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Rare case of an adult male Montagu's Harrier *Circus pygargus* over-summering in West Africa, as revealed by GPS tracking

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Abstract Over-summering within or near the African wintering range by immature, non-breeding individuals occurs regularly in several species of long-distance migratory raptors, yet the extent of over-summering in Africa by adult birds remains unclear. In this study, we describe a case of an adult Montagu's Harrier over-summering in Africa, as revealed by GPS tracking. By relating detailed knowledge of the bird's movements to remotely sensed environmental data (normalized difference vegetation index, NDVI), we show that over-summering in this case was likely related to an exceptionally difficult breeding season the previous year rather than an effect of adverse weather conditions encountered during the winter or a failed attempt to migrate. Various factors are discussed as potential driving forces behind the bird's intra-African movements. Finally, we relate the documented case to a large number of North European Montagu's Harriers studied by telemetry and show that over-summering in Africa by adult individuals is indeed a rare event.

Keywords GPS tracking · Remote sensing · Raptor migration patterns · *Circus pygargus* · Behavioural ecology · Over-summering

Zusammenfassung

Seltener Fall von Übersommerung eines adulten Wiesenweihenmännchens *Circus pygargus* in Westafrika enthüllt durch GPS-Tracking

Übersommerung innerhalb oder nahe ihrer afrikanischen Überwinterungsgebiete kommt bei immaturren, nicht-brütenden Individuen verschiedener langstreckenziehender Greifvogelarten regelmäßig vor. Das Ausmaß von Übersommerung bei adulten Vögeln in Afrika ist jedoch noch undeutlich. In dieser Studie beschreiben wir einen Fall von Übersommerung eines adulten Wiesenweihenmännchens in Afrika, der sich dank GPS-Verfolgung offenbarte. Durch die detaillierten Kenntnisse der Bewegungsmuster des Vogels in Beziehung zu setzen zu ökologischen Daten aus der satellitengestützten Fernerkundung (Normalized Difference Vegetation Index, NDVI), zeigen wir, dass die Übersommerung in diesem Fall wahrscheinlich eher im Zusammenhang mit einer außergewöhnlich schwierigen Brutsaison im vorausgegangenen Jahr stand, als eine Folge von widrigen Wetterbedingungen im Winter oder einem fehlgeschlagenen Zugversuch war. Diverse Faktoren werden als potentielle treibende Kräfte hinter den inner-afrikanischen Bewegungen des Vogels diskutiert. Schließlich setzen wir den hier dokumentierten Fall in Bezug zu einer großen Anzahl von nordeuropäischen Wiesenweihen, die anhand von Telemetrie verfolgt worden sind und zeigen, dass Übersommerung eines adulten Individuums in Afrika in der Tat ein seltenes Ereignis ist.

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Introduction

Migratory routes connect European breeding sites with non-breeding sites in Africa through the movement of more than two billion birds each year (Webster et al. 2002; Hahn et al. 2009). Migration allows birds to exploit northern seasonal resources during the breeding season, and it is a very common behaviour in terms of both number of bird families and total number of individuals involved (Newton 2010). However, not all individual migrants return to the breeding grounds in spring, as some may defer migration and remain in Africa during the European summer. Such over-summering has been reported mainly for non-breeding subadult birds of large and long-lived species, including several species of migratory raptors (e.g. Österlöf 1977; Gschweg et al. 2008; Mellone et al. 2011). Over-summering also occasionally occurs in adult raptors (Thiollay 1989; Fransson 2001), yet to our knowledge, detailed information on individual cases is lacking in the scientific literature.

Several ideas have been put forward to explain why individuals remain at or near their winter quarters in Africa during the breeding season. Migration entails a high mortality risk (Klaassen et al. 2014), and by deferring migration, subadult non-breeding birds may generally increase their chances of survival until sexual maturity is reached (Newton 2010). However, reasons for adult breeding birds staying the summer in Africa are probably specific to each individual. Poor body condition, whether due to difficult conditions in Africa or as a consequence of an exhaustive breeding effort the previous year, might impede spring migration. The same is true for exceptionally harsh weather conditions. In order to understand the causes leading to over-summering by adult birds, detailed information on individual movements and behaviour is needed, ideally in combination with information on relevant environmental conditions.

