How individual Montagu's Harriers cope with Moreau's Paradox during the Sahelian winter

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Summary

1. Hundreds of millions of Afro-Palaearctic migrants winter in the Sahel, a semi-arid belt south of the Sahara desert, where they experience deteriorating ecological conditions during their overwintering stay and have to prepare for spring migration when conditions are worst. This well-known phenomenon was first described by R.E. Moreau and is known ever since as Moreau's Paradox. However, empirical evidence of the deteriorating seasonal ecological conditions is limited and little is known on how birds respond.

2. Montagu's Harriers *Circus pygargus* spend 6 months of the year in their wintering areas in the Sahel. Within the wintering season, birds move gradually to the south, visiting several distinct sites to which they are site-faithful in consecutive years. At the last wintering site, birds find themselves at the southern edge of the Sahelian zone and have no other options than facing deteriorating conditions.

3. We tracked 36 Montagu's Harriers with GPS trackers to study their habitat use and behaviour during winter and collected data on the abundance of their main prey, grasshoppers, in Senegal. Since grasshopper abundance was positively related to vegetation greenness (measured as normalized difference vegetation index, NDVI), we used NDVI values as a proxy for prey abundance in areas where no field data were collected. Prey abundance (grasshopper counts and vegetation greenness) at wintering sites of Montagu's Harriers decreased during the wintering period.

4. Montagu's Harriers responded to decreasing food availability by increasing their flight time during the second half of the winter. Individuals increased flight time more in areas with stronger declines in NDVI values, suggesting that lower food abundance required more intense foraging to achieve energy requirements. The apparent consequence was that Montagu's Harriers departed later in spring when their final wintering site had lower NDVI values and presumably lower food abundance and consequently arrived later at their breeding site.

5. Our results confirmed the suggestions Moreau made 40 years ago: the late wintering period might be a bottleneck during the annual cycle with possible carry-over effects to the breeding season. Ongoing climate change with less rainfall in the Sahel region paired with increased human pressure on natural and agricultural habitats resulting in degradation and desertification is likely to make this period more demanding, which may negatively impact populations of migratory birds using the Sahel.

Key-words: acridivorous birds, deterioration, GPS-tracking, long-distant migrant, Sahel, sub-Saharan Africa, West Africa

Introduction

Each autumn, hundreds of millions of Palaearctic migratory birds head south to spend the winter in more

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favourable conditions closer to the equator. However, ecological conditions in the Sahel, the semi-arid belt south of the Sahara desert and a zone used by many sub-Saharan migratory species for overwintering (Zwarts *et al.* 2009), seem not to be all that beneficial. The Sahel is characterized by a rainy season usually lasting from June to October; hence, migrants arrive during the best period (Morel 1973). However, from November to May, the Sahel zone dries up continually, and thus, ecological conditions deteriorate during the wintering stay of migratory birds (Zwarts *et al.* 2009). Moreau was one of the first to wonder how all the Palaearctic migrants could (i) sustain themselves in the Sahel and (ii) prepare for spring migration in environmental conditions that are continuously deteriorating during their stay (Moreau 1972). This is the so-called Moreau's Paradox, which was widely embraced (e.g. Alerstam 1990; Fry 1992; Berthold 1993; Salewski, Almasi & Schlageter 2006; Rappole 2013). Twenty years later, Fry (1992) summarized the observations of Morel and Moreau and discussed partial resolutions of Moreau's Paradox: (i) the Sahel contains important wetlands, (ii) insect biomass in *Acacia* savanna continues to increase long after the rainy season (November), (iii) African native birds emigrate southward at the time migrants arrive, thus reducing competition, and (iv) insectivorous migrants can become frugivorous and feed on berries of widespread trees during winter and in preparation for spring migration. More recently, Zwarts *et al.* (2015) confirmed Moreau's Paradox: highest densities of insectivorous birds are reached in the most desiccated areas of West Africa where they are found in thorny tree species that are supposed to host high insect numbers. These findings suggest that there might be no paradox for certain species and explain why so many migrants spend the winter in the Sahel. However, so far there remain many questions on the second part of Moreau's Paradox: how can migrants prepare for spring migration if conditions are deteriorating during the wintering period. No studies have demonstrated whether prey availability really decreases, how wintering birds react to such changes, and whether this has consequences for individuals. In the past, we have witnessed large declines in breeding population sizes in Europe of many migrants wintering in the Sahel, as a result of droughts in the 1970s and 1980s (Zwarts *et al.* 2009). The ongoing human pressure on these habitats (Vickery *et al.* 2014), together with the predicted declines in rainfall in this century (Hulme *et al.* 2001), continue to put pressure on these species.

In the northern Sahel, the drying out starts earlier than in the south because rainfall is less and the dry season starts earlier (rainy season north: July–September; 300 km further south: June–October) (Zwarts *et al.* 2009). Therefore, birds initially wintering in the northern Sahel move southwards during the wintering season (e.g. Catry *et al.* 2011; Trierweiler *et al.* 2013). However, for many species that prefer open savanna landscapes, moving even further southwards at the end of their wintering season is not an option in the western Sahel since habitats further south become increasingly closed and forested. These species have to cope with deteriorating conditions and might adapt to this by changing space use. One could expect that birds which experience decreasing prey availability would increase foraging time or effort by either roaming further or increasing the time spent foraging within the same area, possibly also accompanied by a switch to other prey species. Recent technological advancements give us the possibility to investigate the behaviour of individual birds remotely. Using detailed GPS-tracking data, we are able to calculate behavioural measures such as the time flying, the distance covered and area used on a daily basis.

