



Migrating Montagu's harriers frequently interrupt daily flights in both Europe and Africa

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Time budgets are a powerful but hitherto seldom used way to study how migrants organise their bi-annual travels. We studied daily time budgets of travelling Montagu's harriers *Circus pygargus*, based on GPS tracking data, in which we were particularly interested in how time budgets differ between regions and seasons, and are affected by wind. We found that Montagu's harriers used a relatively broad daily time window for travelling by starting daily travels just after sunrise and ending daily travels just before sunset. Occasionally, flights were extended into the night. Montagu's harriers frequently interrupted their daily flights for on average 1.5 h d⁻¹. These interruptions occurred in all regions and seasons. The tracking data during interruptions suggested two different behaviours: in 41% of all interruptions the birds were moving (presumed foraging,) and in 32% they were stationary (presumed resting; the remaining interruptions could not be classified). The interruptions for foraging indicate that Montagu's harriers have a fly-and-forage migration strategy (i.e. combine travelling and foraging on the same day), but the interruptions for resting illustrate that their travels comprise of more than fly-and-forage behaviour alone. The large number of interruptions for foraging in the Sahara Desert indicates that this region is less hostile for a migrating raptor than presumed previously. Importantly, harriers spent more time on interruptions for resting on days with stronger headwinds, suggesting that interruptions for resting serve a function of waiting for more favourable weather conditions. Daily variation in time budgets was largely explained by wind; harriers flew more hours per day, and interrupted their flights fewer hours per day, on days they experienced stronger tailwinds. In contrast, time budgets were similar between regions and seasons, suggesting that wind rather than landscape and season shape travel routines of Montagu's harriers.

An important element of the migration strategy of a bird is its daily travel routine, i.e. how the migrant organises its daily travels. Daily travel routines vary notably between and within species, in both the timing as well as the duration of daily flights (Alerstam 1990, Newton 2010). How ecological conditions and species characteristics shape daily travel routines is poorly understood, possibly as these remain poorly described, especially at the individual level. With the development of tracking technologies that allow us to follow the movements of individual migrants in unprecedented spatio-temporal detail (Robinson et al. 2009, Bridge et al. 2011) this knowledge gap can start to be filled.

The daily time budget is a detailed description of the timing and duration of different behaviours during the day. Describing variation in daily time budgets is a potentially powerful way to understand which factors affect migratory performance. Klaassen et al. (2008) tracked ospreys *Pandion haliaetus* using GPS-based satellite tracking technology, and found that the daily time budgets of migrating ospreys differed for migration through Europe and through Africa, illustrating that landscape properties can have a prominent

effect on migratory behaviour. More specifically, in Europe, where foraging opportunities for this fish-eating species are plentiful thanks to the wide distribution of lakes, rivers and streams, the ospreys frequently interrupted their daily flights for opportunistic feeding bouts. In the Sahara Desert, where foraging opportunities are scarce due to the general absence of water bodies, no such interruptions were observed, and the birds were flying all day instead. These regional differences in daily time budgets explained why ospreys covered, on average, 80 km less distance on a travelling day in Europe than in the Sahara (Klaassen et al. 2008).

The traditional view on bird migration is that migrants alternate between flight steps and (relatively long) stationary stopover periods for fuelling (Alerstam 1990, Dingle 1996, Åkesson and Hedenström 2007). The ospreys behaved differently by combining travelling and foraging on the same day, trading-off potential flight time with opportunistic foraging bouts, a behaviour called fly-and-forage migration (Strandberg and Alerstam 2007). The ultimate form of fly-and-forage migration may be found in aerial foragers, such as swallows and swifts, which can search for food while

at the same time covering migration distance, due to their ability to hunt on the wing (Rudebeck 1950–1951, Dorst 1962, Rubolini et al. 2002). Combining travelling and foraging not only saves time and energy, but also reduces the effective daily energy consumption as food intake will counterbalance the energy expenditure during the travel (Strandberg and Alerstam 2007). However, combining travelling with foraging also comes at the cost in the form of a reduction in effective travel speed in the migration direction because of deviations from the straight path when locating foraging habitats or prey, and because of time losses associated with searching for and handling prey (Strandberg and Alerstam 2007). In order to understand fly-and-forage behaviour it is important to balance these costs and benefits within an optimal migration framework (Alerstam and Lindström 1990, Strandberg and Alerstam 2007, Alerstam 2011). For example, for the ospreys, interrupting the daily flight for foraging came at the cost of flying 2.7 h and an 80 km less covered per day in Europe compared to Africa. However, a simple energy budget suggested that a fly-and-forage migration strategy nevertheless was favourable for an osprey that is able to forage efficiently during the interruptions, as it would reduce the need for full stopover days to such an extent that the overall resulting migration speed is higher (Klaassen et al. 2008).

