

A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel

Christiane Trierweiler^{1,2,3,4*}, Wim C. Mullié^{5,†}, Rudi H. Drent^{1,‡}, Klaus-Michael Exo³, Jan Komdeur², Franz Bairlein³, Abdoulaye Harouna⁶, Marinus de Bakker⁷ and Ben J. Koks⁴

¹Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands; ²Behavioural Ecology and Self-organisation Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands; ³Institute of Avian Research 'Vogelwarte Helgoland', An der Vogelwarte 21, 26386, Wilhelmshaven, Germany; ⁴Dutch Montagu's Harrier Foundation, PO Box 46, 9679 ZG, Scheemda, The Netherlands; ⁵Project Biological Management of Locusts and Grasshoppers, Agriculture Directorate, Ministry of Agriculture, Dakar, Senegal; ⁶PO Box 153, Zinder, Niger; and ⁷Groningen Centre for Spatial Information, University of Groningen, Landleven 1, 9747 AD, Groningen, The Netherlands

Summary

1. Mid-winter movements of up to several hundreds of kilometres are typical for many migratory bird species wintering in Africa. Unpredictable temporary food concentrations are thought to result in random movements of such birds, whereas resightings and recoveries of marked birds suggest some degree of site fidelity. Only detailed (e.g. satellite) tracking of individual migrants can reveal the relative importance and the causes of site choice flexibility and fidelity. The present study investigates how mid-winter movements of a Palaearctic-African migratory raptor, Montagu's harrier *Circus pygargus*, in the Sahel of West Africa are related to the availability of food resources.

2. Thirty harriers breeding or hatched in northern Europe were satellite tracked (2005–2009). On average, four home ranges, each separated by *c.* 200 km, were visited during one overwinter stay in the Sahel. Wintering home ranges were similar in size to breeding season home ranges (average over wintering and breeding home range size *c.* 200 km²), and harriers showed high site fidelity between years.

3. Most preferred habitat types in the Sahel were mosaics of grass- and cropland, indicating similar habitat preferences in both the breeding- and wintering seasons.

4. The main prey of Montagu's harriers in the Sahel were grasshoppers *Acrididae*. Highest grasshopper numbers in the field occurred at relatively low vegetation greenness [normalized difference vegetation index (NDVI) values 0.17–0.27]. We used NDVI as a proxy of food availability for harriers.

5. During their overwinter stay, Montagu's harriers moved in a South–South-western direction between consecutive home ranges. The birds selected areas within the range of NDVI values associated with high grasshopper numbers, thus tracking a 'green belt' of predictable changes in highest grasshopper availability.

6. Contrary to earlier hypotheses of random movements in the Sahelian-wintering quarters, the present study shows that Montagu's harriers visited distinct home ranges, they were site-faithful and tracked seasonal changes in food availability related to previous rainfall patterns, caused by the shifting Intertropical Convergence Zone. Itinerancy may be the rule rather than an exception among insectivorous birds wintering in African savannahs.

Key-words: acridivorous birds, annual cycle, kernel home range, *Ornithacris cavroisi*, satellite telemetry

*Correspondence author. E-mail: christianetrierweiler@yahoo.com

†Deceased on 9 September 2008.

‡Current address: BP 45590, Dakar-Fann, Senegal.

Introduction

Itinerancy is a phenomenon defined as stepwise movements of migratory birds within their non-breeding (wintering) ranges, at a scale of up to several hundreds of kilometres (Moreau 1972). Itinerancy is well known for a number of Palaearctic-African migratory species in sub-Saharan Africa, but driving factors and ecological circumstances have been poorly studied (Moreau 1972; Curry-Lindahl 1981; Jones 1995; Rappole & Jones 2002). A major driving factor is thought to be temporary food availability, although evidence is lacking, mainly because of logistical challenges for ecological monitoring at large scales in remote areas (Rappole & Jones 2002; Newton 2008).

New tracking technologies such as satellite telemetry enable tracking individual birds through space and time over large distances, often for years. At the same time, geospatial data from remote sensing, such as the Normalized Difference Vegetation Index (NDVI) can be used to assess habitat availability and as a proxy for food availability as well (Pettorelli *et al.* 2005; Szép & Moller 2005; Rasmussen, Wittemyer & Douglas-Hamilton 2006; Balbontin *et al.* 2009). Thus, for the first time, both methodologies can be combined to reveal the extent of itinerant movements and their underlying causes.

Among Palaearctic-African migratory bird species, many raptor species have been subject to detailed tracking studies. Many studies have collected data on the breeding and migration ecology of such species, but their wintering ecology has received less attention (Meyburg, Meyburg & Barbaud 1998; Kjellén, Hake & Alerstam 2001; Gschwend *et al.* 2008; Strandberg *et al.* 2008). Here, we study the wintering ecology of Montagu's harriers *Circus pygargus*, which breed in the Palaearctic and winter in sub-Saharan Africa. The harriers spend some 6 months per year in semi-arid and open habitats of Western, Eastern or Southern Africa (Moreau 1972; Clarke 1996; Trierweiler & Koks 2009). The main prey of these birds during the non-breeding season in sub-Saharan Africa are grasshoppers, or migratory locusts, as particularly observed during outbreaks (Thiollay 1989; Cormier & Baillon 1991; Arroyo & King 1995). Gregarious migratory locusts may store more fat and thereby deliver more energy than non-migratory ones, but they can develop chemical defences by consuming native toxic plants (Steedman 1988; Sword *et al.* 2000). Recent data reveal a more detailed perspective on the role of migratory locusts in the diet of Montagu's harriers. In years without migratory locust outbreaks, non-migratory grasshopper species were identified as main preys of Montagu's harriers wintering in Niger and Senegal (Mullié 2009; Mullié & Guèye 2009; Trierweiler & Koks 2009). As locust recession years prevail, non-migratory grasshoppers may generally be a much more reliable and predictable food source than migratory ones (Moreau 1972; Clarke 2002). According to Thiollay (1989), grasshopper

numbers are highest in the northern Sahel zone in the beginning of the dry season, whereas peak grasshopper abundances in the middle and late dry season are found in the more southern Sudan and Guinea zones, respectively. Thiollay (1989) suggested that this seasonal southward shift in peak abundance of grasshoppers is tracked by migratory birds that prey on grasshoppers (Mullié 2009), thereby causing itinerancy in these birds.

Our study aimed to describe spatial and temporal patterns of regional movements of Montagu's harriers in West Africa, based on data of 30 Montagu's harriers satellite-tagged in breeding areas in The Netherlands, Germany, Denmark, Poland and Belarus and tracked throughout their overwinter stay in West Africa. The overwinter movements of the harriers were revealed using satellite telemetry.

We investigated whether Montagu's harriers were selective in their choice of habitats in the Sahel and tested whether their movements were correlated with the availability of their grasshopper prey, as indicated by NDVI. As leaf-eating grasshoppers depend on green vegetation, we used vegetation greenness (NDVI) as a proxy for grasshopper densities and vegetation cover, and thus food availability for Montagu's harriers, similar to studies in Swainson's Hawk *Buteo swainsoni*, which consume grasshoppers during non-breeding periods in South America (Johnson, Nickerson & Bechard 1987; Sarasola & Negro 2005; Sarasola *et al.* 2008).