Montagu's Harriers *Circus pygargus* spend more than 6 months in the Sahel (Trierweiler & Koks 2009). Satellite tracking of individual birds has revealed that they are itinerant using distinct sites (on average four) to which they are site-faithful in consecutive years (Trierweiler *et al.* 2013). During the wintering season, sites are located progressively further southwards following a shifting 'green belt' of vegetation harbouring highest food abundance (Trierweiler *et al.* 2013). Wintering harriers prefer open landscapes and avoid forested areas (Limiñana *et al.* 2012a; Trierweiler *et al.* 2013; Augiron *et al.* 2015), thus lack the possibility to move further south when conditions continue to deteriorate during winter. From their last wintering site in the southern Sahel, birds depart directly north at the onset of spring migration (March). This means that they have to maintain themselves and prepare for migration within an area at the time of worst ecological conditions. Montagu's Harriers are acridivorous during the winter, feeding mainly on local grasshopper species (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013). The most abundant grasshoppers during the dry season are species with diapausing adults, from mid-October onwards only adults are present which are depleted by predation during the season (Mullié 2009; Mullié & Guèye 2010).

The aim of our study was to investigate whether Moreau's Paradox is a real paradox for Montagu's Harriers, thus whether ecological conditions indeed deteriorate towards the end of their wintering period and how birds react to those changes. Therefore, we concentrate on the final wintering site where individuals reside before spring departure. We hypothesize that at this time and place, individuals experience deteriorating conditions. This may impact their foraging behaviour and even have carry-over effects to consecutive seasons. We predict that birds have to increase their foraging effort in response to decreasing prey abundance. To investigate this, we combine field data on prey availability collected at wintering sites in Senegal with high-resolution GPS-tracking data of Montagu's Harriers. Hence, our study provides a prime example of Moreau's Paradox, illustrated at the level of individual birds, giving insights into how migrants deal

with deteriorating ecological conditions at the end of their wintering period.

Materials and methods

STUDY SITES

In 2014 and 2015, we conducted fieldwork in five wintering areas of Montagu's Harriers in central-western Senegal, situated between 14·8° N and 13·6° N and 16·7° W and 15·4° W (Fig. 1a,b). The climate in this region is characterized by a wet season from June to October followed by a dry season from November to May. Mean annual rainfall in Kaolack (14·15° N 16·08° W) since 1919 was 709 mm, but 647 mm during the last 20 years. We considered 2014 a wet year since it was wetter than the 47 years before and 2015 a dry year because it was drier than the last 16 years (Fig. S1, Supporting Information). Areas were chosen because GPS-tagged Montagu's Harriers from breeding populations in the Netherlands, Denmark, Germany and France were or had been using these areas as their last wintering sites. The main study site was the area of Khelcom, also known as Mbégué (14·44–14·74° N and 15·42–15·64° W, ca. 55 000 ha) which is the most important known wintering area of Montagu's Harriers in West Africa, harbouring over 5000 individuals (Mullié & Guèye 2010; Augiron *et al.* 2015). In Khelcom, individual

roosts support between several hundred up to 4000 harriers (January 2015). This area consists of a mosaic of herbaceous savanna, fallow land and cropland [mainly groundnut *Arachis hypogaea* and millet *Pennicetum glaucum*; for a detailed description, see Mullié & Guèye (2010)]. The relatively high percentage of fallow land (Herrmann & Tappan 2013) created a temporarily ideal habitat for wintering harriers and hosts high densities of grasshoppers (Mullié 2009). The second important study site was near Diofior in the region of Fatick (14·15–14·28° N and 16·57–16·66° W), at the edge of the Sine Saloum delta. This region, known for its salt production, is dominated by deltaic flats where wetlands bordered by halophytic vegetation are interspersed with ridges covered by shrubby savanna vegetation. The flats and wetlands dry up during the dry season leaving vast areas of bare salty sand flats, or *tann*. Agriculture is limited to upper and less salty soils surrounding the delta region. Harrier roosts in this area were much smaller, supporting between 50 and 300 birds, with several small roosts being located at distances of about 10 km. Our other three study sites were located near Nioro du Rip (13·85° N 15·69° W), Kaffrine (14·05° N 15·39° W), and Payama (13·65° N 15·57° W). The landscape of these more south-western sites is characterized by low plateaus separated by wide, shallow depressions (Tappan *et al.* 2000). The areas around Nioro du Rip and Kaffrine are dominated by agriculture, also mainly groundnut and millet production, where little bushland or fallow land remains. The landscape in the area near Payama, the
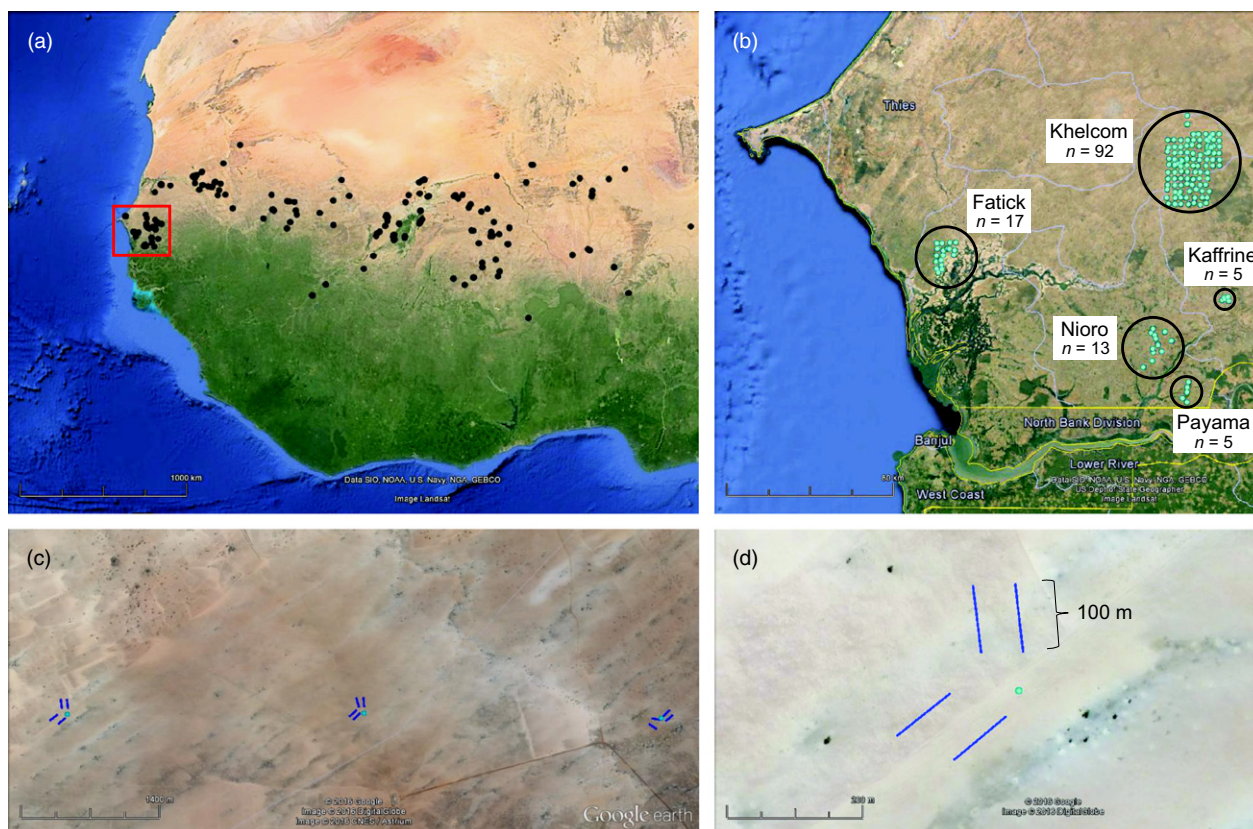