A next step in understanding factors shaping daily travel routines in general, and fly-and-forage migration in particular, is to reconstruct daily time budgets for a range of migrant species. We analysed GPS-tracking data from Montagu's harriers *Circus pygargus* migrating between breeding areas in NW-Europe and wintering areas in Sub-Saharan west Africa. Because the migration of Montagu's harriers has been studied by tracking radar (Spaar and Bruderer 1997), satellite telemetry (Limiñana et al. 2007, Trierweiler et al. 2014) and GPS-tracking (Vansteelant et al. 2015) in recent years, its general migration behaviour is fairly well known. It is mainly a diurnal migrant, like most raptors, but since the species migrates by a combination of flapping and soaring flight (Spaar and Bruderer 1997), its travelling is not restricted to hours with favourable soaring conditions to the same extent as obligate soaring migrants (Kerlinger 1989, Bildstein 2006). Satellite telemetry has revealed that Montagu's harriers indeed occasionally extend their diurnal travels even into the night (Trierweiler et al. 2014). Thus, we expect the harriers to start their daily flights relatively early, end their daily flights relatively late, resulting in a relatively broad daily window for travelling. Correspondingly, we expect the harriers to travel more hours per day compared to raptors relying more strongly on soaring flight (Mellone et al. 2012). One potential factor influencing the time flying per day is day length itself, which could even explain regional and seasonal differences in daily travel routines (Bauchinger and Klaassen 2005). We expect that the time of the onset of the daily flight is correlated with the time of sunrise, the time of the end of the daily flight correlates with the time of sunset, and the time flying per day correlates with day length. In addition, favourable weather conditions are expected to generally promote travelling, in which tailwind repeatedly has been identified as a dominant variable explaining variation in hourly to daily travel distances (Mellone et al. 2012, Vansteelant et al. 2015). We therefore expect that favourable

tailwind conditions promote an early start of the daily flight, a late end of the daily flight (with possible extension of the flight into the night under very favourable conditions), and longer daily flight times.

Interruptions of the daily flight for foraging is only expected in case the disadvantage of a reduction in effective travel speed is (more than) outweighed by the advantage of efficient foraging during the interruptions (Strandberg and Alerstam 2007). Factors like efficient foraging and high energy content of the food are likely to promote fly-and-forage behaviour. Montagu's harriers are opportunistic foragers (Arroyo 1997), feeding on a range of high-energy-content-prey including voles and mice, passerines, reptiles and insects (Clarke 1996, Mirski et al. 2016). Assuming that Montagu's harriers can capture these prey efficiently, we expect fly-and-forage behaviour in areas where prey are abundant. Thus, similarly to ospreys, we expect Montagu's harriers to interrupt their daily flights for foraging in Europe, where prey are expected to be abundant, but not where foraging opportunities are believed to be limited, for example during the crossing of the Sahara Desert (Moreau 1972, Zwarts et al. 2009). The trade-off between travelling and foraging might be different for spring migration, when birds generally migrate faster compared to autumn possibly because of competition for early arrival at the breeding ground (Nilsson et al. 2013) which could for example result in a sprint migration when approaching the breeding area (cf. Alerstam 2006). In addition, voles typically peak in autumn and have low densities in spring (Cornulier et al. 2013), thus also food abundance might differ between seasons, which additionally might affect the decision to interrupt daily flights. Hence, we expect fly-and-forage behaviour to be less dominant during spring compared to autumn migration. Finally, independent of season, we expect fewer interruptions and thus longer daily flight times when wind conditions are favourable.

We generally expect that Montagu's harriers cover larger daily distances when travelling more hours per day. In this way, regional and seasonal variation in daily time budgets would result in regional and seasonal variation in travel speeds, congruent to the osprey example. Although we can expect differences in daily travel routines between regions for autumn (cf. above), expectation for spring migration are less clear. If indeed the Montagu's harrier joins the general pattern in migratory birds that spring migration is faster than autumn migration (Nilsson et al. 2013), our detailed description of daily time budgets would illustrate how this difference comes about. Intriguingly, a large satellite telemetry study (Limiñana et al. 2007, Trierweiler et al. 2014) and the first GPS-logger analysis including only a limited number of individuals (Vansteelant et al. 2015), found no significant regional and seasonal differences in travel performance. This suggests that either there is no regional and seasonal variation in daily travel routines, for example because Montagu's harriers do not engage in fly-and-forage migration at all, or that something else is going on.

Our first aim is to provide a detailed description of the daily time budgets of the Montagu's harrier, including how time budgets differ between regions and seasons, and how they are affected by wind, including information on at what time of the day they start and end their daily flights. This description of the daily time budgets of Montagu's harriers

will be more extensive than was provided for the osprey (Klaassen et al. 2008), where only regional differences in time daily budgets were explored. However, for autumn migration, we can compare time budgets of Montagu's harriers and ospreys, specifically whether time budgets vary regionally also in Montagu's harriers. The second aim is to explore how daily time budgets affect the daily travel distance, and how this varies among regions and between seasons, to establish the link between daily time budgets and travel performance. The ultimate aim is to use the novel information on daily time budgets of Montagu's harriers to understand which factors shape daily travel routines and thus migration strategies in birds in general.

Methods

Study system

We study a small breeding population of Montagu's harriers of about 30–50 pairs in northeast Groningen, the Netherlands (latitude: 53.12°, longitude: 7.08°) occurring in an intensively farmed landscape (Koks et al. 2007, Wiersma et al. 2014). GPS-logger tracking studies were initiated to study habitat use (Schlaich et al. 2015). The Montagu's harrier is a species of conservation concern in the Netherlands, and one of the target species for farmland biodiversity policy in the province of Groningen in particular (Wiersma et al. 2014). For this study, data were included from autumn migration 2009 to spring migration 2015. Two males were tagged just east of the Dutch–German border in the polder of Rheiderland (Germany) and one male, originally tagged in the Netherlands, bred near Diepholz (Germany).