Recent developments in tracking techniques have greatly improved our knowledge of the movement patterns of individual raptors (Catry et al. 2010; García-Ripollés et al. 2010; Klaassen et al. 2014), and Montagu's Harriers *Circus pygargus* have been tracked intensively to study the species' migration system (Limiñana et al. 2007; Trierweiler et al. 2007; Klaassen et al. 2014; Trierweiler et al. 2014) and wintering ecology (Limiñana et al. 2012a; Trierweiler et al. 2013; Schlaich et al. 2016). Furthermore, ecologists have found ways to combine field-based studies with remote sensing data, and since such large-scale data sets are now easily accessible, they are widely used in ecological research (Kerr and Ostrovsky 2003). Trierweiler et al. (2013) used remote sensing data on the normalized difference vegetation index (NDVI) to show that

Montagu's Harriers track a high abundance of resident grasshoppers, the harriers' main prey in winter, by gradually moving southwards during the winter period.

Here we report an unprecedented case of over-summering in an adult male Montagu's Harrier tracked from its breeding location in Denmark. The bird spent a year and a half in West Africa, during which time it visited several different sites. These intra-African movements are described in detail and related to concurrent environmental conditions, leading to a discussion of the driving forces behind the harrier's over-summering behaviour, and whether it attempted to migrate to Europe in spring but failed to do so or deliberately stayed in Africa.

Methods

We studied a small breeding population of Montagu's Harriers in Denmark, currently consisting of 20–30 pairs. This population breeds at the northwestern limit of the species' breeding range and forms part of the North European meta-population (see Trierweiler et al. 2014). The Montagu's Harrier is categorized as endangered on the Danish Red List of threatened species (Wind and Pihl 2004), and breeding pairs have been monitored closely for two decades through a national conservation and research programme run by DOF-BirdLife Denmark (Rasmussen et al. 2015). Between 2011 and 2014, nine adult Montagu's Harriers were fitted with UvA-BiTS GPS trackers to study the birds' space use and habitat choice, ultimately to optimize local conservation efforts. UvA-BiTS (University of Amsterdam Bird Tracking System) is a flexible GPS tracking system with two-way interaction between the GPS trackers and a local antenna system (Bouten et al. 2013). Data is downloaded remotely when a tracker is within range of a local antenna system, and is otherwise stored on the device until it connects again. This means that no information on the position of a tracked bird can be retrieved until it returns to the study area. Consequently, birds can be overlooked if dispersing to other areas.

In July 2011, an adult male Montagu's Harrier was caught near its nest in Ballum, southwest Denmark, and fitted with an UvA-BiTS GPS tracker. This individual, named "Jeppe" (GPS tracker ID #583), had been ringed as a nestling in the same area in July 2008, so upon recapture it was in its fourth calendar year. During the breeding season of 2011, Jeppe bred successfully, raising three chicks. In 2012, Jeppe was not observed in the breeding area and was presumed dead or breeding elsewhere. In May 2013, it returned to the study area to breed, and the GPS data spanning the period between September 2011 and May 2013 were downloaded. From September 2011 to

February 2013, the tracker had recorded GPS positions every 30 min during the day and once per hour during the night. From 11 February 2013, when the memory of the tracker was nearly full, the position frequency decreased to one position every 6 h. Hence, from 11 February 2013, Jeppe's movements were recorded at a lower resolution. Jeppe's breeding attempt in 2013 was unsuccessful, and the bird has not been observed since.

GPS data on Jeppe's movements were processed in R 3.1.2 (R Core Team 2014). Positions with trajectory speeds (speed between two subsequent GPS fixes) higher than 25 m/s were regarded as outliers and removed from the data set. Positions with altitudes higher than 5 km and instantaneous speeds higher than 25 m/s (both as measured by the GPS) were also discarded. Arrival and departure dates at different sites were determined manually using Google Earth (<https://earth.google.com/>). Maps were produced using the package 'RgoogleMaps' version 1.2.0.6 (Loecher and Ropkins 2015). In order to investigate whether the timing of Jeppe's movements coincided with the timing of regular migratory movements, we inspected migratory movements of eight additional male Montagu's Harriers from Denmark ($n = 1$) and the Netherlands ($n = 7$) tracked using UvA-BiTS GPS trackers between 2011 and 2013.