Materials and methods

SATELLITE TELEMETRY

A total of 30 Montagu's harriers [19 females (16 adults, 3 juveniles) and 11 males (7 adults, 4 juveniles)] from 9 breeding areas in North-west and North-east Europe were tracked using satellite transmitters from summer 2005 to spring 2009 (11 were tagged in The Netherlands, 7 in Germany, 2 in Denmark, 4 in Poland, 6 in Belarus). The solar satellite transmitters of 9.5 or 12 g weight were of the PTT-100 series (Microwave Telemetry Inc., Columbia, MD, USA). Transmitters were programmed to on/off cycles of either 10:48 or 06:16 h. During every transmission cycle, a variable number of fixes of variable quality [indicated by the ARGOS location error estimate 'location class' (LC), CLS 2011] was received from each transmitter. Two filtered data sets were created: (i) for analyses of temporal movement patterns, (ii) for spatial analyses.

IDENTIFICATION OF HOME RANGES IN THE WINTERING AREAS (DATA SET 1)

Arrival of migrants in the wintering area was defined in data set 1 as the beginning of the first stay of >1 day in the same home range south of the Sahara (south 18°N). Average arrival dates were in the months September (females) to October (males; Trierweiler 2010). Home range centres were defined as the average of latitudes and longitudes of at least two consecutive positions that did not deviate more than 0.1 decimal degrees (Trierweiler 2010; C. Trierweiler & R.H.G. Klaassen unpublished). The resulting average position (geographical centre of the

home range) was the reference point of the arrival. When the bird was within a 40-km radius of this geographical centre, it was assumed that it had arrived in a home range (Appendix S1). Departure from the wintering area was defined as the end of the last stay of >1 day in the same home range south of the Sahara. The average departure date (no difference between females and males) was in the month of March (Trierweiler 2010).

Data set 1 had a relatively high temporal resolution (with a maximum of one fix per day). Only the highest quality signal (smallest ARGOS location error estimate) for every transmission period was selected (Fuller, Seegar & Schueck 1998; Strandberg *et al.* 2008; Trierweiler 2010; C. Trierweiler & R.H.G. Klaassen unpublished). Outliers (fixes implying implausible large distances and high speeds moved) were identified graphically by plotting date against latitude and longitude and were removed manually. The resulting data set consisted of 2879 fixes representing 31 stays in the wintering area of 22 birds in four different non-breeding periods: 2005/2006, 2006/2007, 2007/2008 and 2008/2009. Our sample included 12 adult and 2 juvenile females as well as 6 adult and 2 juvenile males. No data from the stay in the wintering area were retrieved from the remaining 8 birds: the cause was death or transmitter failure in the breeding areas ($n = 5$) or on first tracked autumn migration ($n = 3$). Death or transmitter failure occurred at the same proportion for females and males. The loss among juveniles was higher than in adults (in our original sample were 77% adults and 23% juveniles, in the remaining sample were 82% adults and 18% juveniles), which can be explained by higher juvenile mortality. Different subsets of the data were used for subsequent analyses, each according to the information and precision required. When including only birds that survived the stay in the Sahel, 28 tracks of 19 birds remained (death/transmitter failure in the wintering area of 1 adult male and 1 adult female; poaching of 1 adult female was confirmed by Nigerian authorities). When including only tracks that ended with the departure of the bird from the wintering area, 25 tracks of 17 birds remained. When including only tracks that did not contain periods without signals of >8 days, and which ended with the departure of the bird from the wintering area, 23 tracks of 16 birds remained.

HOME RANGE CONTOURS AND MOVEMENT PATTERNS IN THE WINTERING AREA (DATA SET 2)

Data set 2, which was used for spatial analyses, was a more strictly filtered data set (maximum one fix per day) with a lower temporal resolution but higher spatial reliability (accuracy) than data set 1. The set was filtered by The Douglas Argos-Filter (<http://alaska.usgs.gov/science/biology/spatial/douglas.html>), retaining fixes with smallest ARGOS error estimates (ARGOS LC 3, 2 and 1, see CLS 2011) and for other fixes using a hybrid-filtering procedure of minimum Redundant distance (assuming that fixes at <2 km distance are spatially redundant) and constraints that prevent overly large travel distances and overly small angles (distance, angle and rate of travel). Arrival dates in – and departure dates from home ranges were taken from data set 1. Data set 2 was used for home range calculations and consisted of 2460 fixes corresponding to 127 wintering home range visits of 22 birds. A bird could visit the same home range more than once, both within the same season and in different seasons. The resulting lack of independence was dealt with statistically by including individual and/or home range ID as random effect into models.

Fixes within home ranges were taken from data set 2 and loaded in ESRI ArcMap 9.3.1 (ESRI Inc., Redlands, CA, USA) software. Kernel home ranges were calculated using likelihood cross validation (CV) to estimate the smoothing parameter h (Horne & Garton 2006, 2007). When the data set contained plausible outliers with a small ARGOS location error estimate (outliers with LC 3, 2 or 1), least squares cross validation (LSCV) was used to estimate h , which in the present case produced more robust surface area estimates than CV (Trierweiler 2010). The smoothing parameters CV h and LSCV h were calculated with Animal Space Use 1.3 software (Horne & Garton 2006, 2007). With Hawth's Analysis Tools 3.27 (www.spatialecology.com), 90% and 50% home range contours were generated in ArcMap. For home ranges with $n < 15$ fixes, no kernel home ranges were calculated because of potentially large errors in the surface area calculation (in the present data set, such errors were shown to occur especially at sample sizes <15, Trierweiler 2010). Instead, data points were buffered with 1.7 km (the average LC over the whole data set) and referred to as 'buffered fixes' home ranges in the following. The total wintering range per bird was calculated using the more conservative minimum convex polygon (MCP) method, calculated by Hawth's Tools over all fixes of one individual during one wintering season ('track MCP'). A MCP including 100% of the data from all of the study birds was used as a measure of the species' regional wintering range ('all MCP'). These MCPs were buffered with 1.7 km.

To check the reliability of overwinter home range sizes calculated from satellite telemetry data, we calculated a sample of breeding home ranges from satellite telemetry data. The average 50% kernel breeding home range size derived from satellite data was $51 \pm 9 \text{ km}^2$, the 90% kernel $250 \pm 49 \text{ km}^2$ ($n = 11$). Satellite tracking may be liable to overestimates because of the relatively large error estimates of satellite fixes (on average 1.7 km in our data set). Preliminary results from GPS logger tracking (error estimates of only several metres) of Montagu's harriers indicate home range sizes around 120 km^2 , supporting the view that home range size calculated from satellite telemetry data may be around two-fold overestimates (R.H.G. Klaassen pers. comm.). On the other hand, comparisons of relative sizes of breeding vs. wintering home ranges calculated from satellite telemetry seem justified, as estimation errors should be equal in both seasons. Absolute home range sizes calculated from satellite telemetry are at this time the only available estimates for the non-breeding season. Furthermore, wintering home ranges calculated from satellite telemetry are at this time the best available indications of the birds' positions in the Sahel: As home ranges are based on several satellite fixes, they are more reliable and more suitable for studies of habitat selection than the use of single fixes, which may be prone to considerable error (Limiñana *et al.* 2008; Trierweiler 2010).

SPATIAL ANALYSES OF HABITAT USE IN RELATIONSHIP TO HABITAT TYPE AND GREEN VEGETATION

The proportions of different habitat types and vegetation 'greenness' within the home ranges of Montagu's harriers were calculated using digital maps of land cover and NDVI in ArcMap (see below).