Montagu's harriers were captured near the nest either using a mist net in combination with a stuffed raptor, or a snare-trap mounted on a perch. Birds were fitted with 12–14 g UvA-BiTS GPS loggers (Bouten et al. 2013, <www.uva-bits.nl>) using a full-body harness made from 6 mm wide teflon ribbon strings (Kenward 1987), and were released within 20–40 min after capture. We never observed nest desertion or failure in relation to capture events. GPS-loggers were programmed to collect GPS-positions every 30 min, every 15 min or every 5 min between 6:00 and 19:00 GMT, and every hour to two hours during the night. In a few cases, high-frequency data (GPS-fixes every 3 s) were collected for a small latitudinal band in the Sahara Desert in order to be able to study flight behaviour, but these data were subsampled to 5, 15 or 30 min (depending on the measurement scheme for that particular bird in that particular season) for the current analysis.

Data analysis

Migrations were annotated by manually inspecting daily maps, in which we distinguished between stopover and migration days. Full stopover days were defined as days when birds used the same night roost during subsequent nights (i.e. <1 km between roosts). In a few cases, birds used different night roosts during subsequent nights, but as both the distance between roosts (<20 km, the maximum distance a Montagu's harrier would range from the nest during

the breeding season, Dutch Montagu's Harrier Foundation pers. comm.) and the time migrating (<1 h) indicated that these were not true migration days, they were excluded from the analysis. In addition, days at which the bird arrived at a breeding, stopover or wintering site were excluded from the analysis as we particularly were interested in full migration days. Also, migration days that included overnight flights were excluded as these mainly occurred during extensive sea crossings when the birds have no possibilities to land (see also 'Discussion'). Finally, days on which the birds showed unusual behaviours such as aborted sea crossings and return flights were excluded. The final dataset consisted of 795 travel days.

We considered that the bird had commenced its daily migratory flight when it had moved at least 5 km away from the roosting site. The time of departure was the time halfway the first GPS-position at more than 5 km from the roost and the preceding position. We defined that the bird had completed its daily migratory flight when it arrived within 5 km from its night roost. The time of arrival was the time halfway between the first GPS-position within 5 km from the roost and the preceding position.

To construct daily time budgets, migration days were subdivided into segments (5 min to 1 h) defined by subsequent GPS-positions. Subsequently, every segment was annotated. For segments before and after the migratory flight we distinguished between resting (mean instantaneous speed as given by the GPS-logger lower than a threshold of 2 m s⁻¹, indicating no flight activity) and foraging (mean instantaneous speed higher than 2 m s⁻¹, indicating flight activity, Supplementary material Appendix 1, Fig. A1). For the segments of the daily migratory flight we distinguished between travelling (segment ground speed > 100 m min⁻¹, Supplementary material Appendix 1, Fig. A2) and interruption (segment ground speed < 100 m min⁻¹). Segment ground speed rather than instantaneous speed was used to distinguish between travelling and interrupting because if birds forage during interruptions, this cannot be distinguished from travelling as Montagu's harriers forage on the wing. We adopted a relatively conservative ground speed threshold of 100 m min⁻¹ in order to avoid that slow migratory progress would be classified as an interruption, and thus that we would overestimate the number of interruptions. The airspeed of a flying Montagu's harrier is about 11 m s⁻¹ (Alerstam et al. 2007), thus one would expect a harrier to travel about 660 m min⁻¹ in wind still conditions.

GPS-tracks for all interruption events were inspected manually. During certain interruptions the birds were mobile, making non-directed movements typical for a harrier searching for food (Dutch Montagu's Harrier Foundation pers. comm.), giving the impression that indeed the birds were foraging. During other interruptions, however, the birds were stationary and most likely sitting still. As foraging and resting are behaviours with very different ecological meanings, we aimed at classifying all interruptions as either for foraging or for resting. However, for short interruptions, existing of 1–3 segments, we found it difficult to interpret the tracks, especially in the case they included a movement. Does a single movement really indicate foraging behaviour, or is it the arrival to or departure from the resting location? Thus, because we had the feeling we could not

reliably classify interruptions consisting of 1–3 segments, we introduced a third category ‘short interruptions’.

For every migration day, we subsequently determined the number of hours resting, foraging, travelling and interrupting (the latter subdivided into ‘foraging’, ‘resting’ and ‘short interruption’). This formed the basis for the time budgets constructed per region and season. In addition, we calculated, for every day, the time of sunrise and sunset (civil twilight; sun angle of -6°), using the ‘crepuscule’ function in the ‘Mapprool’ R package (Bivand and Lewin-Koh 2015), and calculated the (perceived) day length by subtracting the time of sunrise at the morning roost location from the time of sunset at the evening roost location. Wind data were obtained from the NCEP/NCAR reanalysis project, as provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA (www.cdc.noaa.gov), using the ‘NCEP.interp’ function in the ‘RNCEP’ R package (Kemp et al. 2012). These data consist of west–east (u-winds) and south–north (v-winds) wind components, which were combined into single wind vectors (i.e. direction and strength of the wind). Wind data were extracted for a pressure level of 925 hPa, which corresponds to an altitude of about 750 m a.s.l. This altitude was chosen as 90% of the movements of Montagu’s harriers occur at altitudes between 0 and 1500 m, as based on 39 000 GPS-registrations of migrating harriers (Dutch Montagu’s Harrier Foundation pers. comm.). Data were extracted for the morning position closest to 06:00, the noon position closest to 12:00 and the afternoon position closest to 18:00. Data were subsequently averaged in which noon values were given twice as much weight as the morning and afternoon values, mimicking the wind conditions the birds experienced during the day in a simplified way (following Klaassen et al. 2010). From the average daily wind vector the tailwind component was calculated, which is the wind vector parallel to the direction of the daily segment (cf. Klaassen et al. 2010). Finally, we calculated daily distance as the (loxodrome) distance between the morning and evening roost (following Klaassen et al. 2010, Mellone et al. 2012). Differences between Europe and Africa were analysed after geographical borders.