To investigate the environmental conditions encountered by Jeppe during its stay in Africa, we looked at Moderate-resolution Imaging Spectroradiometer (MODIS) NDVI data, which provides a remotely sensed measure of the level of greenness and is available at high spatial and temporal resolution. Trierweiler et al. (2013) and Schlaich et al. (2016) used NDVI as a proxy for grasshopper abundance in Sahelian wintering sites (with grasshopper densities peaking at intermediate NDVI values). Here we do not use NDVI as a proxy for grasshopper density per se, but rather as an indication for the general ecological conditions Jeppe experienced at the different sites, assuming that conditions are unfavourable at very low NDVI values (Tøttrup et al. 2012; Thorup et al. 2017). This approach was adopted because Jeppe covered a larger geographical range than the Sahel, including tropical woody savannah (see "Results"), and a larger temporal window of the year, for which we have no information on grasshopper densities and thus do not know the relationship between grasshopper abundance and NDVI. We used the R package 'MODISTools' (version 0.94.6, Tuck et al. 2014) to download NDVI data for a 1.25×1.25 km area (i.e. a 5×5 array of 250×250 m pixels) centred at each site visited by Jeppe to reconstruct the conditions the bird had experienced during the study period. In addition, we downloaded NDVI data for Jeppe's main "regular" wintering site for a range of years (2001–2014), in order to inspect whether

the site was exceptionally dry during the winter of 2011/2012.

Results

Route

In May 2013, the male Montagu's Harrier Jeppe returned to its Danish breeding grounds after having spent more than 17 months in West Africa. During the winter of 2011/2012, the harrier used three different wintering sites in Mauritania and Senegal (sites A, B and C, see Fig. 1; Table 1). Instead of departing north from its main wintering site (C), Jeppe moved more than 200 km south in March 2012 at the onset of other male harriers' northbound spring migration (Fig. 2). After spending more than a month in Guinea-Bissau (sites D and E), the bird moved almost 600 km north and then roamed a large area in the central part of southern Mauritania (sites F and G) from May to July 2012. During July, in the middle of the European breeding season, Jeppe moved even further north to the northern edge of the Sahel (sites H and I). The bird remained four months at site I, where it also stayed during the autumn migration period of the other harriers (Fig. 2). During the remaining part of the following winter, Jeppe used four different sites (J, K, A and G). Site A was the only site visited in both winters, yet one of the sites used during the summer (site G, Fig. 1) was also revisited. Jeppe departed from site G on spring migration on 17 March 2013 and arrived at the breeding site in Denmark on 29 April 2013, with speed and timing comparable to other tracked harriers (Fig. 2).

Environmental conditions

NDVI values for Jeppe's main wintering site (site C) in 2011/2012 did not differ markedly from other years' values (Fig. 3). This is true for the summer peak as well as for the level during the winter period. These NDVI values suggest that precipitation at site C reached average levels during the summer of 2011, and that site C was not exceptionally dry during the time Jeppe visited the area during the winter of 2011/2012.

The NDVI values Jeppe encountered during its 17 months' stay in Africa varied considerably both in space and over time (Fig. 4). During the first winter (2011/2012), Jeppe left a particular site each time NDVI dropped to a baseline level of around 0.2. As a consequence of moving southward, the bird repeatedly encountered new green areas. By the southward movement from site C to sites D and E, Jeppe moved into tropical woody savannah habitat with notably higher NDVI values (note that these sites are much greener year-round compared to sites in the

Fig. 1 Map of Jeppe's movements during its 17 months in West Africa from October 2011 to March 2013. Wintering sites 2011/2012 are dark blue, summering sites 2012 are red, and wintering sites 2012/2013 are light blue. Symbol size is proportional to length of stay. Smaller dots connected by the black line represent GPS positions

