequency distribution of instantaneous speeds). The percentage of positions in flight was corrected by day length to determine the number of hours spent flying per day. Cumulative daily distance was calculated as the sum of distances between positions during a day. Temporal patterns in daily home range size, hours flying per day, and daily distance were analysed using LMM with 'site category' as fixed effect and 'year' as well as 'site ID' nested in 'individual' as random effects by means of R-function 'lmer' from package 'lme4' v. 1.1-17 (Bates *et al.* 2015) in combina-

tion with package 'lmerTest' v. 3.0-1 (Kuznetsova *et al.* 2017) and R-function 'testInteractions'.

We calculated the total size of wintering site home ranges (using all positions at a wintering site) using the Biased Random Bridge Movement Model (BRBMM; Benhamou 2011) which is a movement-based kernel density estimation to estimate the Utilization Distribution (UD) of an animal with serial autocorrelation of the relocations using R-function 'BRB' from package 'adehabitatHR' v. 0.4.15 (Calenge 2006). Tmax was set to 15 times the GPS-interval since home range size became stable from this value onwards for the different intervals (data not shown). We used the surface area of the 90% contour of the UD retrieved using R-function 'getverticeshr' from package 'adehabitatHR' to determine total home range size. Differences in total home range size between first, intermediate and last sites were analysed using LMM with 'site category' as fixed effect and 'year' as well as 'site ID' nested in 'individual' and 'number of days' as random effects and R-function 'testInteractions'. Spatial patterns in total home range size were modelled using a Linear Model (LM) with 'latitude' and 'longitude' as fixed effects. The effect of environmental variables on total home range size was investigated using LMM with 'NDVI' or 'habitat score' as fixed effects as well as 'site ID' nested in 'individual' as random effects. If total home range size differed between dry and wet years, it was also analysed using LMM with 'yearNDVI' as a fixed effect as well as 'site ID' nested in 'individual' as random effects.

Site fidelity

The dataset of repeated tracks comprised of 33 individuals of which 19 were tracked in two years, six in three years, six in four years and two in five years. In total, these birds used 164 different wintering sites. Each geographical site was given a 'site ID' and classified into one of the three site categories (first/intermediate/last). A site classified as 'first' in any one year was classified as such in all years. Similarly, a site classified as 'last' was classified as such in all years. In two cases, a site was used as first site in one and as last site in a second year and these two sites were classified as 'last'. Sites that were only used as intermediate sites but never as first or last, were called 'intermediate'.

Overall site fidelity was calculated as the percentage of sites reused by an individual between two years. For this, we took the sites visited by an individual in year 1 and counted how many of those it reused in year 2. If all sites were used in both years, the individual showed 100% site-faithfulness. If for example only one out of two of the sites were re-visited in year 2, it

showed 50% site-faithfulness, irrespective of new sites used in year 2. We did several two-year comparisons for birds with more than two years of tracking, i.e. we compared year 1 to year 2, year 2 to year 3, and so on.

To investigate in more detail how often a site was reused in relation to site category and duration of stay, we created a new dataset using only birds that were tracked in at least three years ($n = 14$). In case a bird was tracked in more than three years, we used its first three years for this analysis. With this balanced dataset we could determine if a site was used in all three years or only in one or two of the three years ('reuse category' 1, 2 or 3). Differences in duration of stay between sites were tested for using a Linear Model with 'reuse category' and 'site category' as fixed effects.

Within-individual differences in relation to environmental conditions

The variation within an individual between years and between individuals was investigated for several variables using within-subject centring in mixed models as described in Van de Pol & Wright (2009). This procedure allows to separate within-individual effects from between-individual effects by using the relative values (observation(ind,year) – mean observation (ind)) as well as the individual's mean as predictor variables in a mixed model with individual as random effect. For example, to explain the number of sites that an individual used in a winter in response to the environment 'yearNDVI', the model looked like this:

lme(number of sites ~ relative 'yearNDVI' + mean individual 'yearNDVI', random =~1|individual)

We used this procedure to investigate within- and between-individual effects of local NDVI on several response variables. For this, we used all sites that were at least used twice ($n = 71$) and calculated a mean NDVI value for the period that the bird had stayed at this site. These NDVI values thus are the mean of a different number of NDVI measurements (one every 16 days) depending on duration of stay. If no NDVI measurement lay exactly within the period that the bird used the site (short visit), we used the first NDVI measurement after the bird had left. For each site, a mean NDVI value was calculated over the years the site had been used, as well as the relative NDVI (difference of the NDVI at the site in that year minus the mean site NDVI).

Home range size and activity measures for GPS-tracked birds were available at 24 sites of 10 individuals used in two ($n = 16$), three (4) or four (4) years. Using one of the following response variables: site

home range size, mean hours flying per day, mean daily distance, we investigated within- and between-individual effects by including 'relative NDVI' and 'mean-site NDVI' as fixed effects and 'siteID' nested in 'individual' as random effect.

Timing of movements between sites was investigated for all birds, irrespective of tracking method. Within-individual differences in timing of movement between sites in relation to NDVI were tested in the same way. We used the departure date from first sites as well as the duration of stay at first sites (subset of 20 sites from 17 individuals), the duration of stay at intermediate sites (subset of 19 sites from 16 individuals) and the arrival date at last sites (subset of 32 sites from 30 individuals) as response variables. 'Relative NDVI' and 'mean site NDVI' were included as fixed effects and 'siteID' nested in 'individual' as random effect. All model output is given in Table 1.

RESULTS

General description of strategy of itinerancy
The Montagu's Harriers we tracked from their West European breeding sites used wintering sites between 5.9°N and 18.1°N and between 17.1°W and 17.6°E (Figure 1A). During a winter, birds used on average 3.3 ± 1.1 (range: 1–6) different sites (for site use patterns see Figure 2). The average number of site visits was a bit higher (3.5 ± 1.3, range: 1–8) because 14 individuals out of 72 (19.4%) revisited sites during the same winter. In total, 23 sites were revisited, most of them only once (21 occurrences) and two of them twice. Revisits occurred in 13% of tracks (17 out of 129 tracks) where birds revisited a single site during a winter (11 tracks) or even revisited two sites (6 tracks). Use of a single wintering site occurred only in 3% of the tracks (4 out of 129), twice by an individual in two consecutive years, once by an individual tracked in a single year and once in an individual that had five sites in the next year. Consecutive sites were on average 229 ± 238 km apart (10–1434 km, median: 135 km, $n = 321$ movements between sites). The travel distance between sites did not change with date during the course of the winter (LMM: $t_{195} = -1.255$, $P = 0.211$). Mean direction between consecutive sites was 194° ± 73° (SbW, range: 5–359°, $n = 321$ movements between sites). Direction changed with date over the season (LMM: $t_{195} = -5.213$, $P < 0.001$). Movements between sites in the first half of the winter (before 15
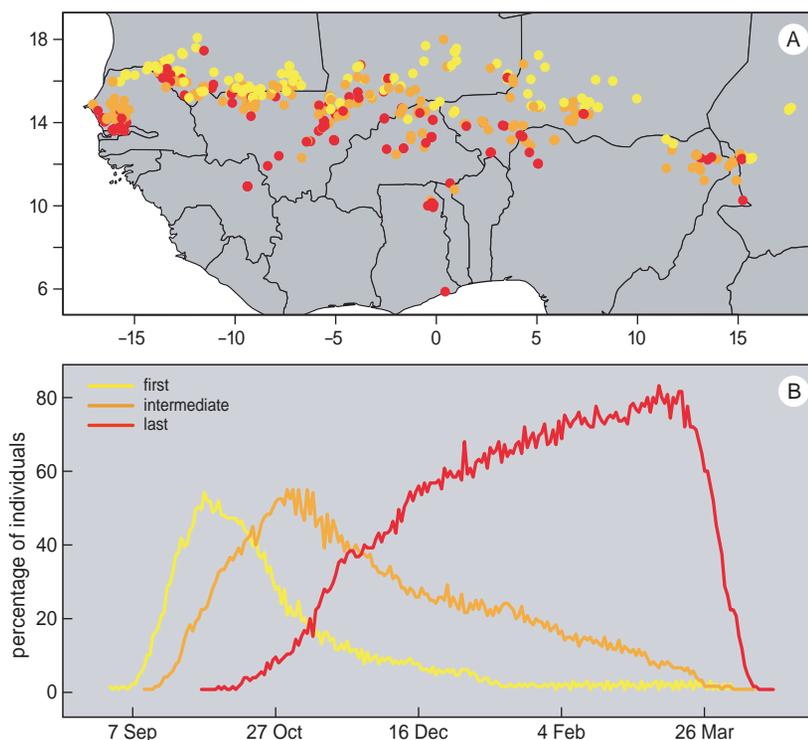
Figure 1. (A) Wintering sites of European GPS- and satellite-tracked Montagu's Harriers (129 winters). (B) Percentage of individuals at first, intermediate and last sites during the wintering season.
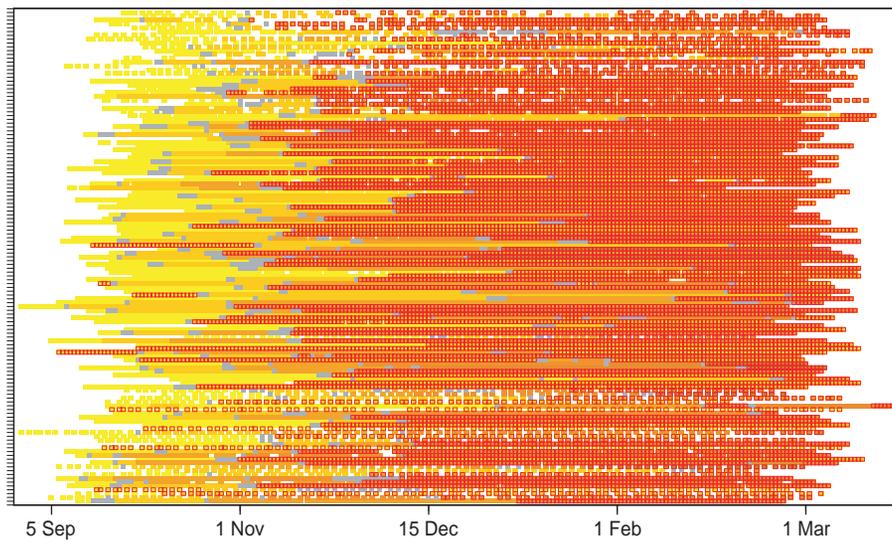
Figure 2. Site use pattern of European GPS- and satellite-tracked Montagu's Harriers (129 winters). Each row resembles one winter. For y-axis labels see Table S3. Colours indicate different sites: first sites yellow, consecutive sites in darkening orange colours. Days at last sites are marked with a red rectangle. Travel days between consecutive sites are indicated in grey. Days with no available data are visible as white rectangles.