Fig. 1. (a) Montagu's Harrier wintering areas in the Sahel of West Africa. Black dots indicate wintering areas of GPS-tracked Montagu's Harriers. An individual visits several consecutive areas during the winter, thus being reflected by multiple points on the map. The red rectangle encloses our study sites in Senegal. (b) Study sites in Senegal with sampling points for grasshopper transect counts marked in light green. (c) Alignment of sampling points at approximately 3 km distance from each other, each surrounded by four transects. (d) Typical position of four grasshopper transects of 100 m length around sampling point.

southernmost site close to the border with the Gambia, is much less open and characterized by laterite plateaus alternated with dense woody vegetation and some agriculture. In all those three areas, smaller roosts with several up to 50 birds were observed.

GRASSHOPPER TRANSECT COUNTS

At the two main study sites, Khelcom and Fatick, we conducted grasshopper transect counts on a grid of sampling points at a distance of approximately 3 km to each other covering the core of the area used by GPS-tagged Montagu's Harriers (Khelcom $N = 92$ points, Fatick $N = 17$ points; Fig. 1b,c). The grid in Khelcom was considerably larger since more individuals were present in the area (of which some were tagged in this area). The other three sites were each the wintering site of a GPS-tracked harrier equipped on its breeding grounds. During the first visit in search of the birds, sampling points, mostly also with around 3 km distance between each other, were established in places that were used by the tracked individuals in the year before (Nioro $N = 13$, Kaffrine $N = 5$, Payama $N = 5$).

At each sampling point, four transects, each of 100 m length, were walked by two observers with a minimal distance of 50 m between transects (Fig. 1d). For each transect, the start and end positions were marked with a GPS during the first visit in January 2014. The same transects (with an accuracy of <10 m) were walked in the middle of the wintering season of harriers (end of January/beginning of February) and at the end of the wintering season (end of March/beginning of April) in 2014 and 2015, respectively. Thus, the same transects were counted twice per season in two consecutive years. Transects were in homogenous habitats, and habitat characteristics were noted on a standardized form (Appendix S1). All grasshoppers within 1 m each side of the transect line were counted. We distinguished two size categories of grasshoppers: less or equal to 3 cm or larger than 3 cm. Approximate grasshopper biomass was calculated by multiplying the encountered numbers by wet weights of the two most common grasshopper species observed in the area of Khelcom (Mullié & Guèye 2010; category small: *Acorypha clara*, 0·9 g; big: *Ornithacris cavroisi*, 2·6 g). Since the species encountered during transect counts depend on green vegetation, we used normalized difference vegetation index (NDVI) as a proxy for food availability (cf. Trierweiler *et al.* 2013, see below).

GPS-TRACKING DATA OF MONTAGU'S HARRIERS

Between 2009 and 2015, we collected GPS-tracking data using UvA-BiTS GPS trackers (Bouten *et al.* 2013; www.uva-bits.nl) from 36 Montagu's Harriers (25 males and 11 females). Birds were captured during the breeding season in the Netherlands (53·2° N 7·2° E, $N = 17$), France (46·2° N 0·4° W, $N = 8$) and Denmark (55·1° N 8·7° E, $N = 6$), plus five at their wintering site in Senegal (Khelcom). One male captured in the Netherlands spent the three following breeding seasons in Germany (52·6° N 8·37° E). One Danish male stayed in Africa during one summer (I.H. Sørensen, A.E. Schlaich, R.H.G. Klaassen, H. Heldbjerg & B.J. Koks, in prep) and was removed from the data set for further analyses. Since several individuals were tracked in more than 1 year, the total number of year*individual combinations in the data set was 53. Of those, only 43 had complete data (in five

cases, the end of the winter was missing; in two cases, the start was missing; and in three cases, both the start and the end were missing). In addition, we excluded two individuals as insufficient data were collected per day to calculate daily measures, thus keeping, in total, 41 complete year*individuals. To analyse whether foraging behaviour changed during the individuals' stay at their last wintering site where they might experience deteriorating conditions within the same area, we considered only year*individual combinations where the bird stayed longer than 60 days at its last wintering site. Those summed up to 31 year*individual combinations. Arrival and departure at different wintering sites were determined visually (see Fig. S2 for an example), with the first wintering site being defined as the first site south of 18° N in which the bird stayed for at least 3 days. Start of spring migration and arrival date at the breeding site were also determined visually, with the first having been obvious in all cases, since birds stay in their wintering area until they abruptly head north (Fig. S2c).

The GPS loggers were programmed to collect GPS positions at an interval of 5 min ($N = 2$ tracks), 10 min (9), 15 min (16) or 30 min (4) during the day and at maximum once per hour during the night. Intervals differed because memory storage increased with newer trackers. Only positions during daylight were used for the analyses, with daylight being defined as being between nautical dawn and nautical dusk. By subsampling the 5-min interval data of one bird to intervals of 10, 15, 20 and 30 min, we checked whether the different daily measures were a function of the recording interval. Since this was not the case (data not shown), we only subsampled the 5-min interval data to 10-min intervals to keep three common intervals (10, 15 and 30 min). Data were checked for outliers visually and by calculating trajectory speed (between two consecutive GPS positions) and discarding points with trajectory speeds higher than 25 m s^{-1}.