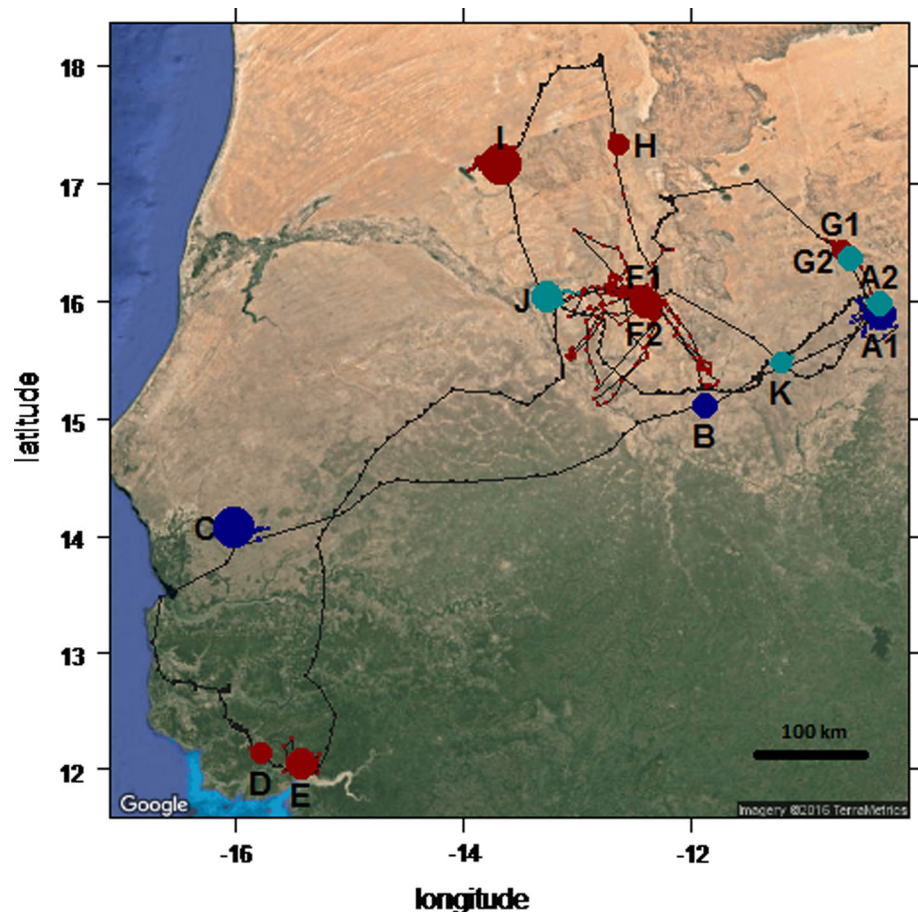


Table 1 Overview of Jeppe's arrival and departure dates to and from sites visited during the 17 months in Africa

| Site | Country | Arrival | Departure |
|------|---------------|------------|------------|
| A | Mauritania | 07.10.2011 | 10.11.2011 |
| B | Mauritania | 10.11.2011 | 24.11.2011 |
| C | Senegal | 25.11.2011 | 18.03.2012 |
| D | Guinea-Bissau | 23.03.2012 | 28.03.2012 |
| E | Guinea-Bissau | 29.03.2012 | 04.05.2012 |
| F | Mauritania | 06.05.2012 | 09.05.2012 |
| G | Mauritania | 10.05.2012 | 16.05.2012 |
| F | Mauritania | 17.05.2012 | 02.07.2012 |
| H | Mauritania | 02.07.2012 | 06.07.2012 |
| I | Mauritania | 08.07.2012 | 17.11.2012 |
| J | Mauritania | 17.11.2012 | 28.01.2013 |
| K | Mauritania | 31.01.2013 | 07.02.2013 |
| A | Mauritania | 09.02.2013 | 27.02.2013 |
| G | Mauritania | 27.02.2013 | 17.03.2013 |

Sahel). Jeppe returned to the Sahel (sites F and G) prior to the onset of the rainy season, while NDVI was still at a very low level—even lower than the baseline level that apparently induced Jeppe's movements during the winter.