December) were on average directed SSW ($207 \pm 57°$) and movements between sites after 15 December were directed SSE with a wider spread ($158 \pm 97°$; significant difference in frequencies, Pearson's Chi-squared test: $\chi^2_{15} = 86.6$, $P < 0.001$; Figure S5). Mean arrival date at the wintering grounds was 23 September $\pm$ 9 days (range: 30 August – 19 October, $n = 129$) and did not differ between the sexes (LMM: $t_{127} = -1.4$, $P = 0.164$). Spring departure was on average on 30 March $\pm$ 8 days (range: 5 March – 20 April, $n = 129$). Males departed on average 4.5 days earlier than females (LMM: $t_{127} = -3.25$, $P < 0.01$). The winter period had a total length of 188 ± 12 days (151–213 days, $n = 129$) of which 9 ± 7 days (0–37 days, $n = 125$) were days on which birds moved between wintering sites. Site visits lasted on average 52 ± 47 days (3–196 days, $n = 450$ visits). Length of stay at the last site of a wintering season (103 ± 49 days, 4–196 days, median = 113, $n = 129$) was significantly longer than at intermediate sites (33 ± 29 days, 3–153 days, median = 24 days, $n = 196$) or first sites (29 ± 23 days, 3–105 days, median = 25 days, $n = 125$; Pearson's Chi-squared test: $\chi^2_1 = -63.65$, $P < 0.001$; Figure 1B).

Habitat composition at wintering sites
Habitat composition varied greatly between wintering sites (Figure 3A and B). Sites ranged from being composed mostly of bare and sparsely vegetated habitat types to being exclusively located in agricultural habitats (Figure 3B). These are extremes on a continuum of

possible habitat compositions, in which no clearly separated groups could be distinguished. Hence, we summarised habitat composition by grouping sites dominated by one of the main dominant habitat groups (Figure 3C). Of first sites, around 30% were dominated by sparsely vegetated habitats. This decreased to about 10% for intermediate and last sites. Sites dominated by agricultural habitats increased significantly from 20% for first sites to nearly 50% for intermediate and last sites. Sites dominated by natural habitat types were mostly found among first sites (46%), this decreased for intermediate and last sites to about 30%. Frequencies of dominant habitats differed significantly between the three subsets (Chi-squared test: $\chi^2_6 = 49.65$, $P < 0.001$). The frequencies differed significantly between first and intermediate sites (Chi-squared test: $\chi^2_3 = 36.26$, $P < 0.001$) as well as between first and last sites (Chi-squared test: $\chi^2_3 = 39.53$, $P < 0.001$), but not between intermediate and last sites (Chi-squared test: $\chi^2_3 = 1.19$, $P = 0.755$).

Site selection by harriers
Overall, sites used by Montagu's Harriers contained more grassland, mosaic vegetation/cropland, mosaic shrubland/grassland, sparse vegetation and cropland than expected from the average cover of these habitats at random sites within the whole wintering range (MCP-all). Habitats that occurred less than expected were bare area, mosaic cropland/vegetation, woodland and shrubland (Compositional analysis: $\lambda = 0.258$, $P =$

0.01; Figure S6). First sites used by harriers contained more grassland, sparse vegetation, bare area, mosaic shrubland/grassland and mosaic vegetation/cropland than random first sites (MCP-first). Habitats that occurred less than expected were woodland, cropland and mosaic cropland/vegetation (Compositional analysis: $\lambda = 0.057$, $P = 0.01$; Figure 4B). The picture was different for intermediate sites where the area of mosaic vegetation/cropland, grassland, cropland, mosaic shrubland/grassland, and sparse vegetation was larger than for the corresponding random sites (MCP-intermediate). Less abundant were mosaic cropland/vegetation, bare area, woodland and shrubland (Compositional analysis: $\lambda = 0.276$, $P = 0.01$; Figure 4B). Last sites consisted more than expected of cropland, mosaic vegetation/cropland, mosaic cropland/vegetation, mosaic shrubland/grassland, and sparse vegetation compared to random sites (MCP-last). Last sites consisted less than expected of grassland, bare area, shrubland and woodland (Compositional analysis: $\lambda = 0.166$, $P = 0.01$; Figure 4B).

Overall, habitat diversity was significantly higher at sites used by Montagu's Harriers compared to random sites (Figure S7; 450 harrier wintering sites, 3295 random sites; *t*-test: $t_{565.19} = -6.188$, $P < 0.001$). Habitat diversity was highest at last sites (mean: 0.96, $n = 129$), followed by intermediate sites (0.82, $n = 196$) and first sites (0.81, $n = 125$; Figure 4C). It differed significantly between first and last sites ($t_{248.68} = -2.794$, $P < 0.01$) as well as between intermediate and last sites ($t_{303.32} = -2.777$, $P < 0.01$) but not between first and intermediate sites ($t_{208.08} = -0.216$, $P = 0.829$). Habitat diversity at first and last sites, but not at intermediate sites, was significantly higher than at random sites within their respective MCPs (Figure 4A and 4C; first: $t_{10046} = 2.083$, $P = 0.037$; intermediate: $t_{218.5} = -0.939$, $P < 0.349$; last: $t_{139.82} = -3.772$, $P < 0.001$).