CALCULATION OF DAILY FORAGING PARAMETERS

Foraging parameters such as time spent flying, distance covered and home range size were calculated for each day. Days with fewer than 75% of expected positions (54 for 10-min interval, 36 for 15-min interval and 18 for 30-min interval) were removed from the data set. Using instantaneous speed, we determined for each position if the bird was sitting or flying by means of a threshold of 1·2 m s^{-1} (local minimum of a two-peaked frequency distribution of speed values, see Fig. S3 for an example of a frequency distribution of instantaneous speeds). Time spent flying per day (in hours) was calculated as the percentage of positions spent flying in order to correct for length of day. Daily cumulative distance was calculated by summing up the distances between consecutive positions during each day. Distance between positions was calculated using function *distMeeus* from ʀ package *geosphere* version 1.5-1 (Hijmans 2015). Daily home range size was calculated as 95% kernel density estimation using ʀ package *rhr* version 1.2 (Signer & Balkenhol 2015). The bandwidth parameter h was determined by reference bandwidth estimation using function *rhrHref*.

NORMALIZED DIFFERENCE VEGETATION INDEX DATA

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) were 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 point of grasshopper sampling, $9 \times 9 = 81$ pixels of 250×250 m (~5 km²) were downloaded for the years 2014–2015. The mean of those 81 pixels was calculated for each 16-day period, and the values for the period corresponding to the actual grasshopper count dates were added to the grasshopper transect data set. Mean NDVI at each study site (Fig. 2) was calculated by averaging the values of all sampling points in the area. No NDVI values could be retrieved for transects counted in March 2015 due to a gap in available NDVI data.

As grasshopper numbers were negatively correlated with NDVI (see Results), we used vegetation greenness as a proxy for grasshopper abundance in areas where no field data on grasshoppers were collected. Indeed, the abundance of grasshoppers will not strictly be determined by the greenness of the vegetation at the exact moment of the transect counts, but will also have been influenced, for example by the amount of rainfall during the preceding rainy season, the greenness in the previous dry season or the number of grasshoppers in the previous year. Nevertheless, it has been shown that NDVI is a valuable tool to gain insight into trophic interactions on a global scale (Pettorelli *et al.* 2005), to locate potential grasshopper and locust habitats (Tappan, Moore & Knausenberger 1991; Waldner *et al.* 2015) and could be used as proxy for food availability (Szép & Moller 2005; Trierweiler *et al.* 2013).

For each wintering site of all GPS-tracked Montagu's Harriers, $25 \times 25 = 625$ pixels of 250×250 m (~39 km², mean home range size) around the mean latitude/longitude of that site were downloaded for the years the bird was present at that site. The

average of the 625 pixels was calculated for each 16-day period, and to each day of the harrier data set, the value of the corresponding period was added.

STATISTICAL ANALYSES

All analyses were performed in R 2.15.2 (R Core Team 2014). Grasshopper abundance and biomass were log-transformed and modelled using linear mixed models (LMM) with *month* (January or March) and *year* (2014 or 2015) as fixed effects and *session* (2014·1, 2014·2, 2015·1 and 2015·2) and *transect ID* nested in *sampling point* and *area* as random effects by means of R function *lmer* from package *lme4* version 1.1-7 (Bates *et al.* 2015). Confidence intervals were retrieved using R function *confint.merMod* from the same package. The relation between grasshopper biomass (log-transformed) and NDVI was tested using a generalized additive mixed model (GAMM) with *session* and *transect ID* nested in *sampling point* and *area* as random effects by means of R function *gamm4* from package *gamm4* version 0.2-4 (Wood & Scheipl 2014). Changes in NDVI values during the stay of harriers at their final wintering site were modelled using a GAMM with *year* and *individual* nested in *year* as random effects. The trend of daily measures (time spent flying, cumulative distance and kernel home range size) over time, as well as the relation of time spent flying and NDVI, was also investigated by means of GAMMs with *year* and *individual* nested in *year* as random effects. The relation between departure date and NDVI, latitude of the final wintering site, breeding latitude and sex and the relation between arrival date and departure date, latitude of the final wintering site, breeding latitude and sex was tested using linear models (LM).
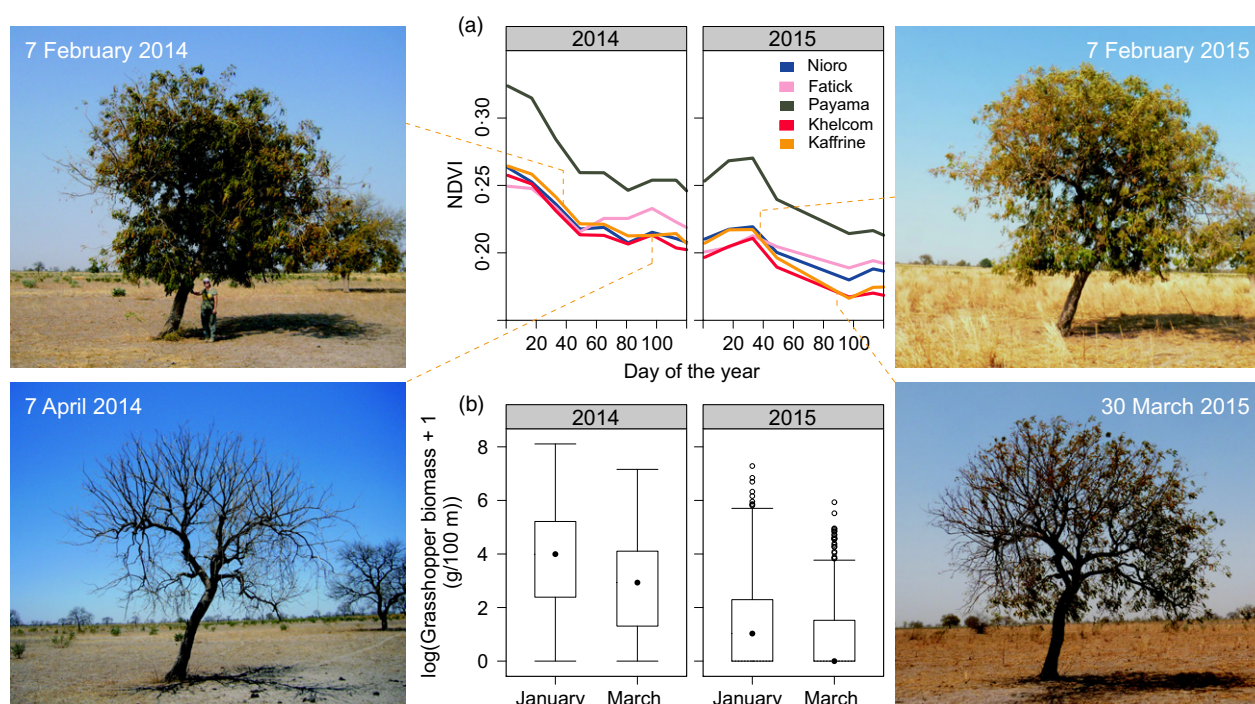