Statistical analyses

A linear mixed-effect model (LMM) approach was adopted in which statistical significance was obtained by likelihood ratio tests of the full model including the dependent variable in question against the reduced model excluding the variable, following Zuur et al. (2009). Random effects included were ‘individual’ and ‘year’. In addition, an interaction with season was included. All analysis were performed in R (R Core Team), using the ‘lme4’ package (Bates et al. 2015).

Data are stored in the UvA-BiTS’ Virtual Lab for Bird Movement Modelling www.uva-bits.nl and available upon request.

Results

In total, 54 tracks of 19 individuals were obtained, which included 30 autumn and 24 spring migrations (Fig. 1). The total number of analysed travel days was 402 and 393 for autumn and spring, respectively.

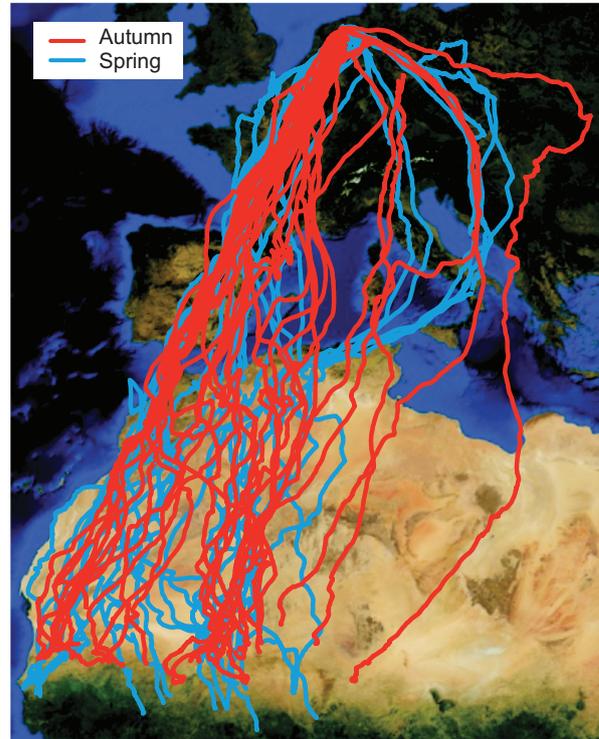


Figure 1. Map showing 30 autumn (orange) and 24 spring (blue) tracks of 19 individual Montagu’s harriers tracked using GPS-loggers.

Timing of the daily flight

On most days, Montagu’s harriers departed within 1–2 h after sunrise (Fig. 2). Departures before sunrise were rare (< 1% of all cases). In 41% of all cases the birds left late (> 2 h after sunrise), which in an extreme case was only just after noon. In most cases, daily flights ended within 1–2 h before sunset. Travelling after sunset was irregular but not uncommon (15%). In 30% of all cases the birds had already ended their flight more than two hours before sunset. The earliest time a flight was ended was just before noon.

Time of onset and end of the daily flight were not or only weakly related to the time of sunrise and sunset, respectively (Supplementary material Appendix 1, Table A1; but note that the positive relationship between time of onset of migration and time of sunrise was marginally significant for spring migration, $p = 0.05$). Similarly, duration of migration (time between onset and end, thus including flying and interruptions, see below) was not related to the length of the day (Supplementary material Appendix 1, Fig. A3, Table A1; note that for autumn migration a negative correlation between time migrating per day and day length was found). Time of onset of the daily flight was also not related to tailwind during morning hours, neither in autumn nor in spring (Supplementary material Appendix 1, Fig. A4, Table A1). However, time of end of the daily flight was related to tailwind conditions in the afternoon, in which birds ended their daily flights later on days with stronger afternoon tailwinds, although this was only found for autumn migration (Supplementary material Appendix 1, Fig. A5, Table A1). Similarly, average tailwind conditions during the day had