Overall, vegetation greenness (NDVI) was slightly lower at sites used by Montagu's Harriers compared to random sites (Figure S8; 5400 NDVI values at harrier wintering sites, mean 0.23; 17,556 NDVI values at
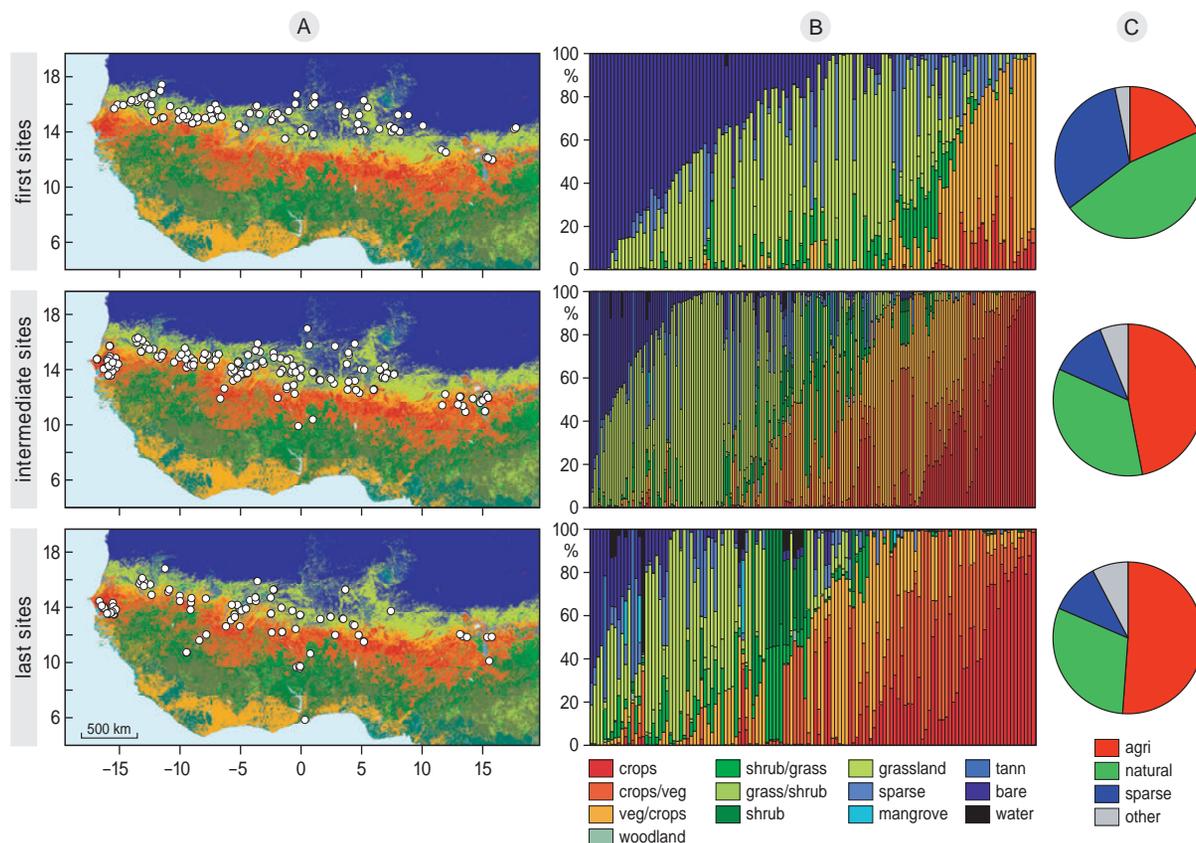
Figure 3. Habitat composition at wintering sites of GPS-tracked Montagu's Harriers for first ($n = 57$), intermediate (99) and last sites (59). (A) Location of wintering site centroids shown on GlobCover land use map. (B) Habitat use per site, each bar represents one site, ordered according to habitat score for graphical purposes. (C) Dominant habitats.
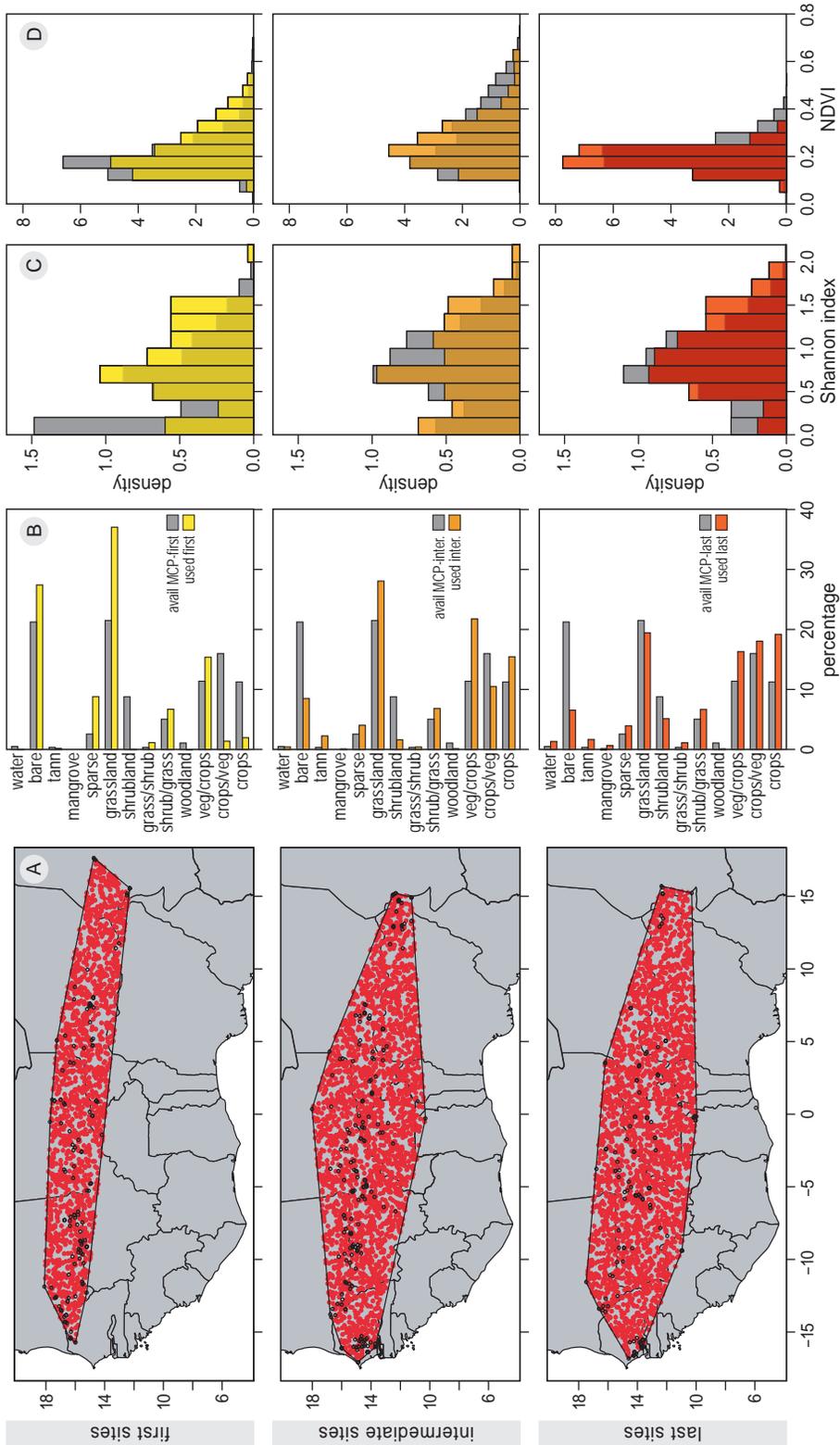
**Figure 4.** (A) Montagu's Harrier wintering sites (black points) and 100% MCP for first, intermediate and last sites. (B) Habitat used at harrier sites compared to wintering range MCPs. (C) Habitat diversity calculated as Shannon's diversity index for harrier wintering sites compared to random sites (grey bars). (D) NDVI (Normalized Difference Vegetation Index) at harrier wintering sites compared to random sites (grey bars).

random sites, mean = 0.24; *t*-test: $t_{565.2}$ = −6.19, $P < 0.001$). Vegetation greenness was highest at intermediate sites (mean = 0.26, *n* = 2352), followed by first sites (0.23, *n* = 1500) and last sites (0.19, *n* = 1548; Figure 4D). It differed significantly between first and intermediate sites (*t*-test: $t_{3352.2}$ = −9.33, $P < 0.001$), first and last sites (t_{2096} = 14.38, $P < 0.001$), as well as intermediate and last sites ($t_{3448.3}$ = 28.97, $P < 0.001$). Vegetation greenness at first sites was significantly higher than at random sites within the respective MCP (Figure 4AD; 4142 NDVI values at random sites within MCP-first, mean: 0.20; $t_{2409.6}$ = −10.11, $P < 0.001$). On the contrary, at intermediate and last sites vegetation greenness was lower compared to the corresponding

random sites (intermediate: 6600 NDVI values at random sites within MCP-int, mean = 0.29; $t_{5205.2}$ = 9.59, $P < 0.001$; last: 6804 NDVI values at random sites within MCP-last, mean = 0.21; $t_{2965.4}$ = 11.55, $P < 0.001$).