Land cover

For the whole of West Africa, habitat types were taken from the GlobCover land cover data set V2.2 (GlobCover Land Cover V2

2008 data base; European Space Agency GlobCover Project, led by MEDIAS-France; 2008; <http://ionia1.esrin.esa.int/>) based on satellite scenes from 2004 to 2006, with a resolution of 300 m. The accuracy of the map (i.e. whether the map categories were correct according to independent reference data sources) was assessed by MEDIAS to be on average 67% (<http://postel.mediasfrance.org>). Harrier home range polygons were overlaid onto this map to determine the habitat types that harriers used. We decided to analyse habitat selection on two spatial scales: (i) a broad view and (ii) a detailed view. (i) The broad view investigated habitats in the individual's region of choice during the wintering season against the background of habitats available in the whole Sahel (Aebischer, Robertson & Kenward 1993). The habitats selected by the individual were represented by habitats contained in the complete home range it visited during the wintering season from autumn arrival to spring departure (minimum convex polygon of its whole track in the Sahel, 'track MCP'). The habitats potentially available to the individual were represented by habitats contained in the complete home range visited by all tracked individuals during the whole wintering season (minimum convex polygon of all tracks, 'all MCP') (ii). The detailed view investigated habitats in an individual's separate wintering season home ranges against the background of habitats available in the individual's Sahelian region of choice. Habitats selected in the separate home ranges were calculated from 90% kernel together with 'buffered fixes' home ranges. Habitats potentially available were taken to be habitats in the individual's track MCP (analysing a broad view of resource use, Sunde & Redpath 2006).

Normalized difference vegetation index

During the dry season (October–May/June), the vegetation in the West-African Sahel and northern Sudan Zone gradually desiccates, starting in the North of the zone and proceeding to the South. The resulting changes in 'greenness' of the vegetation can be quantified (on a scale of 0–1) using the NDVI, obtained from satellite measures of solar reflection of live plants vs. other objects on the earth's surface (Pettorelli *et al.* 2005). For the present analyses, we used 'raw' NDVI grid values ($\text{NDVI} * 250$, in order to avoid rounding errors because of calculations with values close to zero; as delivered by the US Geological Survey) of 10-day NDVI composite pictures. NDVI maps with a resolution of 8 km for all 10-day periods with harrier telemetry data available were downloaded from <http://igskmncngs600.cr.usgs.gov/adds/> (Tucker *et al.* 2005).

Previous studies (summarized in Maiga, Lecoq & Kooyman 2008) showed that low resolution (8 km) NDVI data can be used to identify areas suitable for grasshopper development. To verify that NDVI measures are correlated with field grasshopper abundance in Montagu's harrier's wintering range, grasshoppers were counted by observers walking along line transects that were randomly chosen in Niger, in natural and agricultural habitat types, 1.5 m to the left and right of the observer (transects were located between 10–17°N and 1–13°E; average transect length 0.8 ± 0.04 km length, $n = 328$ transects, with total length 277 km, January–February 2007; Trierweiler & Koks 2009). Polygons representing these transects were intersected with NDVI raster maps in ArcMap, NDVI was averaged per transect. Counts of grasshoppers >3 cm in body length per km of transect were related to NDVI values. Smaller grasshoppers were assumed not to be an important food source for harriers: Mullié & Guéye

(2010) found that small-bodied grasshoppers (<0.73 g fresh mass) represented <2.6% of the prey mass of Montagu's Harriers in Senegal, while they represented 61–68% of the grasshopper community in the field. A number of grasshoppers (reference sample) were captured in the field in order to determine in the lab which species they belonged to (species identification by S. Gagaré, AG-HRYMET, Niger).

Using raster statistics in ArcMap, the NDVI values for 90% kernel together with 'buffered fixes' home ranges were calculated as the average NDVI value for each wintering season 10-day period for each home range that was visited at least once in that season. To allow comparison of NDVI values of home ranges used at different times during the season, they were calculated for all home ranges irrespective of harrier presence at any given time, provided that the bird was present in the wintering range as a whole. In addition, NDVI values were calculated for 157 randomly drawn points (corresponding to the 127 harrier winter home range visits plus an extra 30 points) within the wintering range (all MCP). The points were buffered with 1.7 km.

The difference of NDVI in a home range at time t (a given 10-day period when the bird was present in a given home range) and at time $t-1$ (the previous measurement of that bird, at least one 10-day period earlier) was calculated (hereafter referred to as ' Δ NDVI') for all home ranges and 10-day periods with harriers present. Each Δ NDVI value was assigned a movement score: either the harrier stayed in the home range or moved to a new home range in that period of time.

STATISTICAL ANALYSES

Latitudinal positions of all birds during the overwinter stay in West Africa were analysed using a two-level random-intercepts regression model with a normal error structure in MLwiN 2.02 (Centre for Multilevel Modelling, University of Bristol, UK). Distances and directions between two home ranges were calculated using loxodromes (Imboden & Imboden 1972) between the geographical centres of the two areas (Alerstam, Hake & Kjellén 2006). Circular statistics and Rayleigh's test were produced in R (R development core team 2007; package circular, Agostinelli & Lund 2011). Compositional analyses were used to analyse habitat selection and carried out in R (package adehabitat, function `compiana`, Calenge 2006). NDVI values during the non-breeding season were used 'raw' (multiplied by 250 to reduce rounding errors) and were log-transformed, then analysed using multilevel random-intercepts regression models with a normal error structure in MLwiN 2.02. To analyse the relationship of grasshopper counts and NDVI, a Poisson model with log link function was fitted to the count data with $x = \text{NDVI} * 250$. The effect of Δ NDVI on staying/moving of the bird (coded as 0/1) was tested in a multilevel random-intercepts regression model with logit link function and binomial error structure with $x = \Delta \text{NDVI} * 250$. Averages are presented as ± 1 SE. P -values were assumed to be significant at $\alpha < 0.05$.

Results

TEMPORAL AND SPATIAL MOVEMENT PATTERNS IN THE SAHEL

The wintering range of Montagu's harriers satellite-tagged in Northern Europe lay between 9.9 and 17.4°N and

between 16.9°W and 15.7°E (Fig. 1a, b). The mean number of home ranges visited during one wintering season in West Africa was 4.0 ± 0.7 per bird (1–12 home ranges visited, based on 23 tracks of 16 birds, 2006–2009). The maximum number of home ranges visited during one season was 12, by an adult female. The average surface area of 90% kernel density of wintering season home ranges was similar to or even smaller than average breeding home ranges (wintering, $158 \pm 18 \text{ km}^2$, $n = 68$; breeding, $250 \pm 49 \text{ km}^2$, $n = 11$). As the given home range sizes are based on satellite telemetry data, which are liable to overestimation (see Methods), the actual absolute home range sizes may be even considerably smaller. A typical example of home range visit patterns is

shown in Fig. 1(c). There were only two birds that deviated in their home range use from the general pattern: One adult female (F1) used only one home range, and another female (F2) used only two home ranges in close proximity (<50 km apart) during one season. The mean distance between the geographical centres of subsequent home ranges was $208 \pm 34 \text{ km}$ ($n = 23$ tracks, 16 birds). In five of 25 tracks ($n = 17$ birds), the same home range was visited two ($n = 6$ home ranges) or three ($n = 2$ home ranges) times within the same season. On average, each single home range visit lasted 45.1 ± 5.7 days (average over 78 home range visits of 16 birds). The longest visit in one home range lasted 181 days (the only home range of F1).