Fig. 2. (a) Normalized difference vegetation index (NDVI) in five wintering areas of Montagu's Harriers in Senegal during the winters 2013/2014 and 2014/2015. Dashed lines indicate periods of fieldwork. Pictures were taken in area 'Kaffrine'. (b) Grasshopper biomass (log-transformed) in the middle (January) and at the end (March) of the wintering period of Montagu's Harriers in 2014 and 2015 in five areas in Senegal. $N = 2193$ transects of 100 m length.

Results

SEASONAL TRENDS IN FOOD AVAILABILITY

Normalized difference vegetation index values in the five study areas in Senegal decreased over the course of the wintering period and were lower in the dry winter 2014/2015 than in the wetter winter 2013/2014 (Fig. 2a). We found that the abundance of grasshoppers decreased from January to March by 56% and 68% in the winters 2013/2014 and 2014/2015, respectively, and was lower in 2015 compared to 2014 (Table 1a, Fig. 2b; mean values in January and March: 2014 77·68 and 34·28, 2015 13·13

and 4·2). The same pattern was observed for biomass (Table 1b, Fig. 2b; mean values in January and March: 2014 181·49 and 60·09, 2015 23·36 and 7·21). Finally, grasshopper biomass was also positively correlated with NDVI values before reaching a plateau at higher NDVI values (Table 1c, Fig. 3), confirming both a seasonal decrease in grasshopper abundance and lower values during winter 2014/2015 compared to winter 2013/2014.

FORAGING EFFORT RESPONSE OF MONTAGU'S HARRIERS TO FOOD AVAILABILITY

Montagu's Harriers tracked by GPS loggers were wintering in the Sahel between Senegal in the west and Niger in the east (Fig. 1a). At their final wintering site, birds experienced decreasing NDVI values during the course of their stay (Table 1d, Fig. 4a,b).

Montagu's Harriers flew, on average, between 2·25 and 8·43 (mean 4·98) hours per day at their final wintering site, and almost all individuals increased the amount of flight time gradually between January and spring departure at the end of March/beginning of April (Table 1e, Fig. 4c,d; for individual graphs see Fig. S4). On average, birds flew 1·74 times more during the last 10 days than during the first 10 days of their stay at their last wintering site, thus nearly doubling the time they spent flying. In addition, both cumulative daily distance (1·97 times, Table 1g, Fig. S5a) and kernel home range size (9·59 times, Table 1h, Fig. S5b) also increased between January and March.

Individuals increased their flight time when local NDVI values dropped at their final wintering site (Table 1f, Fig. 4e,f; for individual graphs see Fig. S6). The steepest increase in flight time was observed in the range of NDVI values in which grasshoppers were mostly affected in our Senegal data set (0·19–0·25, compare Figs 3 and 4e,f),

Table 1. Summary statistics of models on within-winter changes in grasshopper abundance and biomass, as well as Montagu's Harriers' behaviour at their last wintering site

Variable	Estimate	SE	t-value	Lower CI	Upper CI
(a) Grasshopper abundance (GLMM)					
Intercept	3·125	0·396	7·887	2·286	3·976
Month	−0·558	0·072	−7·704	−0·681	−0·434
Year	−1·767	0·072	−24·403	−1·89	−1·643
(b) Grasshopper biomass (GLMM, estimates shown in Fig. 2b)					
Intercept	3·674	0·495	7·421	2·665	4·695
Month	−0·715	0·196	−3·656	−1·027	−0·403
Year	−2·096	0·196	−10·718	−2·408	−1·784

	EDF	F-value	P-value
(c) Grasshopper biomass (GAMM, estimates shown in Fig. 3)			
s(NDVI)	3·82	36·7	<0·001
(d) Seasonal NDVI changes in individual wintering area harriers (GAMM, Fig. 4b)			
s(date)	3·97	546·5	<0·001
(e) Seasonal pattern in hours flying per day for individual harriers (GAMM, Fig. 4d)			
s(date)	5·43	121·8	<0·001
(f) Hours flying per day for individual harriers in relation to local NDVI (GAMM, Fig. 4f)			
s(NDVI)	7·02	33·19	<0·001
(g) Seasonal pattern in cumulative distance per day flown by individual harriers (GAMM, Fig. S5b)			
s(date)	3·76	61·24	<0·001
(h) Seasonal pattern in kernel home range size of individual harriers (GAMM, Fig. S5d)			
s(date)	4·17	29·72	<0·001