Home range size and activity measures

Daily home range size was smallest at intermediate sites (mean = 25.7 km²), slightly larger at first sites (28.6 km²; LMM: first-intermediate: χ^2 = 1.52, P = 0.218) and significantly larger at last sites (51.22 km²; first-last: χ^2 = 13.62, $P < 0.001$; intermediate-last: χ^2 = 30.47, $P < 0.001$; Figure 5B). Montagu's Harriers flew least at first sites (mean = 3.86 hours per day),
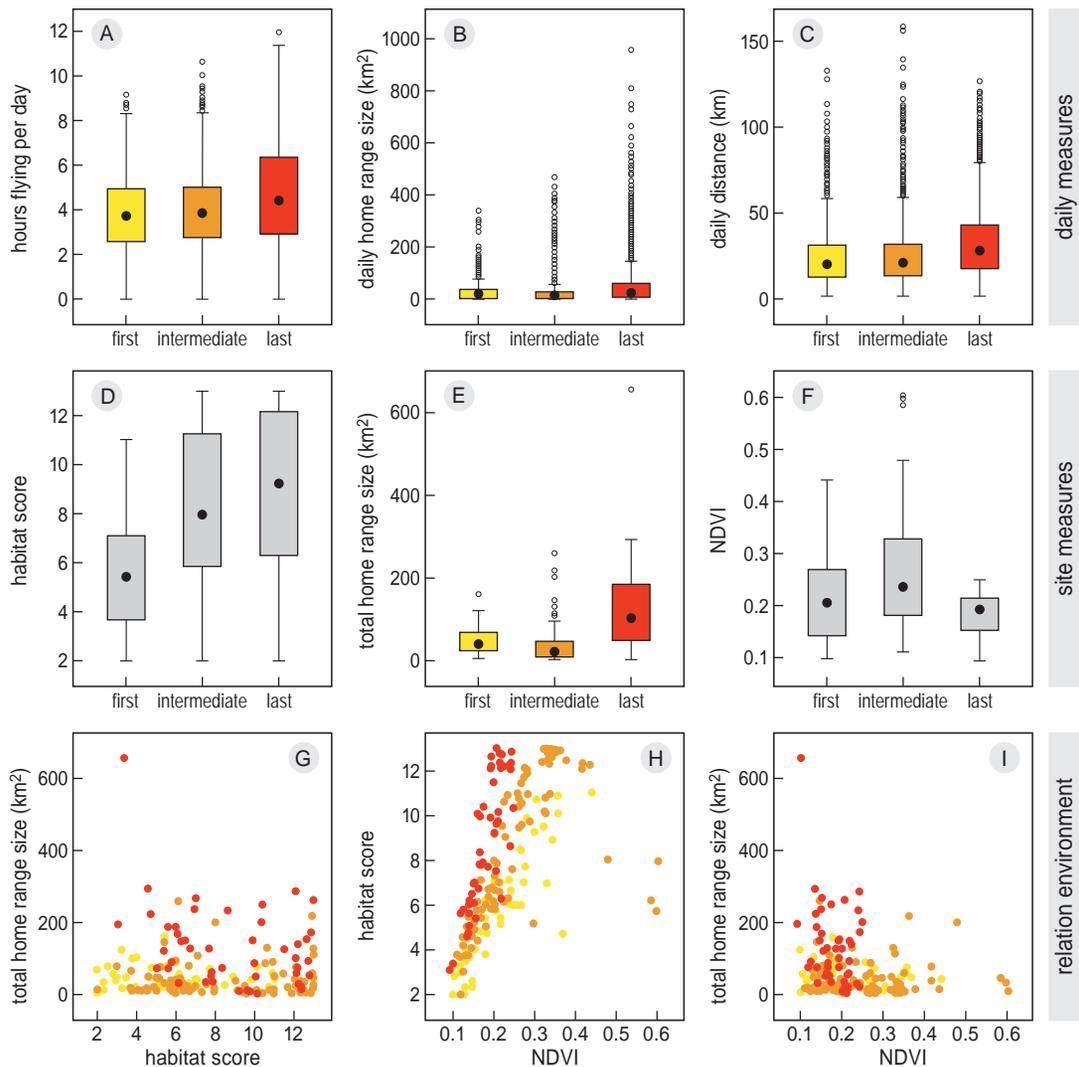
Figure 5. (A–C) Daily activity measures of GPS-tracked Montagu's Harriers, (D, F) environmental variables and (E) total site home ranges. (G, I) Relation between total home range and environmental variables, as well as (H) between environmental variables.
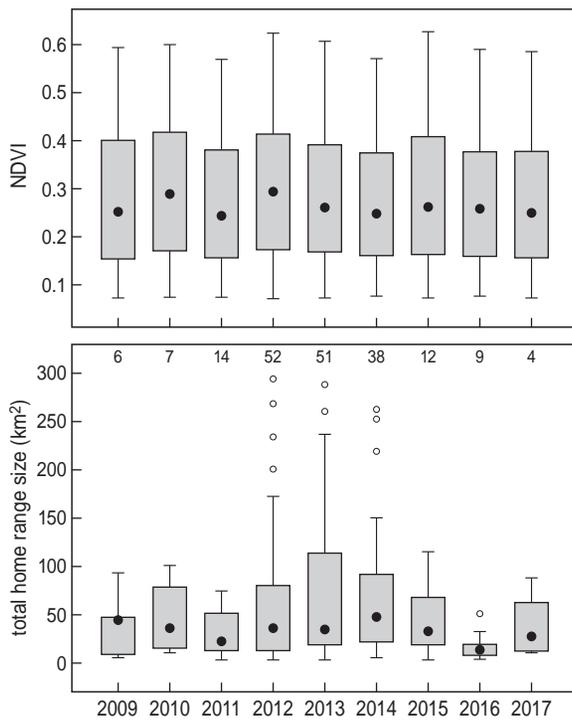
Figure 6. Yearly vegetation greenness (yearNDVI; top) and total home range size (bottom) for the years GPS-tracked Montagu's Harriers were followed. The number of site home ranges per year is given above the boxplots.

slightly more at intermediate sites (3.93; first-intermediate: $\chi^2 = 18.75$, $P < 0.001$) and much more at last sites (4.71; first-last: $\chi^2 = 6.02$, $P = 0.014$; intermediate-last: $\chi^2 = 52.93$, $P < 0.001$; Figure 5A). Daily distance covered was also shortest at first sites (mean = 25.1 km), slightly longer at intermediate sites (25.8 km; first-intermediate: $\chi^2 = 8.81$, $P < 0.01$) and was longest at last sites (33.1 km; first-last: $\chi^2 = 0.46$, $P = 0.50$; intermediate-last: $\chi^2 = 5.17$, $P = 0.046$; Figure 5C).

The median total home range size was 35 km^2 (mean = 63 km^2, range: 3–656 km^2, $n = 193$ sites; Figure S9). Total home range size for first sites (39.7 km^2) was only slightly larger than for intermediate sites (median = 21 km^2; first-intermediate: $\chi^2 = 0.85$, $P = 0.36$). Total home range size for last sites was much larger (101 km^2; first-last: $\chi^2 = 43.19$, $P < 0.001$; intermediate-last: $\chi^2 = 70.00$, $P < 0.001$; Figure 5E). Total home range size did not differ with latitude (LM: $t = -0.048$, $P = 0.962$) or longitude ($t = 0.421$, $P = 0.674$). However, total home range size did decrease significantly with increasing greenness values (LMM: $t_{187.54} = -3.83$, $P < 0.001$; Figure 5F and 5I). But total home range size did not differ with habitat

score ($t_{138.63} = -0.72$, $P = 0.472$; Figure 5D and 5G), despite NDVI and habitat score being positively correlated (Figure 5H). Finally, total home range size did not differ with annual vegetation greenness (yearNDVI; LMM: $t_{2.23} = 0.93$, $P = 0.44$; Figure 6).

Site fidelity

Montagu's Harriers that were tracked in two years, reused 75% of their wintering sites visited in the first year (median = 75%, 1st Qu. = 50%, 3rd Qu. = 100%, $n = 57$ two-year comparisons). Reuse was 60% for first sites (60 two-year comparisons), 50% for intermediate sites ($n = 52$) and 91% for last sites ($n = 64$). For the 14 birds that were tracked in three years, we saw that first and intermediate sites were used once, twice or three times. Last sites, however, were almost always used in all the three years (Figure 7A).
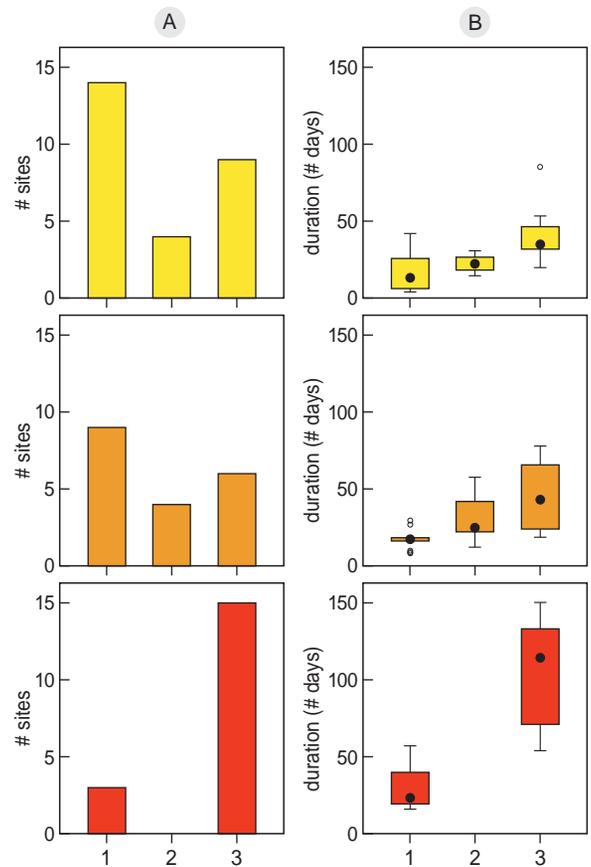
Figure 7. Reuse of geographical sites by individuals tracked in three consecutive years. (A) Sites reused once, twice or thrice during these three years for first (top), intermediate (middle) and last sites (bottom). (B) Length of stay at these sites according to reuse category and site category. Both significantly influenced length of stay (Linear Model: reuse category $F_2 = 39.5$, $P < 0.001$; site category $F_2 = 21.97$, $P < 0.001$).

Within-individual differences in relation to environmental conditions

Montagu's Harriers which were tracked in several years sometimes added or skipped one or more sites compared to the previous year. Neither drier nor wetter years (yearNDVI) explained within-individual or between-individual variation in the number of sites used (Table 1 (a)).

Home range size of harriers followed by GPS trackers did not correlate with annual variation in NDVI when present at these sites (within-individual comparisons). However, we found significant between-individual effects with individuals wintering in drier areas having larger home ranges (Table 1 (b), Figure 8A). The same was true for the time harriers spent flying; no within-individual effects were found but significant between-individual effects with individuals wintering in drier areas flying more (Table 1 (c), Figure 8B). A significant within-individual effect was only found for the mean daily distance flown at a site, with birds flying more kilometres at a site in a drier year, as well as between-individual effects with individuals wintering in drier areas flying more kilometres per day (Table 1 (d), Figure 8C).