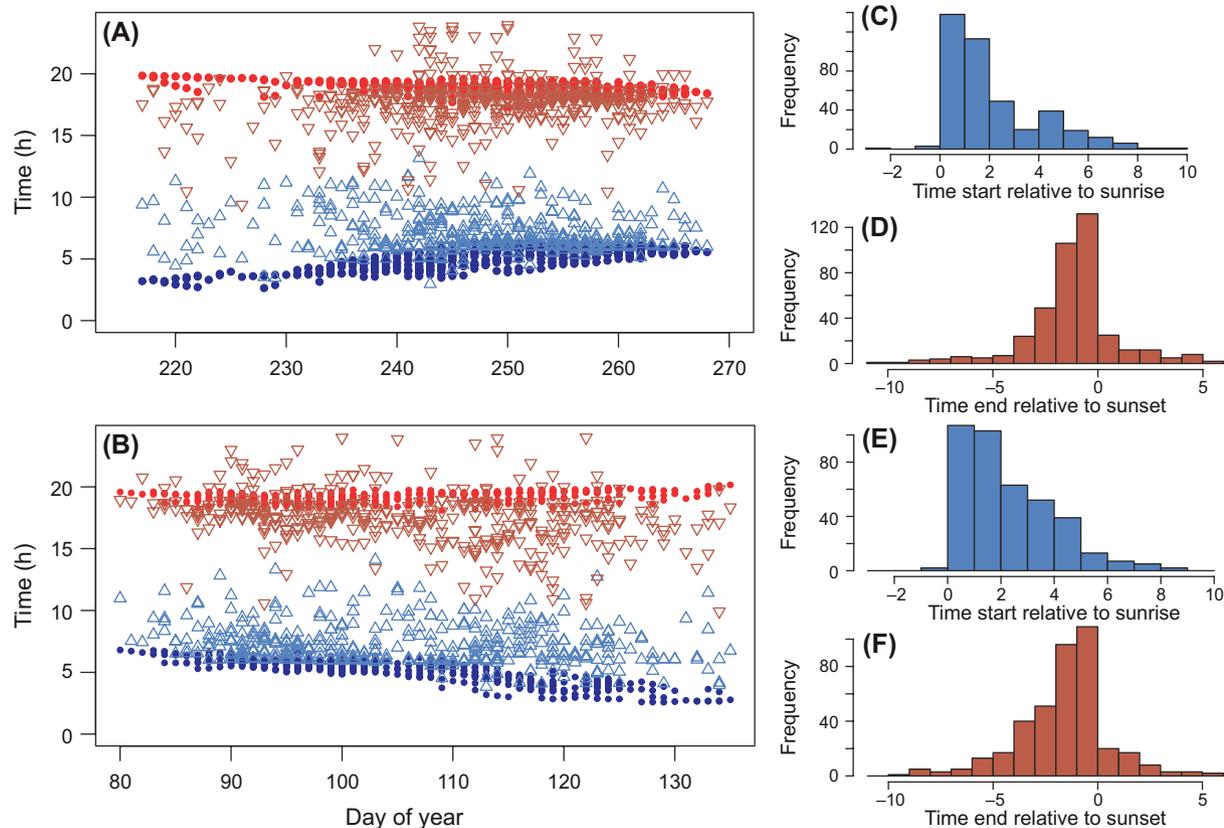


Figure 2. (A, B) Time (GMT) of the onset of the daily flight (light-blue triangles pointing upwards) and the end of the daily flight (dark-red triangles pointing downwards), in relation to time of sunrise (red dots) and sunset (blue dots), over the season, for autumn migration (A) and spring migration (B). (C–F) Histograms on the right provide the corresponding frequency distributions of departure and arrival times in relation to sunrise (C, E) and sunset (D, F) times, respectively, for autumn (C, D) and spring (E, F).

a significant positive effect on the daily duration of migration in autumn, but not in spring (Supplementary material Appendix 1, Table A1).

Interruptions and daily time budgets

Montagu's harriers frequently interrupted their daily flights (Fig. 3–4). Interruptions occurred on 78% of all travel days. The cumulative interruption time was, on average, 1.48 h d⁻¹, which comprises 14% of the average daily migration time. Interruptions were made throughout the day but most frequently just after the onset of the daily flights (Fig. 4). Close inspection of the GPS-tracks revealed that birds were moving (foraging) during 41% and stationary (resting) during 32% of all interruptions. 27% of the interruptions were too short to enable classification. The ratio between interruptions for foraging compared to interruptions for resting generally slightly increased over the time of day, from roughly 50% in the morning to 69% in the afternoon (Fig. 4).

Wind conditions had a clear effect on daily time budgets. Both in autumn and spring, harriers flew more hours per day on days with stronger average tailwinds (Fig. 5, Supplementary material Appendix 1, Fig. A7, Table A1). Conversely, both in autumn and spring the birds interrupted the flights for fewer hours per day on days with stronger average tailwinds (Fig. 5, Supplementary material Appendix 1,

Fig. A8, Table A1). This relationship was mainly caused by time spent on interruptions for resting being significantly longer the stronger the headwind. The corresponding relationship for interruptions for foraging was also negative, but not significantly so (Supplementary material Appendix 1, Fig. A9, A10, Table A1).

Daily time budgets were generally similar among regions and between seasons (Fig. 4, Table 1). Daily flight times were marginally, but significantly longer in Africa (9.4 and 9.0 h for autumn and spring, respectively) than in Europe (8.6 and 8.7 h, respectively) (LMM: $X^2 = 5.57$, $DF = 1$, $p = 0.02$), but did not differ between seasons (LMM: $X^2 = 2.59$, $DF = 1$, $p = 0.11$). Daily cumulative interruption time did not differ among regions (LMM: $X^2 = 0.14$, $DF = 1$, $p = 0.71$) or between seasons (LMM: $X^2 = 1.06$, $DF = 1$, $p = 0.30$). However, the number of interruptions for foraging in relation to number of interruptions for resting did vary between regions in that the harriers interrupted their flights more often for resting in Africa and more often for foraging in Europe (autumn: $X^2 = 66.3$, $DF = 1$, $p < 0.001$, spring: $X^2 = 17.3$, $DF = 1$, $p < 0.001$). There was no such difference between seasons (Europe: $X^2 = 2.16$, $DF = 1$, $p = 0.14$, Africa: $X^2 = 1.97$, $DF = 1$, $p = 0.16$). A most noteworthy result is that interruptions for foraging occurred frequently in Africa, even in the middle of the Sahara Desert (Supplementary material Appendix 2).