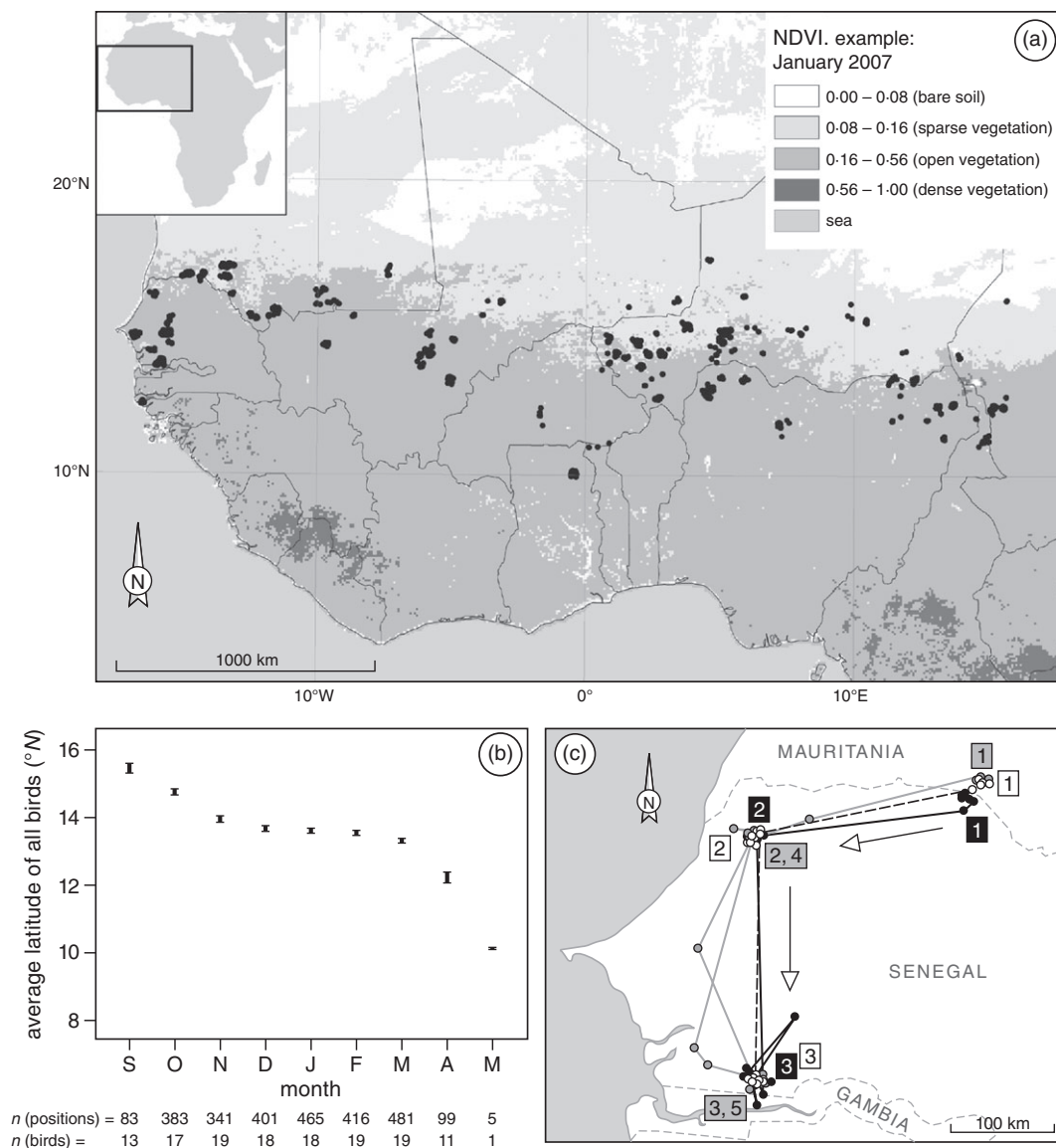


Fig. 1. (a) Satellite fixes (black dots) of staging Montagu’s harriers in West-Africa (2005–2009). The background map depicts the NDVI (resolution: 8 km) of the first 10-day period of January 2007, as an example. The continuous NDVI values (0–1) have here been grouped into five categories representing different land cover types (see legend). (b) Average monthly latitudes over satellite fixes of all tracked birds (2005–2009) ± 1 SE. (c) Movements of a satellite tracked adult Dutch–German Montagu’s Harrier female during three subsequent winters. Circles represent satellite fixes (black: 2006/2007, grey: 2007/2008, open/dashed: 2008/2009), lines connect subsequent fixes. Numbers indicate order of visits of the three home ranges.

The average direction between geographical centres of subsequently visited home ranges was 207° (South–Southwest) and deviated significantly from random (Rayleigh test, $p = 0.21$, $n = 75$ home range changes of 14 birds, excluding F1 and F2, $P = 0.03$). Larger distances tended to be moved earlier in the season [mixed model (with variation on bird's tracks) on day number, $x =$ distance moved, $\beta = -0.005$, Wald $\chi^2_1 = 2.98$, $P = 0.08$, $n = 78$ home range changes]. Birds were located more to the south later in the season (two-level regression on day number, $x =$ latitude, $\beta = -0.001$, Wald $\chi^2_1 = 18.49$, $P < 0.0001$, $n = 2674$ satellite fixes from 28 tracks of 19 birds, excluding birds that died during the season; see averages in Fig. 1b).

All five birds that were tracked in multiple seasons showed site fidelity: they returned to at least one home range that they had visited in the previous season (based on 2 adult females and 1 adult male tracked in 3 seasons, and 2 adult females tracked in 2 seasons; example shown in Fig. 1c).

HABITAT SELECTION IN THE WINTERING QUARTERS

Habitat types available in the species' regional wintering range ('all MCP', Fig. 2a) are shown in Appendix S2. The comparison of habitat use on a broad scale (scale 1, see Methods) showed that habitat use deviated significantly from random (compositional analysis, $\lambda = <0.001$, $n = 31$ tracks, 24 habitat types, $P = 0.001$, Fig. 2a,b). The 'mosaic grassland, shrubland, forest, cropland' category was both the most available in the complete wintering range (14.7%) and the most preferred category. A further eight (35%) habitat types were frequently selected over others (see asterisks in Fig. 2b).

Spatial analyses at a more detailed scale (scale 2, see Methods) confirmed that habitat use deviated significantly from random ($\lambda = 0.293$, $n = 121$ home ranges, 13 habitat types, $P = 0.01$). For this analysis, several similar habitat types with small surface areas were lumped together (reclassified, see Fig. 2c). 'Mosaic cropland, grassland, shrubland, forest' was ranked as the most preferred habitat type (Fig. 2c); this habitat type was not significantly different in preference from 'grassland, savannah'. Other habitat types were not preferred.

CORRELATIONS OF HARRIER DRY SEASON REGIONAL MOVEMENTS WITH VEGETATION GREENNESS

Grasshoppers encountered during counts in Niger (January–February 2007) belonged to at least 11 different species (reference sample of $n = 24$ grasshoppers identified to species level), the most important being *Acorypha clara*, *Ornithacris cavroisi* and *Acanthacris ruficornis citrina*. Grasshopper numbers in transect counts showed a significant quadratic relationship with NDVI [Poisson regression with (SE) on log (grasshopper count) = $-10.5 [1.0] + 0.4 [0.04] * NG - 0.004 [0.0001] * NG^2 + 0.4 [0.03] * \text{transect length}$, where NG is NDVI * 250; NG: Wald

$\chi^2_1 = 118.6$, $P < 0.0001$; NG²: Wald $\chi^2_1 = 103.6$, $P < 0.0001$; transect length: Wald $\chi^2_1 = 241.5$, $P < 0.0001$, Fig. 3]. The highest grasshopper counts (>twice the average) occurred at NDVI values between 0.168 and 0.248 (in the lower range of NDVI values for open vegetation). The highest grasshopper abundance according to the statistical model that was fitted to the count data occurred at NDVI values between 0.168 and 0.272, indicating a good model fit. We conclude that NDVI values are an appropriate proxy for grasshopper abundance. As lower vegetation cover also means a better accessibility of prey for Montagu's harriers, we use NDVI as a proxy for prey availability.