Within-individual differences in the timing of movements between sites were mainly explained by local NDVI values. Harriers departed significantly earlier from a first site in a drier year than from the same site in a greener year (Table 1 (e), Figure 9A), and consequently also remained for a significantly shorter time at a first site when it was drier (Table 1 (f), Figure 9B). The duration of the stay at intermediate sites was not correlated to NDVI (Table 1 (g), Figure 9C). Timing of arrival at last sites tended to be later in a drier year compared to the arrival date at the same site in a greener year (Table 1 (h), Figure 9D). There were no between-individual effects in timing of movement (Table 1 (e–h)).

DISCUSSION

Itinerancy and other wintering strategies

Based on observations of (sudden) increases in bird numbers during ephemeral food peaks (such as migratory locust outbreaks), Moreau (1972) and Newton (2008) suspected that some migratory landbird species perform nomadic movements during the winter period. Nomadism was for example suspected in White Stork *Ciconia ciconia*, Lesser Spotted Eagle *Clanga pomarina* and Lesser Kestrel *Falco naumanni*. Later, tracking studies revealed that these species were itinerant instead (Berthold *et al.* 2001, Meyburg *et al.* 2015, Catry *et al.* 2011). A strategy of nomadism was also expected for Montagu's Harrier (García & Arroyo 1998). But as shown by Trierweiler *et al.* (2013) and in this study, the Montagu's Harrier joins the list of species that are itinerant. Importantly, we believe there remain no species that are nomadic during their non-breeding period in Africa. Instead, itinerancy seems to be the most common wintering strategy.

Residency, with birds using only a single site for the entire wintering period, is another possible wintering strategy. Examples include Osprey *Pandion haliaetus* (Kjellén *et al.* 1997, Alerstam *et al.* 2006), Common Redstart *Phoenicurus phoenicurus* (Kristensen *et al.* 2013), Northern Wheatear *Oenanthe oenanthe* (Schmaljohann *et al.* 2012) and Pied Flycatcher (Ouwehand *et al.* 2016). Importantly, residency often is part of a mixed strategy, with some individuals being resident and others being itinerant. This varies from most individuals being resident (10 out of 12 European Nightjars *Caprimulges europaeus* (Norevik *et al.* 2017), 17 out of 19 European Hoopoes *Upupa epops* (Bächler *et al.* 2010, van Wijk *et al.* 2016), 44 out of 66 Barn Swallows *Hirundo rustica* (Liechti *et al.* 2015) to most individuals being itinerant, e.g. 6 out of 9 Lesser

Table 1. Model output for several variables using within-subject centring in mixed models as described in van de Pol & Wright (2009).

	Within-individual effect NDVI					Between-individual effect NDVI				
	Estimate	SE	*df*	*t*-value	*P*-value	Estimate	SE	*df*	*t*-value	*P*-value
(a) Number of sites	–4.57	8.37	53	–0.55	0.590	–39.18	29.80	28	–1.31	0.200
(b) Home range size	–369.76	351.41	35	–1.05	0.300	–634.86	198.67	13	–3.20	**0.007**
(c) Hours flying	–3.81	3.83	35	–0.99	0.330	–9.88	2.42	13	–4.09	**0.001**
(d) Daily distance	–70.61	25.62	35	–2.76	**0.009**	–104.55	20.34	13	–5.14	**<0.001**
(e) Departure first	123.86	47.37	35	2.61	**0.013**	56.26	112.08	2	0.50	0.670
(f) Duration first	133.06	47.70	35	2.79	**0.009**	84.42	84.52	2	1.00	0.420
(g) Duration interm.	27.23	96.80	26	0.28	0.780	57.19	101.01	3	0.57	0.610
(h) Arrival last	–450.39	250.56	58	–1.80	0.070	–215.66	115.79	1	–1.86	0.310
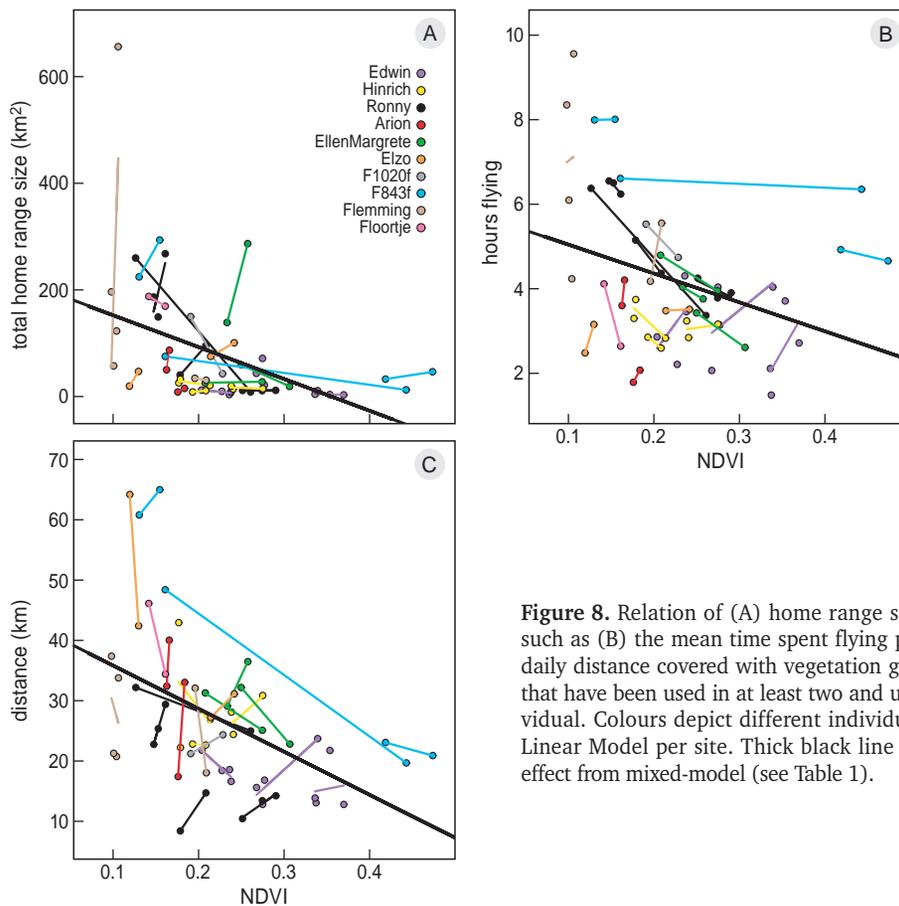
Figure 8. Relation of (A) home range size and activity measures such as (B) the mean time spent flying per day and (C) the mean daily distance covered with vegetation greenness (NDVI), for sites that have been used in at least two and up to four years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 1).

Kestrels (Catry *et al.* 2011, Limiñana *et al.* 2012a) and 11 out of 12 Northern Wheatears (Arlt *et al.* 2015). A mixed strategy also applies for the Montagu's Harrier, although the occurrence of residency is noticeably low; only in 3% of the cases (*n* = 129) a bird had a single wintering site. We conclude that in African-Palearctic migratory landbirds two main wintering strategies exist, itinerancy and residency, which are not a dichotomy of two distinct strategies but rather the extremes on a gradient of mixed strategies from full residency to complete itinerancy.

A factor that complicates the discussion about wintering strategies is that some authors consider part of the sites individuals use in their wintering range as migratory stopovers, especially in cases with large intra-African movements. For example, Tøttrup *et al.* (2012) consider the long stay of Red-backed Shrikes in the Sahel in autumn as a migratory stopover, rather than part of an itinerant wintering strategy. The question is whether this is the case, as the duration of this stay in the Sahel seems to be mainly determined by

food availability in the Sahel and the timing of the late autumn rains in the Kalahari (the shrikes' final destination) rather than by the time required to fuel for the flight from the Sahel to Southern Africa (Thorup *et al.* 2017). One might even argue that the distinction between migration and wintering is artificial anyway, as migrants are animals tracking spatiotemporal variation in favourable conditions, including resources, around the globe throughout the year (Thorup *et al.* 2017). But such a generalisation does not help to understand wintering strategies. Instead, we propose to be explicit about the functions of the sites used by the animals, in particular the relative contribution to 'wintering' and 'fuelling for migration'. In the example of the Red-backed Shrike the function of the stay in the Sahel seems two-fold, with the birds first making use of the lush vegetation in the Sahel at the beginning of the winter and 'waiting' for the conditions in the Kalahari to improve as part of an itinerant wintering strategy, and second preparing (fuelling) for the long flight from the Sahel to southern Africa. In the Montagu's Harrier,

fuelling before moving to the next site seems negligible as the distances between subsequent sites are relatively small (on average 229 km) and harriers travel to a large extent by energy-efficient soaring flight (Vansteelant *et al.* 2015). In addition, as fly-and-forage migrants Montagu's Harriers can forage on the way (Klaassen *et al.* 2017). Preparations for migration are only relevant at their last wintering site, from which they commence their long spring migration (Schlaich *et al.* 2016).