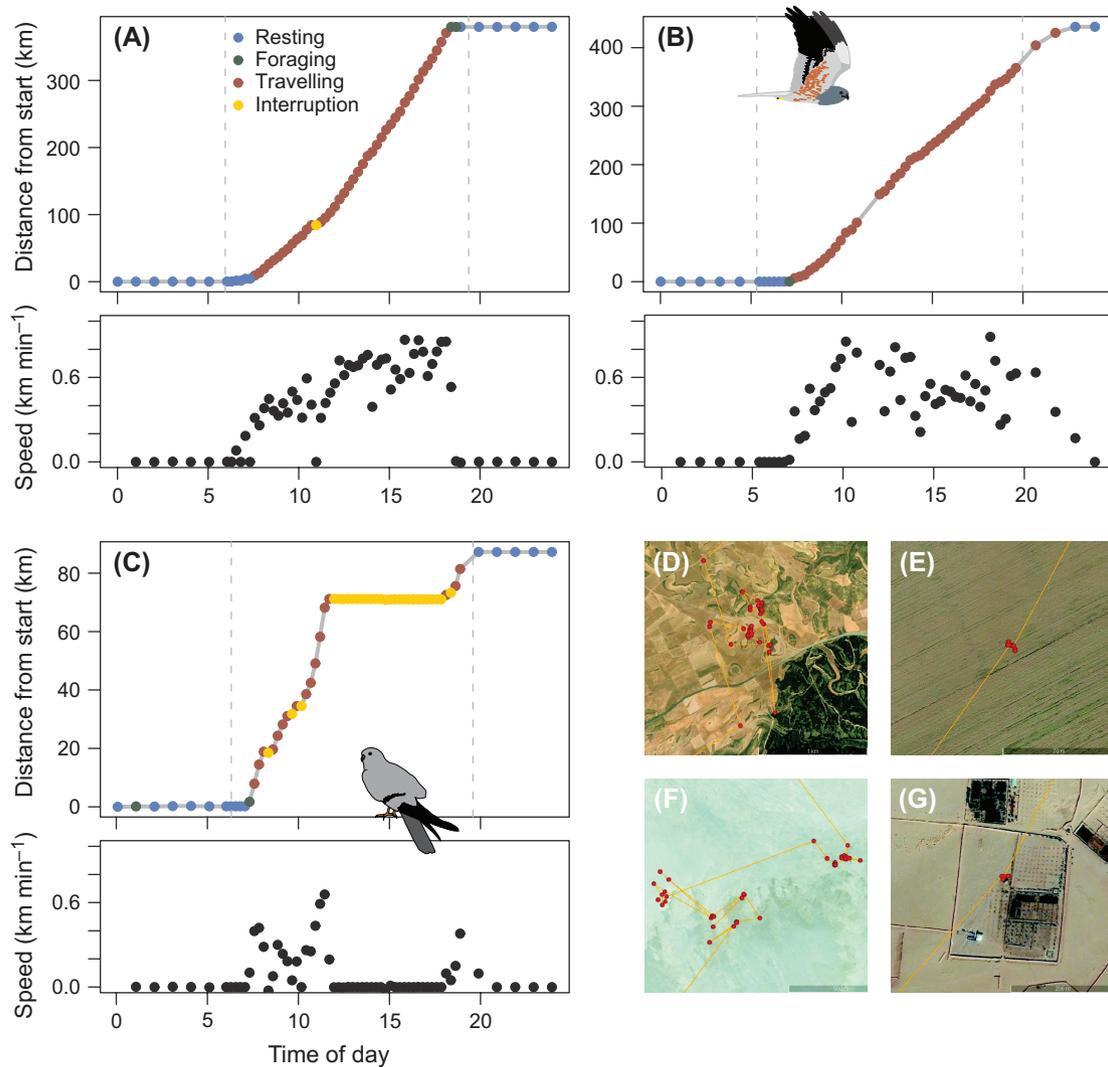


Figure 3. Examples of different types of travel days, including a day with only one very short interruption of the daily flight (A), a day with an extension of the flight into the night (B), and a day with several interruptions of the daily flight, one of them being several hours long (C). For these examples, the upper panel provides the progression (distance) from the night roost over time of the day. The lower panel provides the corresponding segment speed (see main text). The small satellite images (D–G) provide representative examples of GPS-tracks during interruptions, for Europe (upper two panels) and Africa (lower two panels). The left two panels (D and F) show interruptions where the bird was moving locally, suggesting foraging behaviour, the right two panels shows interruptions where the bird was stationary, suggesting resting.

Daily travel distances

The distance the harriers travelled on a day varied between 20 and 790 km. This variation was largely explained by variation in the time flying per day (Fig. 6, Supplementary material Appendix 1, Fig. A11, Table A1). Similarly, we found a strong negative correlation between daily distance and the cumulative daily interruption time (Fig. 6, Supplementary material Appendix 1, Fig. A12, Table A1). In addition, we found a strong positive effect of tailwind on the distance travelled per day (Fig. 6, Supplementary material Appendix 1, Fig. A15, Table A1).