Normalized Difference Vegetation Index, in the home ranges where a Montagu's harrier was present, was significantly different from outside these areas (lower in the beginning of the season and higher later on, Fig. 4, Table 1). Furthermore, the seasonal decline in NDVI (negative effect of 10-day period) was significantly weaker in visited home ranges than outside these home ranges (interaction of harrier presence/absence and 10-day period, Table 1). NDVI in visited home ranges was on average within the range corresponding to highest grasshopper abundance (relatively open vegetation) throughout the non-breeding season (see fitted curves in Fig. 4).

On average, harrier movements between home ranges resulted in a positive difference in NDVI values (positive Δ NDVI, Fig. 5), whereas seasonal changes in the Sahel cause on average decreasing NDVI values throughout the dry season (Fig. 4). The effect of Δ NDVI on staying/moving (coded as 0/1) was tested in a multilevel random-intercepts logistic regression model. Random effects were home range ID ($\chi^2_1 = 0.000$, $P > 0.99$), bird ID ($\chi^2_1 = 7.303$, $P = 0.007$) and winter (season) ID ($\chi^2_1 = 0.000$, $P > 0.99$). Fixed effects were Δ NDVI ($\beta = 0.175 \pm 0.070$, $\chi^2_1 = 6.194$, $P = 0.01$) and day number ($\beta = -0.015 \pm 0.003$, $\chi^2_1 = 36.369$, $P < 0.0001$). There was a trend towards an interaction of Δ NDVI with day number ($\chi^2_1 = 3.758$, $P = 0.05$). There was no significant co-linearity between Δ NDVI and day number ($r = -0.050$, $n = 524$, $P = 0.3$).

Our analyses of habitat use suggest that the harriers, which arrive in autumn often in northern parts of the Sahel with relatively low NDVI values, select subsequent home ranges with higher NDVI values, associated with high food availability. In the first part of the dry season, harriers were able to achieve higher positive differences in NDVI values (Δ NDVI) between home ranges (Figs 4 and 5). In the second half of the dry season, when NDVI values are low throughout the Sahel, differences (Δ NDVI) were smaller.

Discussion

SPATIAL AND TEMPORAL PATTERNS OF MONTAGU'S HARRIERS' REGIONAL MOVEMENTS IN THE SAHEL

Satellite telemetry showed that northern European Montagu's harriers winter in a relatively narrow belt of

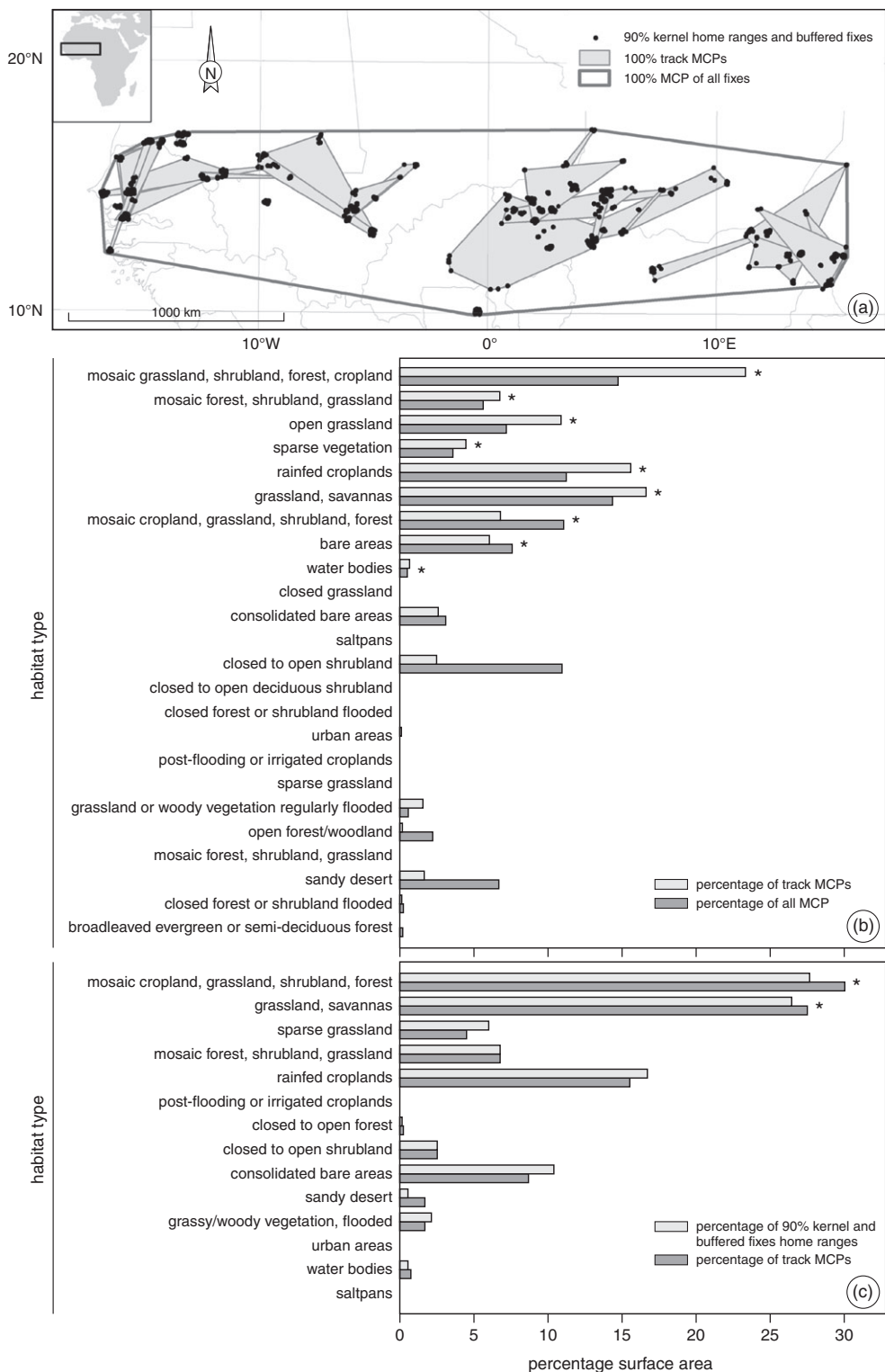


Fig. 2. (a) The 100% MCP of all fixes of satellite tracked Montagu's harriers in West-Africa ('all MCP', black outline) with 100% track MCPs (grey) and 90% kernel home ranges and 'buffered fixes' (black dots, drawn larger than actual size). (b) Percentage surface area of available habitat types in 'all MCP' (see Appendix S2, based on digital map GlobCover landcover V2.2) compared to percentage within track MCPs (i.e. the selection of the harriers; surface areas 3 000 000 and 1 000 000 km², respectively). Habitat types are ordered by descending rank in compositional analysis (most preferred to least preferred). Asterisks indicate the cluster of habitats that were preferred over the other habitats ($\alpha = 0.05$). Note that the compositional analyses are based on the proportional use of habitat types per track (not overall) compared to the available habitat. Selection can thus be significantly positive even though the total used percentage presented in the figure is smaller than the percentage available. (c) As (b), but for habitat types available in track MCPs compared to 90% kernel and 'buffered fixes' home ranges (surface area 13 000 km²). Habitat categories that had zero surface areas in track MCPs were omitted from this analysis, the remaining categories were grouped to avoid a large number of zero occurrences.