Variation in wintering behaviour

Itinerancy showed many faces among individuals. No two individuals behaved exactly in the same way. We found no overlap in sites used by different individuals during the winter. In fact, wintering sites were longitudinally distributed across a width of 3700 km. Directions and distances of movements between sites varied individually, as did the number of sites used during the winter (ranging from 1 to 6 sites) and
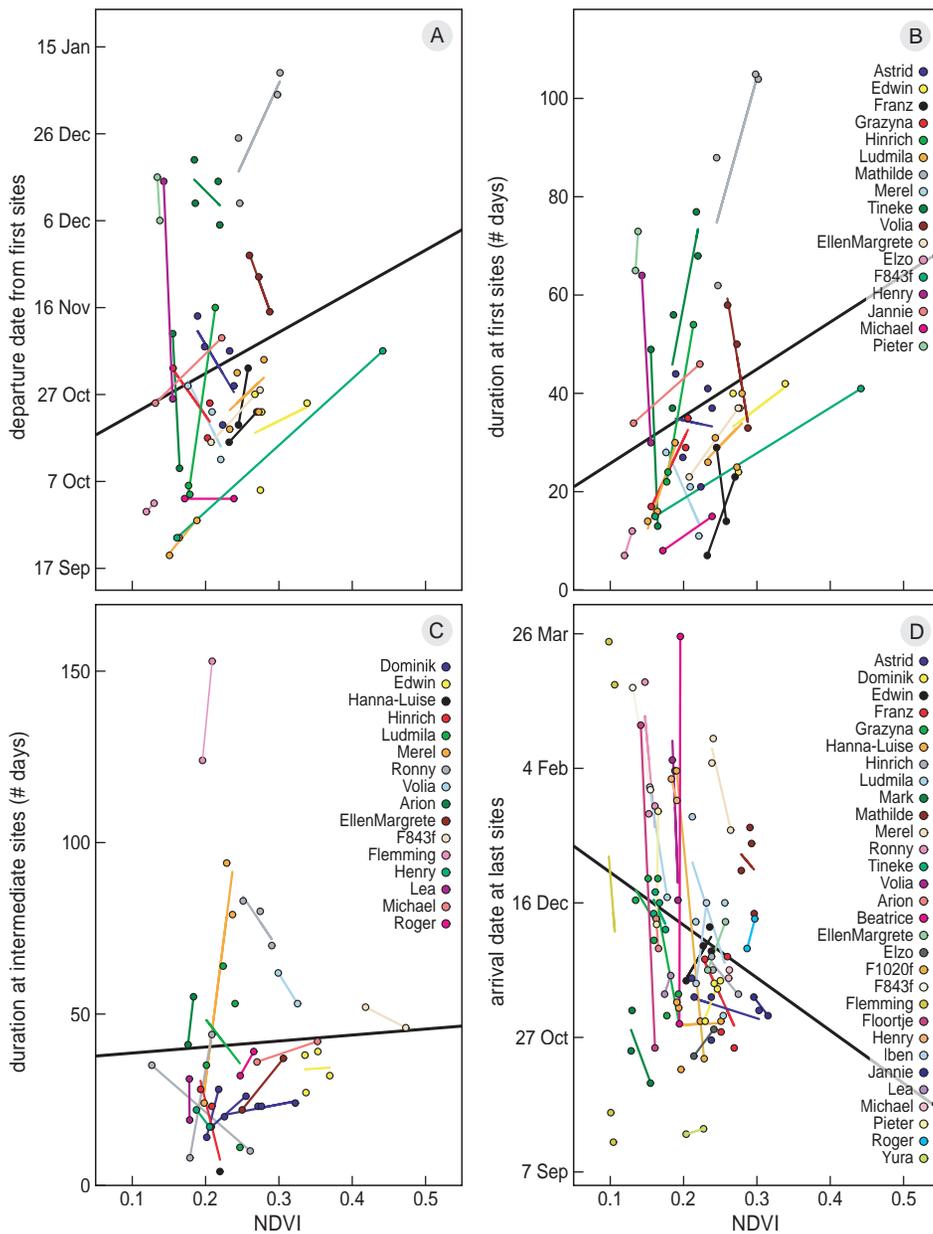
Figure 9. Relation of timing of movements between wintering sites with vegetation greenness (NDVI), for sites that have been used in at least two and up to five years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 1).

timing and duration of site visits (Figure 2). There is no 'average' bird. Instead, variation in behaviour is all important. The many different ways in which a strategy of itinerancy can be realised at the individual level suggest great flexibility of harriers to adjust to changes in spatiotemporal variation of environmental conditions. The remaining question is how these individual strategies develop, a question that can only be answered by tracking individuals from the first year of their lives (Sergio *et al.* 2014). The large number of tracked individuals allowed us some insight into this variation in behaviour and underlines the need to be careful when extrapolating from small sample sizes, an issue in many tracking studies.

Site fidelity of African-Palearctic migratory landbirds

Moreau (1969), and later Sauvage *et al.* (1998), Salewski *et al.* (2000) and King & Hutchinson (2001), compiled overviews of recaptures of ringed passerines and waders between years to check for winter site fidelity. They found evidence for winter site fidelity in 60 species, suggesting that site fidelity is common among African-Palearctic migrants. However, ringing is not particularly suitable to study site fidelity, especially as ringing operations typically are conducted each year at the same sites and the probability that a bird is recovered beyond its ringing site is extremely low. This results in a strong bias towards recaptures at the same site. On the basis of tracking data, Meyburg *et al.* (2015) reported strong winter site fidelity for Lesser Spotted Eagle, similar to Montagu's Harrier. Other tracking studies instead provided evidence for low site fidelity in White Stork (Berthold *et al.* 2002, 2004), European Hoopoe (van Wijk *et al.* 2016) and Common Redstart (Kristensen *et al.* 2013). Tracking is a strong method to study winter site fidelity, but hitherto studies that reported on repeated tracks are notably scarce. Consequently, we have an incomplete picture of winter site fidelity in African-Palearctic migratory landbirds, apart from the fact that both high and low winter site fidelity have been observed, irrespective of wintering strategy (residency versus itinerancy).

Our dataset included repeated journeys of 33 individuals tracked during multiple winters. With the data we are able to confirm the initial suggestion by Trierweiler *et al.* (2013) that Montagu's Harriers are to a large extent faithful to the sites they visit during the African dry season. Site fidelity has the advantage of local knowledge of the landscape, such as where to find food, where to find a place to drink, and where to find a safe place to roost (Trierweiler & Koks 2009). A disadvantage of site fidelity is that birds are less flexible in exploiting annual spatiotemporal variation in resources. Given the fact that Montagu's Harriers show strong site fidelity, we can conclude that local knowledge of the landscape apparently is more important than flexibility in site selection.

Habitat use

We found that wintering sites of Montagu's Harriers generally consisted of mosaics of grassland, cropland, shrubland, and sparse vegetation, as also reported by Limiñana *et al.* (2012b), Trierweiler *et al.* (2013) and Augiron *et al.* (2015). Importantly, sites used by harriers differed from random sites in having a higher habitat diversity. This preference might be related to food abundance, as diverse habitats generally host more biodiversity (Rosenzweig 1995) and therefore potentially more prey species. On the contrary, relatively high numbers of grasshoppers, the most important prey for Montagu's Harriers in Africa (Mullié 2009, Mullié & Guèye 2010), were found in the relative monotonous 'intensively' farmed area of Khelcom in Senegal (Mullié & Guèye 2010), an area also renowned for large communal harrier roosts (Augiron *et al.* 2015, own observations). Clearly, systematic field observations on prey abundance from sites varying in habitat diversity are needed to understand the selection of wintering sites by Montagu's Harriers.

Agricultural habitats stood out as one of the main habitats at the sites used by harriers, especially at intermediate and last sites. First wintering sites were generally located further to the north in the Sahel, where natural habitats dominate the landscape, which explains the lower occurrence of agricultural habitats at these sites rather than changes in habitat preferences (Figure 3). The importance of mixed agricultural habitats is not unique to Montagu's Harriers. Also species like Lesser Kestrel, Northern Wheatear and Whinchat *Saxicola rubetra* are frequently observed in agricultural habitats in the Sahel (Limiñana *et al.* 2012a, Wilson & Cresswell 2010, Blackburn & Cresswell 2015). The surface area of arable land with millet and sorghum has strongly increased in the Sahel in the second half of the previous century in order to feed the ever-growing human population (Brink & Eva 2009, Zwarts *et al.* 2009). This might benefit species that make use of agricultural habitats. On the other hand, the farming system itself has also changed, from an extensive system of shifting cultivation involving fallow land, to a more intensive system of permanent cultivation and a shortening of the crop-fallow cycle (Zwarts *et al.* 2023). Fallow land, representing natural habitat, might

be of particular importance for wintering birds, but we cannot judge the impact of these changes as we have an insufficiently detailed picture of habitat use and habitat selection. The latter is the consequence of the coarseness of the available habitat maps for the Sahel.