Daily distance varied marginally but significantly among regions and between seasons, in which longer distances were covered in Africa (270 km d⁻¹ in autumn and 234 km d⁻¹ in spring) than in Europe (228 km d⁻¹ in autumn and 217 km d⁻¹ in spring) (LMM: $X^2 = 9.4$, $DF = 1$, $p = 0.002$), and

longer distances in autumn (228 km d⁻¹ in Europe and 270 km d⁻¹ in Africa) than in spring (217 km d⁻¹ in Europe and 234 km d⁻¹ in Africa) (LMM: $X^2 = 7.0$, $DF = 1$, $p = 0.008$) (Fig. 6).

Discussion

Timing and duration of the daily travel

As hypothesized for a species that travels by a combination of flapping and soaring flight (Spaar and Bruderer 1997), the Montagu's harrier used a relatively broad daily time window for travelling by generally embarking on daily travels just after sunrise and terminating daily travels just before sunset. Average daily migration time measured 10.4 h, which is comparable to other raptors migrating by a combination

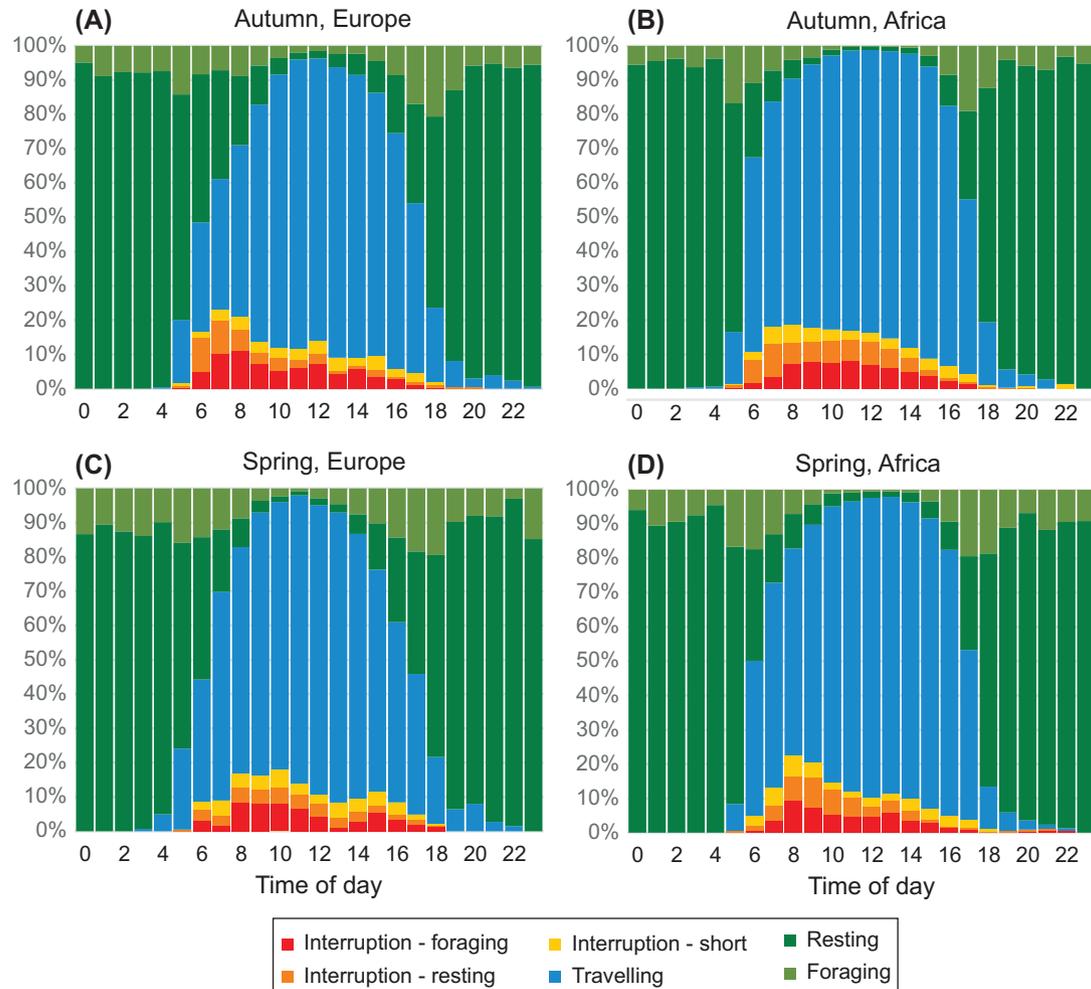


Figure 4. Daily time budgets of travelling Montagu's harriers for different regions and seasons. Per hour, the relative time devoted to different behaviours (see legend) is given. To compile these time budgets, data from different days, individuals and years were pooled (see Methods). Note that only travel days were included. Time is in GMT.

of soaring and flapping flight (osprey: 9.7 h, marsh harrier *Circus aeruginosus*: 10.1 h) but longer compared to obligatory soaring migrants (Egyptian vulture *Neophron percnopterus*: 8.5 h, short-toed eagle *Circaetus gallicus*: 8.4 h), supporting the idea that variation in daily migration time partly is related to the flight strategy (Hedenström 1993, Mellone et al. 2012).

We found no effect of day length on the timing or duration of the daily travel. In contrast to for example passerines (Bauchinger and Klaassen 2005), day length generally seems to have only a marginal effect on daily travel routines in raptors (Mellone et al. 2012). However, we did find that wind conditions had an effect on daily travel routines, i.e. the time the Montagu's harriers terminated their daily travel was positively correlated to afternoon tailwind conditions. This relationship possibly is a combined effect of some birds ending their flight early when wind conditions are unfavourable, and some birds continuing the flight after sunset when wind conditions are favourable. It should be noted that this effect of wind was only found for autumn migration, thus how migrants deal with varying wind conditions might differ between seasons (Klaassen et al. 2010). In addition, wind only seemed to affect the decision to terminate flight as no

effect of morning tailwind conditions was found on the time of the onset of the daily travel. Wind nevertheless should be considered as an important factor influencing daily travel routines (see also below).