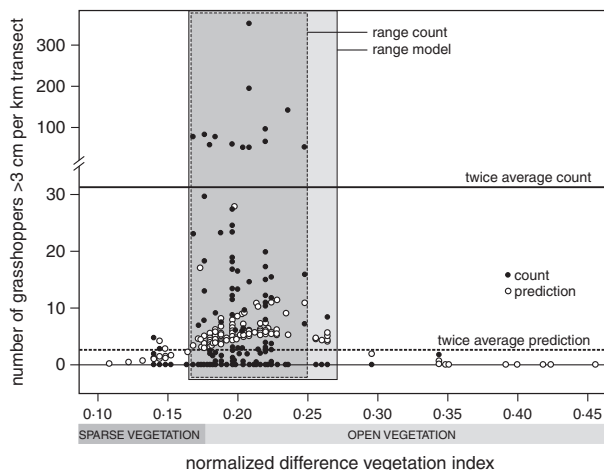


Fig. 3. NDVI plotted against (i) counts of grasshoppers >3 cm length (number km⁻¹ transect counted, Niger, January–February 2007) and (ii) predictions of a statistical model fitted to the count data (see text). The dark grey dashed rectangle indicates the range of NDVI values with highest grasshopper numbers according to counts (>twice average count), the light grey solid according to predictions of the statistical model (>twice average prediction).

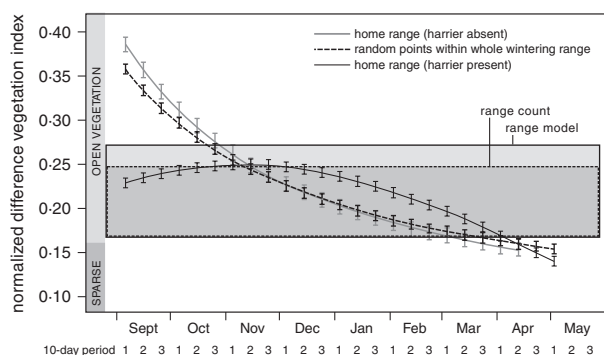


Fig. 4. NDVI through the winters 2005–2009, for home ranges where satellite tracked Montagu's harriers were present (within the same winters only; black line), for home ranges where tracked harriers were absent (grey line), and for 158 random 1.7 km-buffered points in the whole regional wintering range ('all MCP'; dashed line). Curves were fit using random-intercepts multilevel regression models with $y = \log_{10}(\text{NDVI} * 250 + 0.375)$; see Table 2 for parameter estimates). The dark grey dashed rectangle indicates the range of NDVI values with highest grasshopper numbers according to counts (>twice average count), the light grey solid according to predictions of the statistical model (>twice average prediction, see Fig. 3). Error bars represent ± 1 SE.

the Sudano-Sahelian zone in West Africa. Contrary to earlier hypotheses of nomadic movements of Montagu's harriers in the Sahelian-wintering quarters (García & Arroyo 1998; cf. Rappole & Jones 2002), the present study shows that birds chose a small number of distinct, separate home ranges. The average surface area of wintering season home ranges was similar to or even smaller than average breeding home ranges. Satellite telemetry also demonstrated a high degree of site fidelity in home ranges of wintering Montagu's harriers, suggesting a great

Table 1. Significance of random and fixed effects in a three-level mixed-effect regression model with $y = \log_{10}(\text{NDVI} * 250 + 0.375)$. Here, home ranges where the harrier was absent and random points in the wintering range were grouped as 'absence'

Variables	β	SE	χ^2	d.f.	P
Random					
Winter ID	0.001	0.002	0.7	1	0.4
Bird ID	0.011	0.002	24.7	1	<0.0001
Home range ID	0.042	0.000	7192.7	1	<0.0001
Fixed					
Constant	1.869	0.026	5288.1	1	<0.0001
Harrier presence (absence = reference category)	-0.042	0.018	5.7	1	0.02
10-day period	-0.014	0.000	2881.0	1	<0.0001
Harrier presence/absence * 10-day period	0.005	0.002	8.7	2	0.003

$n = 14\ 460$.

importance of familiarity with relatively small areas within the wintering range to these birds.

The home ranges that were visited in the beginning of the stay in West Africa were in general more northern than later visited home ranges. Montagu's harriers showed a directed movement of on average *c.* 650 km (sum of distances between geographical centres of subsequently visited home ranges) in South–South-western direction, during the dry season. If the birds followed retreating vegetation greenness (see hereafter), which occurs along a North–South axis, movements to the South would be expected. Prevailing strong northeast trade winds in the Sahel (called the Harmattan), however, may result in the South–South-western shift. In the following, we discuss the relationship between the selection of home ranges and habitat characteristics, and whether the birds' regional movements tracked seasonal changes in vegetation greenness and food availability.

HABITAT SELECTION IN THE WINTERING QUARTERS

Habitat selection was investigated at two spatial scales. One was that of selection of an individual Montagu's Harrier's wintering range ('track MCP'; average size $32\ 000 \pm 6500$ km²) out of the species' regional wintering range ('all MCP'; 3 000 000 km²). The second was the choice of separate home ranges (average size 158 ± 18 km²) within the individual's wintering range ('track MCP'). In the breeding areas, Montagu's harriers prefer open landscapes, and we show that similar habitat types are preferred in the wintering areas. Thus, the birds occupy a similar niche throughout the year (Salewski & Jones 2006 and references therein). The most important non-breeding season habitat types for the harriers appear to be mosaics of grassland, savannah and cropland, interspersed with shrubland and forest. The preference for

Table 2. Significance of random and fixed effects in three multi-level regression models, modelling log-transformed NDVI ($y = \log_{10} [\text{NDVI} * 250 + 0.375]$) for home ranges where harriers were absent (first), for random areas (second) and for home ranges where harriers were present (third model)

Variables	β	SE	χ^2	d.f.	P
Absent from home range ($n = 1737$)					
Random					
Winter ID	0.001	0.002	0.558	1	0.455
Bird ID	0.014	0.003	27.266	1	<0.0001
Home range ID	0.009	<0.001	837.538	1	<0.0001
Fixed					
Constant	1.140	0.029	1533.267	1	<0.0001
1/day number	204.633	4.872	1763.881	1	<0.0001
Random 1.7 km buffered points ($n = 12\ 166$)					
Random					
Winter ID	0.001	<0.001	1.843	1	0.175
Home range ID	0.047	0.001	6063.457	1	<0.0001
Fixed					
Constant	1.216	0.016	5816.596	1	<0.0001
1/day number	178.146	3.511	2574.192	1	<0.0001
Present in home range ($n = 553$)					
Random					
Winter ID	0.003	0.003	0.941	1	0.332
Bird ID	0.013	0.003	23.227	1	<0.0001
Home range ID	0.007	0.000	245.860	1	<0.0001
Fixed					
Constant	1.011	0.178	32.200	1	<0.0001
Day number	0.005	0.001	26.469	1	<0.0001
Day number ²	<0.001	<0.001	36.067	1	<0.0001

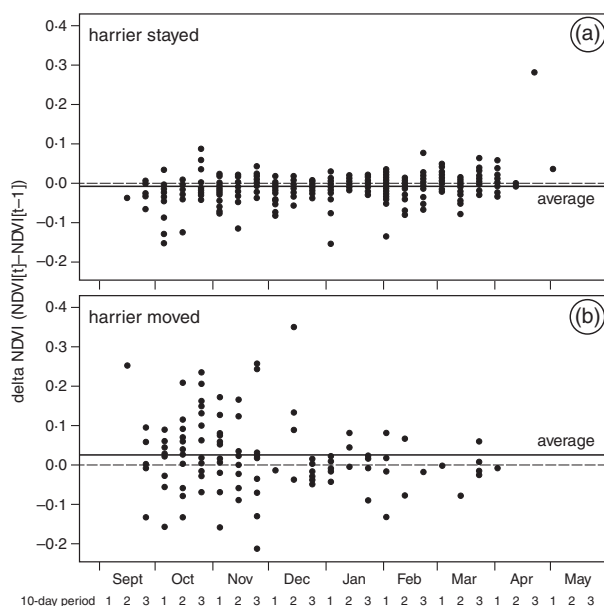


Fig. 5. Δ NDVI ($\text{NDVI}[t] - \text{NDVI}[t - 1]$) throughout the wintering season (2005–2009). Each data point represents one 10-day period for one tracked bird in one winter. (a) Δ NDVI for Montagu's harriers that stayed in the same home range as during the previous measurement. Average Δ NDVI: -0.011 ± 0.002 . (b) Δ NDVI for harriers that moved to a new home range since the previous measurement. Average Δ NDVI: 0.025 ± 0.009 .