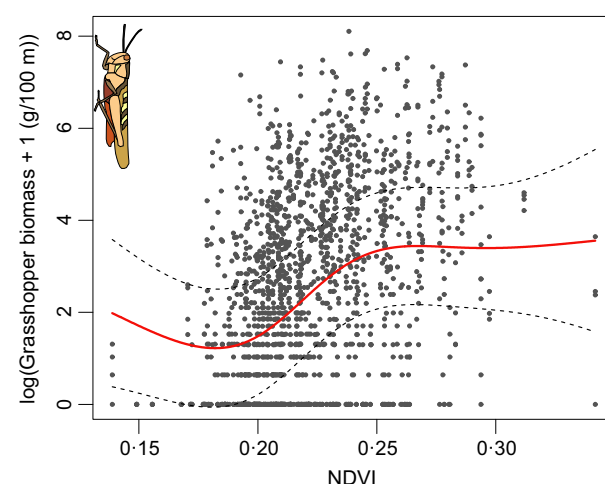|	Estimate	SE	t-value	P-value
(i) Departure date from wintering grounds (LM, Fig. 5a)				
Intercept	81·598	24·115	3·384	0·003
NDVI	−42·8237	19·544	−2·191	0·04
Wintering latitude	−1·099	0·856	−1·283	0·21
Breeding latitude	0·587	0·339	1·733	0·097
Sex	−1·941	2·324	−0·835	0·413
(j) Arrival date at breeding grounds (LM, Fig. 5b)				
Intercept	40·295	25·069	1·607	0·12
Departure date	0·568	0·177	3·215	0·003
Wintering latitude	0·02	0·793	0·026	0·98
Breeding latitude	0·666	0·328	2·032	0·052
Sex	−1·907	2·076	−0·918	0·367

EDF, estimated degrees of freedom.

Fig. 3. Grasshopper biomass (log-transformed) in gram per 100 m counted on transects against normalized difference vegetation index (NDVI) values. Predicted values of GAMM are shown as red line, twice standard error as dashed lines.
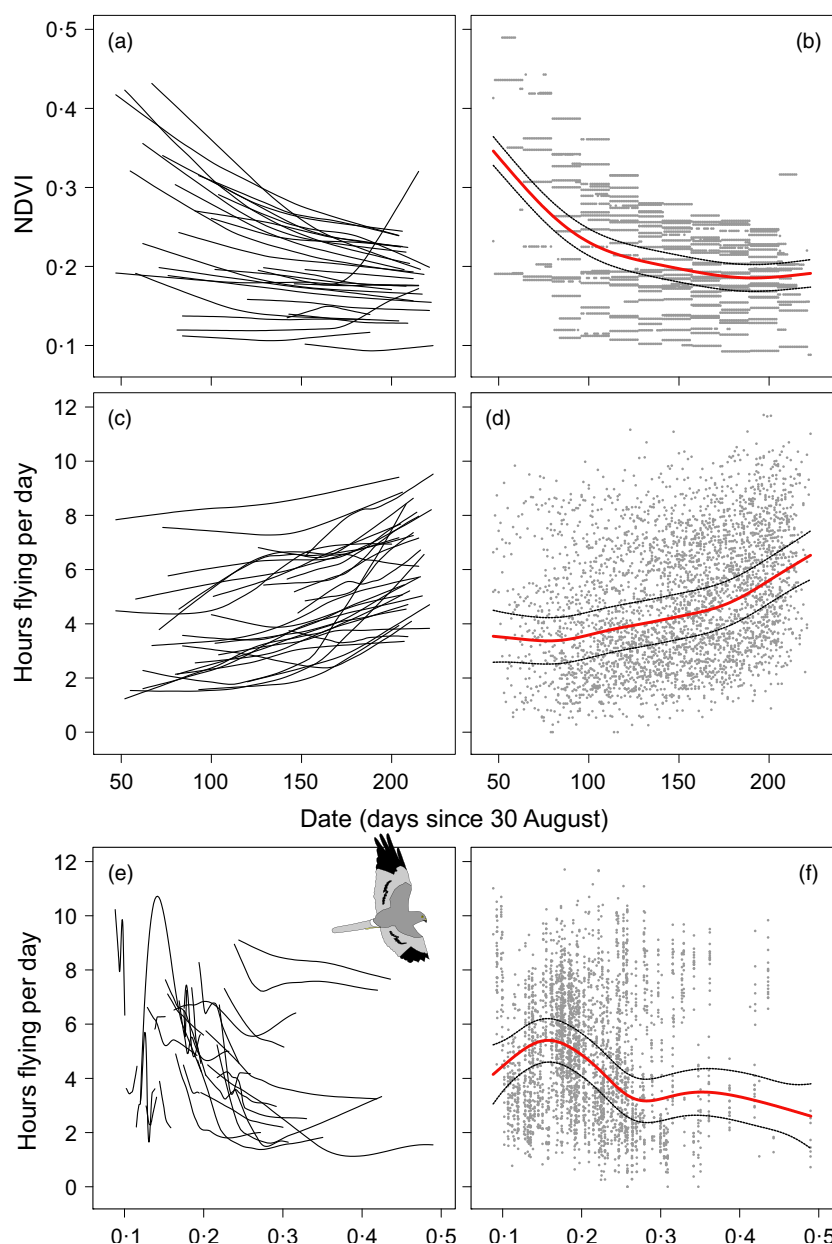
Fig. 4. Seasonal changes in (a and b) NDVI experienced by 31 GPS-tracked Montagu's Harriers at their final wintering site. (c and d) Daily hours spent flying of GPS-tracked Montagu's Harriers at their final wintering site. (e and f) Daily time spent flying of Montagu's Harriers in relation to normalized difference vegetation index (NDVI) used as proxy for grasshopper abundance. Lines are loess smoothed raw data per individual on the left (a, c, e) and raw data overlayed by predicted values of GAMMs (red) and two times standard errors (dashed lines) on the right (b, d, f).

suggesting that the increase in flight time was a direct response to declining prey densities. Montagu's Harriers departed later on spring migration when encountering lower NDVI values (Table 1i, Fig. 5a), and subsequently arrived later in their breeding area (Table 1j, Fig. 5b). Breeding latitude, latitude of the final wintering site and sex did not significantly contribute to these patterns.