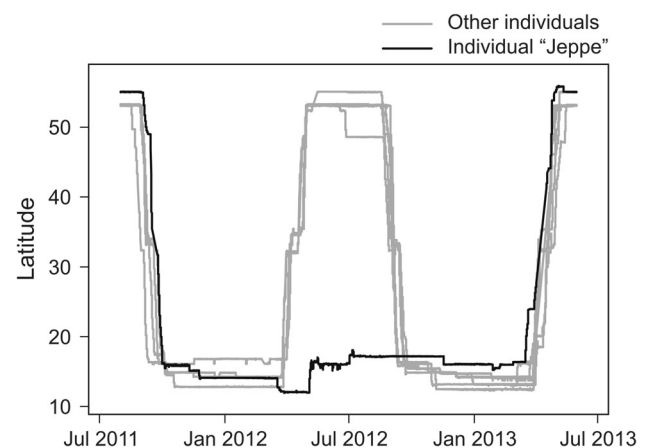


Fig. 2 Latitudinal movements of nine male Montagu's Harriers fitted with GPS trackers between 2011 and 2013. Two males were breeding in Denmark; all others were breeding in the Netherlands

These were the driest circumstances Jeppe experienced during the over-summering period. In July 2012, Jeppe moved further north to areas that are even drier during the dry season (sites H and I). Jeppe arrived here during or just before the rainy season, remained at site I throughout the NDVI peak, and did not leave the site until NDVI had

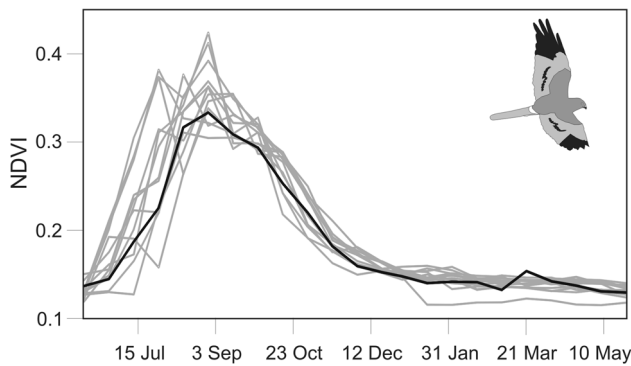


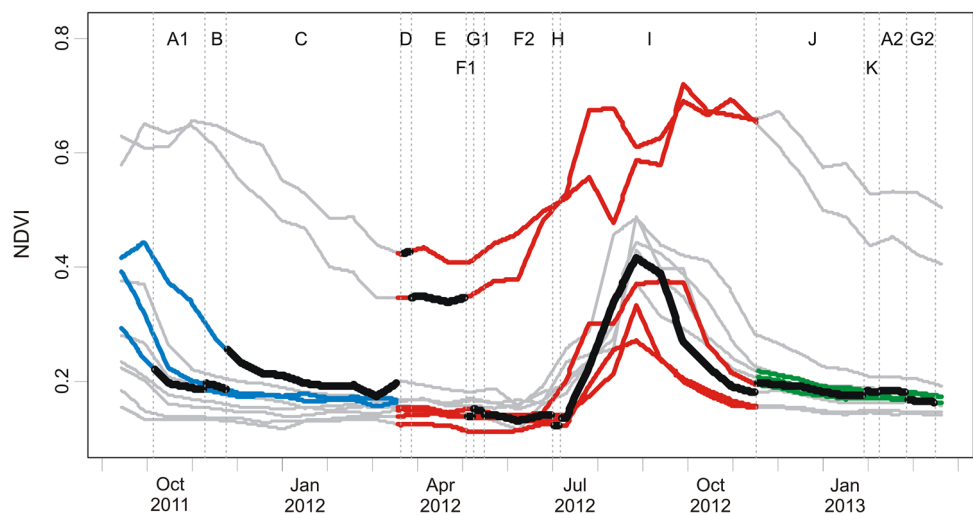
Fig. 3 Annual variation in NDVI for site C, the main wintering site of Jeppe, from June 2001 through to June 2014. Values from June 2011 to June 2012 are shown in black

dropped again to the baseline level (November 2012). During the remaining part of the winter, Jeppe again moved from site to site (J, K, A and G). Particularly notable is the movement from site A to G in February 2013, as this brought Jeppe to a site that had lower NDVI values than the previous one.