mosaic habitat types indicates that heterogeneous habitats were preferred over homogeneous ones. A preference for heterogeneous habitats is consistent with previous observations: Palaearctic migrants in the Sahel generally prefer structurally diverse habitats, presumably because of the higher diversity or density of prey in such habitats (Salewski & Jones 2006 and references therein). The above described preferences are in line with results from fieldwork in Niger (January–February 2006 and 2007), where Montagu's harriers avoided high tree densities and preferred grassland and shrubland, interspersed with trees, as well as some mosaic cropland habitat types (C. Trierweiler, J. Brouwer, B. Koks, L. Smits, A. Harouna, K. Moussa & H. Issaka, unpublished). Cropland may be attractive for harriers during regular cultivation but also, and maybe especially, when it is set aside. Fallow land can be seen as a natural habitat in the early stages of vegetation succession and represents an ideal habitat for many grasshopper species: In Khelcom, central Senegal, for instance, deforestation of a sylvo-pastoral reserve (55 400 ha) and subsequent partial cultivation with a fallow cycle and partial natural succession (1991–2004) resulted in a varied grasshopper community. More than 32 grasshopper species were reported and many predators of grasshoppers were attracted, including Montagu's harriers (Mullié & Guèye 2010). Future research should investigate the relative importance of regular vs. fallow cropland for Montagu's harriers in the Sahel.

RELATIONSHIP OF GRASSHOPPER AVAILABILITY AND VEGETATION GREENNESS (NDVI)

We tested whether the southward shift of Montagu's harriers during the overwinter stay in the Sahel was related to the availability of non-migratory grasshoppers, which are their main prey (Thiollay 1989; Mullié & Guèye 2010). Grasshoppers in the Sahel and Sudan zones can be divided into species groups showing different life-history strategies, related to rainfall and vegetation development (Lecoq 1978; Launois-Luong & Lecoq 1989). Grasshoppers with diapausing adults (species that survive in the dry season as adults, e.g. *O. cavroisi* and *A. clara*) are of particular importance for predators of grasshoppers such as Montagu's harriers (Mullié, Brouwer & Scholte 1995; Mullié 2009). It is, therefore, not surprising that all 40 grasshoppers from 28 Montagu's Harrier pellets (Niger, February 2007) that could be identified to species belonged to *O. cavroisi*. Grasshopper numbers measured in the field related to vegetation greenness (NDVI), presumably because of the dominance of *O. cavroisi*, which feeds on grasses and leaves. We showed this relationship even though grasshopper numbers were measured in transects of just several hundred metres of length (spread over more than 1000 km from east to west), whereas NDVI maps were of much lower resolution (8 km). Highest numbers of grasshoppers in the field were associated with a relatively low range of NDVI values, representing open vegetation.

Although it may be argued that grasshopper detectability during counts may be lower in closed vegetation, the results seem plausible, as the mentioned grasshopper species are known to occur mainly in open landscapes.

VEGETATION GREENNESS WITHIN AND OUTSIDE OF HOME RANGES

When Montagu's harriers settled in their first wintering home ranges, these habitats comprised relatively open or sparse vegetation types of the northern Sahel zone, with a relatively low NDVI. The NDVI in harrier home ranges in the beginning of the dry season was consequently within the range of highest grasshopper numbers (according to our January–February 2007 counts and a statistical model of these counts). Average NDVI over random areas and in home ranges where the harriers were absent, however, were above that range (Fig. 4). There are at least three – not mutually exclusive – possible explanations for the harriers' staging behaviour in the northern Sahel:

- 1 The harriers need to feed as soon as possible after the energetically demanding crossing of the Sahara desert and are forced to stage in the first suitable area they encounter on their way to their final destinations. Their stay can be interpreted as a stopover and their further movements within the wintering range as a continuation of autumn migration.
- 2 The harriers stage in the northern Sahel zone because they encounter attractive habitats. When these habitats deteriorate during the course of the dry season, they move on. Adult birds may have experienced in previous years that early during the overwinter season, southern regions are not so attractive: The relatively lush and dense vegetation in more southerly areas may make prey less accessible (Simmons 2000), and it may not harbour as many grasshoppers. The hypothesis that lush vegetation holds less grasshopper prey is derived from our January–February 2007 counts in Niger, where we found an association of relatively low NDVI values with highest grasshopper numbers (this study). This association is, therefore, based on a situation where, amongst others, the non-migratory grasshopper species *A. clara* and *O. cavroisi* played an important role. Another potential reason for southern regions being less attractive is that grasshoppers in these regions of the Sahel may still be flightless nymphs (and thus not profitable prey) when harriers arrive in sub-Saharan Africa. Mullié and Guèye (unpublished) found that from mid-August until the end of September, 85–95% of the grasshopper community in central Senegal were nymphs. From the end of September until the end of October, the percentage of nymphs in the community gradually reduced to 30%.
- 3 When Montagu's harriers arrive south of the Sahara in autumn, they may encounter grasshopper species of which some, such as *Oedaleus senegalensis* and

Diabolocatantops axillaris, perform migratory movements in north–south directions in relation to rainfall and likely vegetation greenness, mostly from September to October. It is conceivable that this triggers (some of) the movements of Montagu's harriers described in the present study. Data on harrier diet from the northernmost part of the wintering range in September–October are currently lacking. It is, however, known that *O. senegalensis* made up c. 15% of prey numbers of Montagu's harriers in Senegal in November 2009 (W.C. Mullié and F. Noël unpublished). After November, the adults of *O. senegalensis* start dying, and are thereby not likely to play an important role in the harriers' diet later in the season. *O. senegalensis* occurs throughout the wintering range of Montagu's harriers. In 2008, grasshopper densities, in particular *O. senegalensis*, were very high over most of their range in Senegal (average 30–35 individuals m^{-2} in Khelcom, against 5–10 individuals m^{-2} in 2009; Mullié & Guèye 2010). During our counts in Niger in January–February 2007, *O. senegalensis* was not encountered in the field nor as prey in Montagu's harrier pellets. Data for other countries are lacking. Future studies, including more information on relative and absolute abundance of different grasshopper species and on Montagu's harrier diet across the Sahel and throughout the dry season, should evaluate the relevance of this hypothesis.

Taking into account the information we have available in the present study, with highest grasshopper numbers associated with a range of relatively low vegetation greenness, hypotheses (2) and (3) seem to explain the observed patterns best. Therefore, in average years – without outbreaks of, for example, desert locusts (*Schistocerca gregaria*) – the availability of other, partly-migratory or non-migratory grasshopper species (e.g. *O. cavroisi*, *A. clara*, *O. senegalensis*) is the most likely trigger for the harriers' southward movements.