Discussion

In this study, we first describe the seasonal deterioration of environmental conditions at the final wintering sites of Montagu's Harriers wintering in the Sahel. Secondly, we show that deteriorating conditions (i.e. drying out of the landscape) are associated with a decline in grasshopper abundance; the harriers' main prey during winter. Thirdly,

we reveal that harriers respond to these changes in environmental conditions by increasing their daily flight time, distance and home range size during their stay at the last wintering site. Finally, our findings indicate that unfavourable conditions at the final wintering site could have carry-over effects to later annual cycle stages and that in dry years the deterioration of environmental conditions might have fitness consequences by showing that birds in drier areas forage more intensively, depart later on spring migration and arrive later at their breeding grounds.

WHY DO HARRIERS INCREASE FORAGING TIME?

Previous work on satellite tagged Montagu's Harriers revealed that individuals visit several wintering sites during the season following a southwards shifting 'green belt'
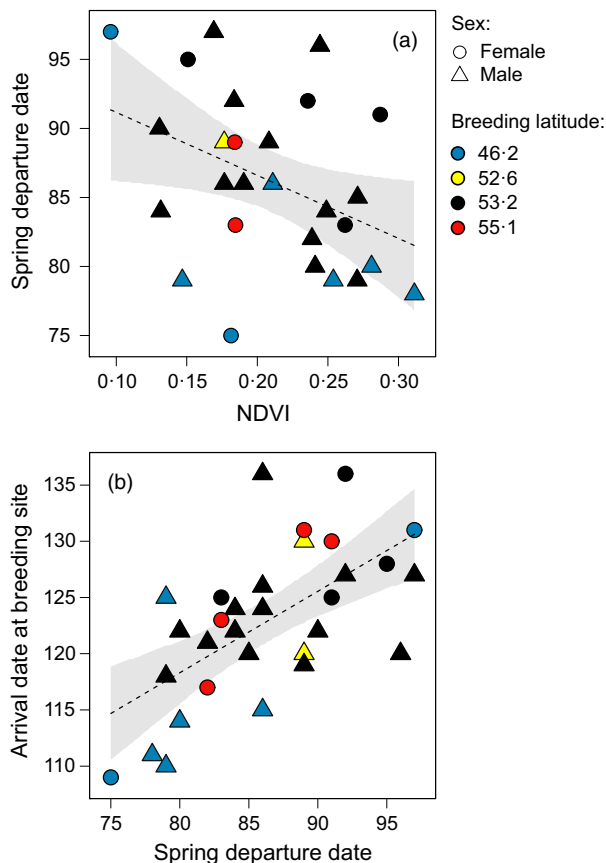
Fig. 5. (a) Departure date (days since 1 January) of Montagu's Harriers for spring migration in relation to mean NDVI values at their final wintering site. (b) Arrival date at the breeding area in relation to spring departure date from the last wintering area. Breeding latitude of individuals is indicated in different colours (blue: France, yellow: Germany, black: the Netherlands, red: Denmark), sex with different symbols. Linear model is indicated by dashed line. For statistics, see Table 1i,j.

of vegetation and thereby stay within the range of NDVI values containing most grasshoppers (Trierweiler *et al.* 2013). In West Africa, this southward shift comes to an end at the southern border of the Sahel, and we show that at those final wintering sites, birds still do experience declining densities of grasshoppers during their stay.

The GPS-tracked Montagu's Harriers increased their daily flight time, distance covered and area used during the stay at their final wintering site. Individual variation in those behavioural measures was enormous, with individuals spending on average from 2·2 up to 8·4 h flying per day. Whether this variation resulted from variation between wintering sites or heterogeneity in individual quality could not be assessed in our study since our data set contained only one bird per area, covering the whole wintering range of the north-western breeding populations between Senegal and Niger (Limiñana *et al.* 2012b; Trierweiler *et al.* 2013). We also have no information on the number of conspecifics and the number of other acridivorous species, and thereby the within- and between-species

competitions in the areas of our GPS-tracked individuals, that may further explain variation.

Additionally, the observed behavioural changes may also be explained by preparation for spring migration. Many migrants do store large fuel loads prior to crossing ecological barriers, such as the Sahara, and these stores are gained during the last weeks before departure (Newton 2008). After departing from their last wintering site, Montagu's Harriers head straight north crossing the Sahara desert (cf. Fig. S2) and normally just stopover in North Africa (Trierweiler *et al.* 2014). However, if the increased flight time over the season was solely to store reserves for migration, we would have expected a stronger increase prior to departure rather than a more gradual increase over 3 months, as birds generally have a high capacity of accumulating fat reserves, at least when foraging conditions are favourable (Kvist & Lindström 2003). In addition, Montagu's Harriers migrate to a large extent by soaring flight (Limiñana *et al.* 2013), a relatively energy-efficient flight mode (Hedenstrom 1993), and are fly-and-forage migrants (Trierweiler 2010), which might further reduce the need to store huge fuel loads, assuming that harriers can find food during the Sahara crossing. We thus conclude that Montagu's Harriers alter their behaviour in response to deteriorating conditions in the Sahel.

MOREAU'S PARADOX

Moreau wondered in 1972 how millions of Palaearctic migrants could winter in the dry Sahel and prepare for spring migration in what seem to be continually deteriorating conditions (Moreau 1972). We discuss three possible ways in which Moreau's Paradox might be resolved.

First, the paradox can be resolved because the assumption of deteriorating food abundance in the course of the dry season is false. This is clearly not the case for Montagu's Harriers (cf. Fig. 2) and other acridivorous species in Senegal. However, it might be true for other areas or other species relying on different food sources. Even though our transect counts covered only wintering areas at the western most range of the wintering distribution of Montagu's Harriers, the similar relationship reported by Trierweiler *et al.* 2013 for Niger and the importance of grasshoppers as prey found in pellets in other areas (Trierweiler & Koks 2009; own unpublished data) make us confident to believe that this is a common pattern. Morel (1973) argued that migrants arrive in the Sahel just at the end of the rainy season when vegetation is rank and invertebrates numerous. During their stay, at least some trees continue to have leaves, flowers and fruit production. Writing mainly about passerines, he further argued that potential competition with local species might be low since these often perform within-African movements (Morel 1973). Within the West African Sahel, Zwarts *et al.* (2015) recently found the highest numbers of insectivorous woodland bird migrants in the driest and most

desiccated parts. They further suggested that migrant Palaearctic birds prefer thorny tree species (e.g. *Acacia* and *Balanites*) that are richer in arthropods. However, it is likely that insect densities on these trees also decline during the dry season, and birds still need to prepare for migration during the worst period of the season. Field data on prey availability and diet choice for insectivorous tree dwelling birds in space and time are still lacking, and hence, we cannot come to a general conclusion.