We relied on the GlobCover land use dataset with a 300-m resolution. Ground-truthing revealed that the accuracy of this dataset is mediocre (73% for the Sahel; Defourny *et al.* 2009). Moreover, the habitat classification for this dataset is rather coarse. For example, the category 'crops' does not provide information on what crop type was grown or whether the land was left fallow. Similarly, the category 'sparse vegetation' described different habitat types at different sites. At some sites it described sparsely vegetated grassy savannah, but we also noticed via ground-truthing that laterite plateaus were included in this category. Laterite plateaus have been noticed as important landscape structures for harriers (own observations), since shrubs on these plateaus host grasshoppers and farming is limited due to barren soil. Unfortunately, as fallow land and laterite plateaus are not identifiable on the land use map we used, we cannot investigate the importance of these habitats and landscape structures, and thus cannot fully exploit the potential of the small spatiotemporal resolution the birds were tracked with. Higher resolution maps with detailed habitat categories allowed formal habitat use and habitat selection analyses, which would provide the important information relevant to conservation on what habitats and landscape elements are used for foraging, resting and roosting. Using detailed high-resolution land use information is the key to future habitat selection analyses of migrants wintering in the Sahel.

The role of the Sahel in the annual cycle of migratory landbirds

Although Montagu's Harriers use several sites during the winter, their strategy of itinerancy is performed rather strictly within the narrow latitudinal band of the Sahel region. This is believed to reflect habitat suitability, with the Sahara north of the Sahel being too dry, and the wooded savannah south of the Sahel being too forested (Montagu's Harriers generally prefer open landscapes (Clarke 1996; see also Figure 3). For landbirds that have a strategy of itinerancy, this restriction to the Sahel is rather unique. There are only few other examples of itinerant migrant landbird species remaining in the Sahel, e.g. the Tawny Pipit *Anthus campestris* (Briedis *et al.* 2016) and the Northern Wheatear (Arlt *et al.* 2015), also habitat specialists of open arid landscapes.

This does not mean that the Sahel is not used by other migrants. On the contrary, itinerant migrants commonly use the Sahel before they continue to more southerly sites outside the Sahel biome. These species typically use the Sahel in the beginning of the winter, just after the rainy season has ended and vegetation is still green and food aplenty (Morel 1973). Examples include the Common Nightingale *Luscinia megarhynchos* (Hahn *et al.* 2014), Thrush Nightingale *Luscinia luscinia* (Stach *et al.* 2012), Common Cuckoo *Cuculus canorus* (Willemoes *et al.* 2014), Common Swift *Apus apus* (Åkesson *et al.* 2012) and Red-backed Shrike (Tøttrup *et al.* 2012). In eastern Africa only, Montagu's Harriers commonly also winter south of the Sahel (Clarke 1996), but as tracking data for these eastern populations is lacking, we have no information about their wintering strategy.

Tracking resources and the effect of annual variation in environmental conditions

The strategy of itinerancy in Montagu's Harriers was first described by Trierweiler *et al.* (2013). Our analyses, based on a much larger dataset, confirm these results. By relating the movements of the birds to vegetation greenness (NDVI), Trierweiler *et al.* (2013) also showed that harriers track a shifting 'green belt' of vegetation greenness indicative of higher grasshopper abundance. In contrast to Trierweiler *et al.* (2013) our dataset included a large number of tracks from the same individual in different winters, which, uniquely, allowed us to analyse effects of annual variation in environmental conditions at the level of individual birds.

We found that individuals responded to variation in environmental conditions by adjusting the timing of their movements (and thus the duration of their stays at sites). When conditions were relatively dry (lower NDVI values), the birds left their first site earlier, but arrived slightly later at their last wintering site. The patterns for intermediate sites were unclear, presumably due to variation in the number of intermediate sites used. But the overall picture suggests that birds adjust the timing of their movements to the environmental conditions encountered. Thus, Montagu's Harriers are not static in the timing of their movements between sites (no fixed behavioural response), but itinerancy is a flexible adjustment to between-year variation in environmental conditions encountered at their different individual wintering sites (plastic behaviour). In other words, behavioural plasticity is the mechanism behind the 'green belt hypothesis' (Trierweiler *et al.* 2013) of how Montagu's Harriers stay within a certain range of NDVI values that indicate highest food abundance.

Several other studies correlated (the timing of) movements between wintering sites with environmental conditions (Red-backed Shrike, Thrush Nightingale and Common Cuckoo (Thorup *et al.* 2017); Pallid Swift *Apus pallidus* (Norevik *et al.* 2018); Great Reed Warbler *Acrocephalus arundinaceus* (Koleček *et al.* 2018); Willow Warbler *Phylloscopus trochilus* (Lerche-Jørgensen *et al.* 2017)). In all these examples, conditions encountered at consecutive wintering sites improved after midwinter movements, suggesting that tracking spatiotemporal 'blooms' in resources is common in migratory landbirds. However, these analyses were made at the population level, and to our best knowledge there are no other studies showing this response within individuals, as we do in the current study.

We used vegetation greenness as a proxy for food availability instead of using direct data on prey availability (as, obviously, the latter is not available at the scale of the Sahel). Although this is a common approach in migration studies (e.g. Thorup *et al.* 2017), we do realize that insectivorous landbirds do not eat vegetation but the insects that rely on it. We should be aware of the potential shortcomings of using a proxy. Since Montagu's Harriers mainly prey on grasshoppers during winter and grasshoppers depend on green vegetation, NDVI seems a valid proxy for food abundance (Trierweiler *et al.* 2013, Schlaich *et al.* 2016). But at the same time we know that some species of shrubs carry green leaves but host no grasshoppers. In addition, more factors than vegetation alone may influence grasshopper abundance. We therefore would like to stress the importance of backing-up remote sensing data with on-the-ground observations of prey abundance.

Future prospects
Recurrences of individual Great Reed Warblers at the same site in Congo but at different times in subsequent years led Moreau (1972) to the question: "How far, one wonders, is it the rule for these intra-tropical movements to be replicated in the successive seasons when they finally came to anchor in the same few square meters of African vegetation?". For the Montagu's Harrier we can now answer this question, profiting from the fact that we had data on repeated journeys. Confirming that they are itinerant and showing high site fidelity, we showed that these migrants indeed replicate their intra-tropical movements but adjust the timing to environmental conditions.

Many open questions remain. We do not yet know what the consequences of this strategy are for the rest of the annual cycle. Are there carry-over effects to migration or even breeding, and what about fitness

consequences? The only hint we have for Montagu's Harriers is that individuals that departed later from drier last wintering sites also arrived later at the breeding grounds (Schlaich *et al.* 2016). How will this develop in the future in the light of further land use changes in the Sahel? Furthermore, we do not know whether conditions at the breeding sites or at the wintering sites are limiting populations of Montagu's Harriers and how this varies between populations. And finally, we do not yet understand how individuals' itinerary schedules originate.