Harriers also used areas with NDVI values above or below the range associated with high grasshopper counts, showing that the range defined from grasshopper counts represents no strict thresholds. The harriers being present outside the range of highest grasshopper numbers may be explained by a seasonal shift in this range. Furthermore, geographical or habitat differences in this range may play a role, which can be expected from the large habitat and seasonal differences present throughout the Sahel during the dry season. Such shifts and differences should be investigated in future studies. Behavioural flexibility of the birds may be another explanation for the fact that harriers did not stay exclusively in this range: the raptors may feed to a variable extent on alternative prey such as birds or reptiles. Further study is needed to investigate the existence and extent of behavioural flexibility.

Our findings support the view that January to March are the months when grasshopper-consuming birds face

limited food supplies in the Sahel (Mulli , Brouwer & Scholte 1995; Mulli  & Gu ye 2010). Mulli  & Gu ye (2010) found that total grasshopper biomass in central Senegal was reduced from 1256 kg dry weight km⁻² in December to 352 kg dry weight km⁻² in May, a reduction of 71.9%. By their regional movements, harriers may partly overcome these constraints. From the beginning of April onwards, however, even harriers may be confronted with low greenness within the habitat types that are available to them, and consequently low grasshopper availability, making the preparation for energy-demanding migration (e.g. acquiring body reserves) difficult. On the other hand, birds, small mammals and reptiles can function as an alternative prey species of Montagu's harriers in the Sahelian-wintering areas (Trierweiler & Koks 2009). It remains as yet unknown whether these food sources relate to the NDVI as well.

FOLLOWING A 'GREEN BELT' OF PREY AVAILABILITY

The non-random regional movements of Montagu's harriers during their non-breeding period in the Sahel appear to be caused by seasonal shifts in food availability. These movement patterns show parallels with spring migration patterns observed in Arctic breeding Barnacle (*Branta leucopsis*) and Pink-footed geese (*Anser brachyrhynchus*; Van der Graaf *et al.* 2006; Duriez *et al.* 2009). The phenomenon of these birds' movements being synchronised with food peaks was termed as 'green wave hypothesis' in the 1970s (cf. Van der Graaf *et al.* 2006). Referring to the green wave hypothesis, we suggest explaining the observed southward movement patterns of Montagu's harriers during the Sahelian dry season by a 'green belt hypothesis', according to which predators of grasshoppers track predictable and reliable peaks in availability of their grasshopper prey. These prey peaks are linked to a range of vegetation greenness (the green belt), which shifts southwards during the Sahelian dry season, ultimately caused by patterns of previous rainfall, in turn, resulting from climatic patterns of a seasonally shifting Intertropical Convergence Zone (ITCZ). Other Palaearctic migrants, whose food sources (e.g. insects) are related to green vegetation, have been shown to respond to climatic gradients in the Sahel with itinerancy before. Examples are extended southward movements of tracked (grasshopper consuming) White Storks (Berthold *et al.* 2001) and of Purple Herons (Zwarts *et al.* 2009) after initial stopovers in the Sahel zone. Passerines using itinerant strategies during wintering in West Africa are, for example, Great reed warblers (Hedenstr m *et al.* 1993), Willow warblers (Salewski, Bairlein & Leisler 2002) and Garden warblers (Ottoson *et al.* 2005). It has, furthermore, been shown that in dry years, densities of Palaearctic migrants in north Senegal (1960–1982) were about 50% lower than in years with normal previous rainfall (but equal under normal and dry conditions in August and March–May), suggesting southerly movements of migrants when they

encounter dry conditions upon arrival in the northern Sahel zone (Mulli  2009).

The 'green belt hypothesis' is supported by our observation that two immature Montagu's harriers, which spent their second calendar year in the Sahel, moved northwards with the shifting ITCZ during the rainy season (C. Trierweiler & K.-M. Exo, unpublished, Dutch Montagu's Harrier Foundation, unpublished). Northward rainy season movements have not been demonstrated in immature Palaearctic migratory raptors in the Sahel before. However, they are well known from intra-African migrants that feed on grasshoppers like the Grasshopper Buzzard *Butastur rufipennis* (Del Hoyo, Elliott & Christie 1992), Abdim's Stork *Ciconia abdimii* (Petersen *et al.* 2008), Cattle Egrets *Bubulcus ibis*, Abyssinian Rollers *Coracias abyssinicus* and African Grey Hornbills *Tockus nasutus* (Jensen, Christensen & Petersen 2008).

The mentioned examples and the present study suggest that the presumably reliable strategy of following a green belt of predictable food availability may be the rule rather than an exception in birds spending their non-breeding season in African savannahs and relying on herbivorous or folivorous prey.

The present study is one of the first using satellite tracking of individual birds to reveal inter-year site fidelity and within-year itinerancy (*sensu* Moreau 1972) in detail and linking these movements to habitat and food availability, respectively. The observed between-year site fidelity to overwinter home ranges, as well as some amazing between-year winter site fidelity in other species (Moreau 1972; Curry-Lindahl 1981; Jones 1998; Salewski, Bairlein & Leisler 2000; Rappole & Jones 2002), suggest relatively predictable food availability in the Sahel between years (Terrill 1990).

However, Montagu's harriers did not show itinerancy between very distant wintering sites (cf. Jones 1995). As the harriers moved between home ranges that were separated by just, on average, 200 km, they still tracked food availability on a relatively large scale. Other migratory animal species have been shown to track food availability on similarly large scales. In birds, it has been shown that the number of migrants in a wintering site may correlate with food availability, which was explained by extended migrations during the wintering period (Wood 1979; Terrill & Ohmart 1984). Experiments in captive migrants revealed that these extended migrations may be triggered by food deprivation (Gwinner, Biebach & von Kries 1985; Gwinner, Schwabl & Schwablbenzinger 1988).

Although we documented itinerancy in Montagu's harriers during their non-breeding period in sub-Saharan Africa, the earlier hypothesis of nomadic movements may still hold under exceptional circumstances. In 'outbreak years' of migratory locusts or alternative prey species such as small mammals, the predators may track these temporary resource concentrations rather than the 'normal' seasonal grasshopper availability: In Senegal, densities of wintering Montagu's Harrier were much higher during a

migratory locust outbreak year than in a recession year (Baillon & Cormier 1993). Similarly, an outbreak of small mammals in Ethiopia resulted in exceptionally high densities of Montagu's harriers (C. Magin cited in Trierweiler & Koks 2009). During our study, and to our knowledge, no outbreaks of, for example, desert locusts or small mammals occurred in our study areas.

FITNESS CONSEQUENCES

Effects of ecological conditions in the non-breeding areas may carry over to the breeding season in migrants. Favourable ecological conditions in the non-breeding areas (measured by higher NDVI values) advance migratory phenology in several species (Gordo & Sanz 2008; Balbontin *et al.* 2009). Variation in food availability in the non-breeding areas has been shown to contribute to survival rates, breeding success and population change in a number of migratory bird species (Peach, Baillie & Underhill 1991; Szép 1995; Bairlein & Henneberg 2000; Norris *et al.* 2004; Schaub, Kania & Köppen 2005). Sahelian habitats changed dramatically during the last decades, mainly because of anthropogenic degradation of natural and semi-natural habitats and because of drought and climate change (Thiollay 1989, 2006; Zwarts *et al.* 2009). Conservation issues result from such changes, also for wintering Montagu's harriers (Limiñana *et al.* 2012). Whether these changes in Montagu's harriers' wintering grounds carry over to the breeding season, thereby influencing population changes in this species, remains to be investigated.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Determination of a threshold for arrival in a home range.

Appendix S2. Habitat types in the regional wintering range of Montagu's harriers in West Africa.

Fig. S1 Histogram of daily travel distances (km day^{-1}) of satellite-tracked Montagu's harriers during their stay in the West-African wintering areas.

Fig. S2 Habitat types in the regional wintering range of Montagu's harriers in West Africa.

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