A second solution to the paradox may be that prey abundance is decreasing, but birds switch to alternative prey. Currently, we have no indication that this occurs in wintering Montagu's Harriers, despite the fact that prey switching certainly occurs in breeding populations. Indeed, breeding Montagu's Harriers can forage on a wide range of prey, with small birds being their main prey in many areas, whereas voles dominate in other areas (Terraube & Arroyo 2011). In populations that depend strongly on Common Voles *Microtus arvalis*, harriers switch to alternative prey like songbirds, reptiles and large insects in years with low vole densities (Millon *et al.* 2002; Koks *et al.* 2007). In winter, the species is highly acridivorous (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013), and our pellet samples from Senegal in 2014 show no obvious switch in diet between the middle and the end of the wintering period (own unpublished data). But in other wintering areas, such as Niger, fewer grasshoppers (<60%) are found in pellets (Trierweiler & Koks 2009), and hence, diet switches may be part of the solution in some ecological conditions. Diet switches might occur in other Sahelian migrants, since some songbirds can switch to berries (e.g. berries of *Salvadora persica*: Morel 1973; Zwarts *et al.* 2015) or nectar (Salewski, Almasi & Schlageter 2006).

Thirdly, prey abundance may be decreasing but birds cope with this by adapting their foraging behaviour. This is what we found for Montagu's Harriers which increased their flight time with decreasing prey abundance. However, in dry areas or years, this seems to come at the cost of a late departure that might subsequently carry-over to later annual cycle stages (Norris & Marra 2007).

ULTIMATE EFFECTS

Local ecological conditions at the end of the winter affect individuals, as we show that harriers wintering in areas with less vegetation and hence lower food abundance departed later in spring (Fig. 5), suggesting a link between food availability and individual condition. Departure date might be strongly influenced by individual annual schedules with birds breeding at more southern latitudes departing earlier and consequently being able to winter in more northern and drier areas, as shown for Pied Flycatchers *Ficedula hypoleuca* (Ouwehand *et al.* 2016). Still, the effect of NDVI on departure date of our harriers remained significant when testing for effects of latitude of wintering and breeding site, as well as sex. In a completely different ecosystem, American Redstarts *Setophaga ruticilla* that winter in habitats with higher food abundance do depart earlier than individuals in low-quality habitats at the same site, and departure is earlier in years with more rainfall (Studds & Marra 2012). For the Sahel system, there is evidence showing that annual mean spring migration time through the Mediterranean is later after dry winters (Both 2010; but see Robson & Barriocanal 2011 for opposite trends), as is spring arrival at breeding sites (Saino *et al.* 2004; Both *et al.* 2006; Gordo & Sanz 2008; Balbontín *et al.* 2009; Tøttrup *et al.* 2012). As timing affects later fitness consequences in most migratory species, Moreau rightly drew attention to the difficulty migrants might have when leaving their wintering grounds during the worst ecological circumstances in the season. Low Sahel rainfall has also been shown to lower overwinter survival in Palaearctic migrant species that spend the winter here (Den Held 1981; Peach, Baillie & Underhill 1991; Zwarts *et al.* 2009), which could be mostly happening through conditions at the end of the winter period hampering preparation for spring migration. Indeed, mortality in Montagu's Harriers is highest during the spring crossing of the Sahara desert (Klaassen *et al.* 2014). The same is not only also true for other migrants, but even more pronounced in drier years (Zwarts *et al.* 2009). We should stress that our data are biased towards individuals that successfully returned to the breeding areas; thus, we cannot infer mortality. The later departure from the driest wintering sites could suggest that other individuals departed in too low condition to successfully migrate to the breeding areas and were never seen again. Alves *et al.* (2012) showed for Icelandic Black-tailed Godwits *Limosa limosa islandica* that individuals in poor condition did not migrate. Late departure can be associated with late arrival at the breeding sites (cf. Fig. 5b; Jahn *et al.* 2013; Lemke *et al.* 2013), and late arriving individuals often have lower reproductive success (Kokko 1999; Smith & Moore 2004). Additionally, it has been shown for several species that breeding performance is indeed lower in years that followed a drier winter (Zwarts *et al.* 2009, p. 472ff and references therein). We thus suggest that wintering in habitats with low food availability before the onset of spring migration may negatively affect fitness. Thus, especially extremely dry years (as during the severe droughts in the 1970s and 1980s) might strongly influence survival and subsequent breeding success. Ongoing climate change with possibly less rainfall in the Sahel region paired with increased human pressure on natural and agricultural habitats resulting in degradation and desertification might make this late wintering period prior to migration more demanding, likely affecting overall population size. For a species that is depending on immense protection efforts in Europe, this might have disastrous effects and we need to investigate small-scale habitat use in wintering areas to gain knowledge that could be used to improve the year-round conservation of the species by means of habitat conservation and management along the flyway.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.144sv (Schlaich *et al.* 2016).

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Supporting Information

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

Appendix S1. Grasshopper transect count form used for sampling in Senegal in 2014 and 2015.

Fig. S1. Annual rainfall (mm) at Kaolack, Senegal (14·15° N 16·08° W).

Fig. S2. Example of a typical winter season of a male Montagu's Harrier wintering in Senegal.

Fig. S3. Example of a frequency distribution of instantaneous flight speeds (in m s^{-1}).

Fig. S4. Daily hours spent flying of GPS-tracked Montagu's Harriers during the whole wintering season.

Fig. S5. Cumulative distance (a and b) and kernel home range size (95%) (c and d) of GPS-tracked Montagu's Harriers at their final wintering site.

Fig. S6. Daily time spent flying and Normalized Difference Vegetation Index (NDVI) at the final wintering site of Montagu's Harriers.