Discussion

This study reveals the first documented case of over-summering in Africa by an adult Montagu’s Harrier. GPS tracking provided detailed information regarding the bird’s movements, which we here relate to season and NDVI values. We found no evidence that this case of over-summering was caused by unusual weather events or patterns of precipitation, and the bird’s behaviour showed no indications of it being injured or trapped at any point. In fact, the bird visited a notably large number of sites during its 17 months in West Africa.

Fig. 4 NDVI values recorded at all sites visited by Jeppe throughout his stay in Africa, with thick black lines indicating values experienced by Jeppe during the time he stayed at each site. Blue lines indicate sites visited during the winter 2011/2012, red lines indicate summering sites, and green lines indicate sites visited during the winter 2012/2013



Over-summering in Africa by adult Montagu’s Harriers is rare, which is emphasised by the fact that the current case constitutes the only example among 90 individuals tracked over 129 winters by either satellite telemetry ($n = 54$ individuals over 72 winters, own data 2005–2016; Trierweiler et al. 2014) or GPS trackers ($n = 36$ individuals over 57 winters, own data 2009–2016; Vansteelant et al. 2015; Schlaich et al. 2016).

Reasons for staying in Africa

Local weather conditions have been shown to affect bird migration in various ways (e.g. Strandberg et al. 2008; Tøttrup et al. 2012; Vansteelant et al. 2015), and it is indeed possible that unfavourable weather conditions during spring migration impeded Jeppe’s departure. However, when faced with unfavourable weather conditions in spring, Marsh Harriers *Circus aeruginosus* tracked by satellite telemetry always made several attempts to cross the Sahara, and although some of these harriers eventually aborted the desert crossing and retreated to staging sites in the Sahel, initial movements were always directed northwards and clearly revealing intentions to migrate (Strandberg et al. 2008). Quite the opposite was seen here, since Jeppe moved further south during the usual spring migration period and did not make any northward movements from its final wintering site in March 2012. Hence, it is unlikely that the over-summering by Jeppe was induced by a failed attempt to migrate due to unfavourable weather conditions at the onset of spring migration.

An alternative explanation is that the conditions experienced by the bird during the preceding winter were generally unfavourable, entailing a poor body condition and thus impeding migration. This may have led Jeppe to explore foraging opportunities further south, attempting to improve its body condition prior to

migrating. In terms of NDVI, conditions at the main wintering site during the winter of 2011/2012 were very similar to other winters (Fig. 3); thus we do not assume that the bird experienced particularly harsh environmental conditions during the winter preceding its over-summering. However, other factors may have resulted in low food availability or in other ways caused suboptimal living conditions.

Finally, the remarkable over-summering behaviour of Jeppe could be the result of an exhaustive breeding effort the previous year. It has been suggested that late breeding might result in an increased mortality risk during autumn migration in Montagu's Harriers, since late breeders have less time to prepare for migration (Limiñana et al. 2012b). Furthermore, breeding is a truly demanding life history stage in raptors and may cause significant post-breeding mortality (Daan et al. 1996; Klaassen et al. 2014). The 2011 breeding season was certainly very demanding for the Danish Montagu's Harriers. The summer was characterized by unusually high levels of precipitation, and monthly rainfall during June through August was 71% above average (DMI 2011). Breeding success was below average, as only 15 fledglings were produced by 25 pairs (Rasmussen and Clausen 2011), yet Jeppe managed to raise three young (one-fifth of the Danish chicks in 2011; only six pairs bred successfully). It is conceivable that this effort somehow forced him to remain the following summer in Africa and thereby defer breeding in 2012. Lending some support to this is the fact that the female Jeppe was paired with in 2011 (a female tracked by satellite telemetry from 2009 to 2014) arrived very late at the breeding grounds and did not attempt to breed in 2012 (own data).

Drivers of intra-African movements

In spring 2012, Jeppe left its main wintering site at the usual time of spring migration. Although this spring movement might be interpreted as migratory restlessness (Gwinner 1996), Jeppe remained at site I and did not express any restlessness during the entire period of autumn migration in 2012. Thus, its movements during spring and early summer 2012 may have been determined by other factors.