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SAMENVATTING

Europese trekvogels gebruiken in Afrika een verscheidenheid aan strategieën om daar de winter door te komen. Individuen kunnen trouw zijn aan één overwinteringsplek, of individuen kunnen meerdere gebieden gebruiken tijdens de winter. Er werd verondersteld dat een deel van de soorten erratisch is, en opduikt op plekken met een tijdelijke overmaat aan voedsel. Zo zouden Grauwe Kiekendieven *Circus pygargus* bijvoorbeeld uitbraken van Afrikaanse treksprinkhanen *Locusta migratoria migratorioides* volgen. Zenderonderzoek heeft echter laten zien dat individuele Grauwe Kiekendieven weliswaar meerdere gebieden gebruiken, maar dat ieder individu tussen de jaren trouw is aan dat 'setje' gebieden. Zo'n strategie van wat je opeenvolgende plaatstrouw zou kunnen noemen ('itinerancy' in het Engels) blijkt bij veel landvogels voor te komen. Op deze manier lijken trekvogels in de winter variatie in ruimte en tijd in het voedselaanbod te benutten. Opvallend genoeg lijkt er geen soort te zijn waarvoor de strategie van rondzwerven van toepassing is. Als individuen plaatstrouw zijn aan hun opeenvolgende overwinteringsgebieden, hoe gaan ze dan om met variatie in het voedselaanbod tussen winters? Zijn ze star in de timing en duur van het gebruik van hun overwinteringsgebieden, of reageren ze op de voor de Sahel zo kenmerkende regenafhankelijke jaarlijkse fluctuaties in het voedselaanbod? Om dat te onderzoeken konden we putten uit de vliegbewegingen van 125 adulte Grauwe Kiekendieven die we tussen 2005 en 2018 in Europese broedgebieden van satelliet- of GPS-zenders hadden voorzien. Bij elkaar opgeteld leverden deze vogels gegevens voor 129 complete winterseizoenen, inclusief 33 individuen die in twee of meer winters konden worden gevolgd. De aankomst in de Sahel viel gemiddeld op 23 september (spreiding 30 augustus tot 19 oktober), zonder verschil tussen mannen en vrouwen. In het voorjaar vertrokken de kiekendieven gemiddeld op 30 maart (spreiding 5 maart tot 20 april), waarbij mannen 4,5 dagen eerder noordwaarts keerden dan vrouwen. De duur van het verblijf op de overwinteringsplekken in Afrika beliep gemiddeld 188 dagen, waarvan negen dagen werden gebruikt om van de ene naar de andere plek te vliegen. Gemiddeld gebruikten de Grauwe Kiekendieven 3,3 verschillende plekken als winterlocatie (met een individuele variatie van 1–6; gebruik van slechts één plek kwam maar in 4 op 129 winterseizoenen voor), waaraan ze in hoge mate plaatstrouw tussen de winters waren (75%). Opeenvolgende winterplekken lagen gemiddeld 229 km uit elkaar (mediane waarde 135 km), met een forse spreiding van 10 tot 1434 km. De verplaatsing in de loop van de winter was gemiddeld zuidwaarts gericht, waarbij de verplaatsingen na 15 december een meer zuidzuidoostwaartse component hadden. De laatste van de winterplekken werd het langst gebruikt (gemiddeld 103 dagen), de intermediaire en eerste plekken beduidend korter, namelijk respectievelijk 33 en 29 dagen. Bij elkaar bestreken de gezenderde vogels uit Europa (van Verenigd Koninkrijk tot en met Belarus) de westelijke en centrale Sahel over een breedte van 3700 km. Hoewel ze in uiteenlopende habitats voorkwamen, verschilde de habitatkeus naar seizoen (en dus winterplek): de noordelijkste plekken waren het meest natuurlijk en het schaarst begroeid (vooral savanne met kale plekken), de zuidelijker gelegen plekken waren gevarieerder met een groter aandeel landbouw. Grauwe Kiekendieven bevonden zich doorgaans in de meer gevarieerde landschappen binnen de regio. De kans is groot dat voedselaanbod daarin de sturende factor was. Het dagelijkse activiteitsgebied van de kiekendieven op de eerste winterplek omvatte gemiddeld 28,6 km^2; ze vlogen er per dag gemiddeld 3,86 uur, waarbij 25,1 km werd afgelegd. Dat verschilde nauwelijks van de intermediaire winterplekken, met respectievelijk 25,7 km^2, 3,93 dagelijkse vlieguren en een afgelegde afstand van 25,8 km. Op de laatste winterplek, waar ze, zoals gezegd, het langst verbleven, bestreken de kiekendieven een grotere oppervlakte (51,2 km^2), vlogen ze langer per dag (4,71 uur) en legden ze grotere afstanden af (33,1 km). Dat lijkt erop te wijzen dat de vogels het in die tijd van het jaar en op die plek niet makkelijk hadden om aan de kost te komen (meer vliegen over grotere afstanden). In relatief droge jaren legden de kiekendieven meer kilometers per dag af binnen hetzelfde gebied in vergelijking met relatief groene (natte) jaren. Bovenal pasten de kiekendieven hun timing aan; in drogere jaren bleven de vogels korter in hun eerste gebied en verplaatsten ze zich eerder naar het volgende gebied. In nattere jaren kwamen de vogels eerder in hun laatste gebied aan. We concluderen dat binnen een strategie

van opeenvolgende plaatstrouw de kiekendieven star zijn in welke gebieden ze gebruiken (ruimtelijke component) maar juist flexibel in de timing en duur van het gebruik van deze gebieden (temporele component). Dit is dus de manier hoe de kiekendieven binnen een strategie van opeenvolgende plaatstrouw omgaan met jaarlijkse fluctuaties in het voedselaanbod. Met dit zenderonderzoek hebben we dus een beter beeld gekregen over hoe de strategie van opeenvolgende plaatstrouw precies in elkaar steekt. En bovenal hebben we geleerd dat de gemiddelde Grauwe Kiekendief niet bestaat.

RÉSUMÉ

Les oiseaux migrateurs européens utilisent des stratégies variées lors de leur séjour en Afrique durant l'hiver boréal. Certains sont fidèles à un unique site d'hivernage, quand d'autres se déplacent entre plusieurs zones au sein d'un même hiver. On a pensé que certaines espèces sont erratiques et se déplacent à la recherche de secteurs où des pics de disponibilité alimentaire temporaires se produisent. Il a semblé par exemple que les Busards cendrés *Circus pygargus* suivent les invasions de Criquets pèlerins africains *Locusta migratoria migratorioides*. Cependant, des études utilisant des émetteurs suivis par satellite ont montré que, bien que les Busards cendrés utilisent plusieurs territoires, chaque individu est fidèle à cet ensemble de territoires d'une année sur l'autre. Cette stratégie d'itinérance entre des territoires hivernaux successifs semble répandue chez de nombreuses espèces terrestres. De cette manière, ces espèces migratrices semblent en mesure exploiter les variations spatio-temporelles de l'offre alimentaire en hiver. Mais si les individus sont fidèles à ces sites d'hivernage successifs, comment s'adaptent-ils aux variations interannuelles de la disponibilité alimentaire ? Le calendrier et la durée d'exploitation de leurs sites d'hivernage sont-ils figés ou répondent-ils aux fluctuations annuelles des ressources alimentaires, qui dépendent des pluies et sont caractéristiques du Sahel ? Pour étudier cette question, nous avons analysé les mouvements de 125 Busards cendrés adultes que nous avons équipés d'émetteurs satellites ou GPS dans les zones de reproduction européennes entre 2005 et 2018. Au total, ces oiseaux ont fourni des données correspondant à 129 saisons hivernales complètes et 33 individus ont pu être suivis sur deux hivers ou plus. L'arrivée au Sahel a eu lieu en moyenne le 23 septembre (entre le 30 août au 19 octobre), sans différence entre les mâles et les femelles. Au printemps, les busards sont partis en moyenne le 30 mars (entre le 5 mars au 20 avril), les mâles repartant vers le Nord en moyenne 4,5 jours plus tôt que les femelles. La durée du séjour sur les sites d'hivernage en Afrique a été en moyenne de 188 jours, dont 9 jours de déplacements d'un site à un autre. En moyenne, les Busards cendrés suivis ont utilisé de 1 à 6 sites différents pour leur hivernage, avec une moyenne de 3,3 sites et les individus étaient très fidèles d'un hiver à l'autre (75%). L'utilisation d'un unique site n'a été constaté que 4 fois sur 129 saisons hivernales. Les sites consécutifs

étaient en moyenne distants de 229 km (valeur médiane de 135 km), avec une variation considérable de 10 à 1434 km. Les déplacements au cours de l'hiver étaient en moyenne dirigés vers le Sud, ceux réalisés après le 15 décembre ayant une composante orientale et étant orientés Sud-Sud-Est. Le dernier des sites d'hivernage a généralement été celui occupé le plus longtemps (103 jours en moyenne), tandis que les temps de séjour sur les sites intermédiaires et initiaux ont été nettement plus courts, avec 33 et 29 jours respectivement. Ces Busards cendrés provenant de longitudes variées, du Royaume-Uni à la Biélorussie, ont couvert le Sahel occidental et central sur une largeur de 3700 km. Bien qu'ils aient fréquenté des habitats divers, leur choix d'habitat a avant tout reflété la saison et donc de la localisation du site d'hivernage : les sites les plus septentrionaux étaient les plus naturels et occupés par une végétation clairsemée (principalement de la savane avec des parcelles dénudées), tandis que les sites plus méridionaux étaient plus variés avec une plus grande proportion d'agriculture. Les Busards cendrés ont montré une tendance à s'établir dans des paysages en moyenne plus variés que ceux disponibles aux alentours. Il est probable que l'approvisionnement en nourriture soit le facteur de choix déterminant. La zone d'activité quotidienne des busards sur leur site d'hivernage initial s'est élevée en moyenne à 28,6 km^2. Ils y ont volé en moyenne 3,86 heures par jour, couvrant 25,1 km. Les valeurs obtenues sur les sites d'hivernage intermédiaires sont proches, avec respectivement 25,7 km^2, 3,93 heures de vol par jour et une distance parcourue de 25,8 km. Sur le dernier site en revanche, où ils ont séjourné le plus longtemps, les busards ont couvert une plus grande surface (51,2 km^2), volé plus longtemps par jour (4,71 heures) et parcouru de plus grandes distances (33,1 km). Cela semble indiquer qu'à cette époque de l'année, les conditions de vie ont été plus difficiles (plus de vols effectués et sur de plus longues distances). Lors des années relativement sèches, les busards ont parcouru plus de kilomètres par jour dans la même zone que lors des années plus humides et verdoyantes. Et surtout, ils ont adapté leur calendrier : lors des années sèches, les oiseaux sont restés moins longtemps dans leur première zone et ont rejoint plus tôt la suivante. Et lors des années plus humides, les oiseaux sont arrivés plus tôt dans leur dernière zone. Cette étude nous permet de conclure que la stratégie d'itinérance des Busards cendrés entre des sites auxquels ils sont fidèles comporte une composante spatiale figée (fidélité aux sites) et une composante temporelle flexible (durée d'utilisation variable des sites). Cette itinérance entre des sites connus constitue donc la stratégie adoptée par le Busard cendré pour faire face aux fluctuations annuelles de la disponibilité alimentaire. L'utilisation d'émetteurs suivis par satellite nous a permis de mieux comprendre plus précisément comment celle-ci fonctionne, mais également d'observer que chaque individu l'applique de façon très personnelle.

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