Jeppe used a notably large number of sites in West Africa during the summer of 2012, each move conceivably driven by prevailing environmental conditions. In the Sahel region, man-made habitat changes have amplified negative impacts of droughts and climate change (Zwarts et al. 2010), and it may be difficult for a harrier to survive here during late spring, as environmental conditions gradually deteriorate until the onset of the summer rains. Jeppe's southward move into tropical

woodland savannah in March 2012 thus appears sensible. However, tropical woodland savannah is not a typical habitat for Montagu's Harriers, and it is remarkable that Jeppe returned to the Sahel in May 2012 *before* the onset of the rainy season. At sites F and G, Jeppe experienced the driest (i.e. least green) conditions during the entire period spent in Africa.

We can only speculate why Jeppe left the green area in Guinea-Bissau to return to a very dry area in the Sahel. Conditions in Guinea-Bissau might have been unfavourable for a harrier, or competition with local breeding birds might have increased during the spring. Alternatively, the northward move was initiated as an attempt to migrate, yet never brought Jeppe further than site F. It is also possible that the Sahel is simply a favourable place for harriers, even when the area is very dry. Indeed, some grasshopper species could be very numerous during dry periods, or the diet of a summering harrier might consist primarily of small mammals, birds and reptiles, and thus be more similar to the typical diet on the breeding grounds.

Sites H and I represent the driest areas visited by Jeppe, and the bird moved to these sites just before or coinciding with the arrival of the summer rains. The bird remained at site I in the northern Sahel throughout the wet season and did not leave until NDVI values dropped markedly. It is very interesting that it opted to spend the rainy season at a site on the northern edge of the Sahel where rains start earlier in the season.

Jeppe's movements during the second winter were quite remarkable. It did not visit the same wintering sites during the two consecutive winters, which contrasts with the site fidelity typical for Montagu's Harriers in winter (Trierweiler et al. 2013), and may indicate that it was exploring unfamiliar territory in order to ultimately increase foraging and survival during subsequent winters. Such explorative behaviour during times of average or high food availability has been described for other bird species (Bennetts and Kitchens 2000; Oppel et al. 2009); thus the number of sites visited does not necessarily imply that Jeppe was experiencing low food levels.

During the first winter, Jeppe left an area as soon as the NDVI had dropped to the baseline level, and subsequently travelled to a more southern and greener site. This corresponds exactly to the Green Belt hypothesis as described by Trierweiler et al. (2013) and Schlaich et al. (2016), in which harriers track moderately green vegetation, as this is where the highest densities of grasshoppers are found. In the second winter, however, the last site Jeppe visited had lower NDVI values than the previous sites, suggesting that Jeppe moved to a drier site instead. This is particularly remarkable, since this was the site Jeppe departed from at the onset of spring migration. However, although NDVI values

seem to provide a good proxy for grasshopper numbers, sites with similar NDVI values can differ considerably, and site G may have been rich in grasshoppers or alternative prey despite low NDVI. Also noteworthy is the fact that Jeppe had already visited both of the last two sites (A and G) during the first half of his extended stay in Africa, yet during different seasons and presumably under quite different conditions. If Jeppe somehow evaluated these areas and later chose to return, the value of such explorative visits may be quite significant. Therefore, field observations on food abundance are still needed to draw firm conclusions about such aspects.

Conclusions

Our detailed documentation of an adult male Montagu's Harrier over-summering in Africa illustrates that even among adult birds, a trade-off exists between travelling back to Europe for a breeding attempt and staying in Africa to recover. It also shows that remaining in Africa during the summer is generally an option. Daily mortality rates of raptors are highest during spring migration and lowest during winter in Africa (Klaassen et al. 2014). Thus, from that perspective, over-summering in Africa might be the best possible option for a migratory bird in suboptimal or poor body condition, or a bird faced with unfavourable weather conditions for migrating. Assuming that mortality rates are lower during summer in Africa than during migration and breeding, over-summering may even result in long-term benefits such as increased familiarity with potential wintering areas. Nevertheless, skipping a breeding attempt is probably a viable option only for long-lived species such as raptors.

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Compliance with ethical standards

The authors declare that they have no conflict of interest. Capturing, handling and tracking of harriers was carried out under license from the national authority (the Ringing Section at the Natural History Museum of Denmark).

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