Interruptions and the fly-and-forage migration strategy

We hypothesized that Montagu's harriers would adopt a fly-and-forage migration strategy as the species seems to fit the general conditions promoting this behaviour (Strandberg and Alerstam 2007). Indeed, we found that Montagu's harriers frequently interrupted their daily flights, in which interruptions comprised 14% of the average daily migration time. Fly-and-forage migration was only expected for Europe, where foraging conditions are believed to be widespread, and not in Africa where foraging opportunities are believed to be scarce (similar to ospreys cf. Klaassen et al. 2008). However, daily time budgets were similar among regions and between seasons, with similar extents of fly-and-forage migration, and thus a dominant fraction of fly-and-forage migration also in Africa.

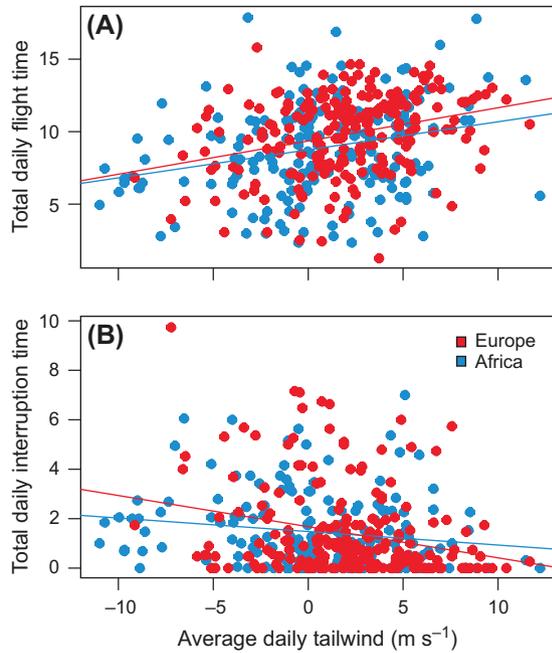


Figure 5. Effect of average daily tailwind on the number of hours flying (upper panel) and number of hours interrupting the flight (lower panel) per day, for autumn migration. See Supplementary material Appendix 1 for additional correlations with wind, including the same correlations for spring migration.

The interruptions seemed to be associated with two different behaviours, foraging and resting. Although the balance between interruptions for foraging and interruptions for resting varied between regions, with relatively more interruptions for foraging in Europe and relatively more interruptions for resting in Africa, both behaviours were observed in all regions and seasons. Thus, our results strongly suggest that even when crossing the Sahara Desert Montagu's harriers regularly interrupt their flights for foraging (see also Supplementary material Appendix 2). Possibly we underestimate the abundance of prey in the Sahara Desert, like reptiles and insects (Mellone et al. 2011) or resting birds (Schmaljohann et al. 2007), or the efficiency of Montagu's harriers to exploit scarce foraging opportunities. Reports from the Sahara Desert often mention that the desert is more vegetated than one might expect, especially the southern range in autumn (K. de Smet and F. Bairlein pers. comm.). Nevertheless, more quantitative information about the abundance and availability of potential prey would be required (Schlauch et al. 2016) to ultimately understand the

frequent interruptions of the daily travels in Africa. It was equally surprising to us that the harriers often are resting during interruptions in Europe. Again, information about the habitat and prey would be required to solve the question why harriers do not use this time for foraging instead.

The observation that the harriers were resting instead of foraging during at least 32% of all interruptions provides a new perspective on their migration behaviour. It would be incorrect to characterise the migration strategy of Montagu's harriers as a fly-and-forage migration strategy (despite fly-and-forage behaviour being an important part of their strategy) but rather as a fly, forage and resting migration strategy.

Although daily time budgets did vary marginally among regions and between seasons (see below), we found a notable variation in flight and cumulative interruption times between days. This short-term variation could be explained by wind; both in autumn and spring harriers flew more hours per day, and conversely interrupted their flights for fewer hours per day, on days they experienced stronger tailwinds. Interestingly, when distinguishing between the different behaviours during interruptions, we found that only interruptions for resting might serve a function of waiting for more favourable weather conditions, which has, to the best of our knowledge, not been demonstrated before on such short time scales. In conclusion, wind generally seems to have an important effect on daily travel routines, not only influencing the timing and duration of the daily travels (cf. above) but also affecting the delicate trade-off between flying and making interruptions. This underlines the dominant effect of wind on migratory behaviour in general (Alerstam 1990, Liechti 2006, Klaassen et al. 2010, Bohrer et al. 2012, Mellone et al. 2012, 2015, Vansteelant et al. 2015).

Comparison between Montagu's harrier and osprey

When comparing daily travel routines in Montagu's harriers and ospreys, there is a striking contrast between the strong regional variation in daily time budgets in ospreys (Klaassen et al. 2008) and the similarity in daily time budgets between regions in the Montagu's harrier. The daily travel speed of ospreys was 115 km d⁻¹ higher in Africa than in Europe, which was explained by 2.7 h d⁻¹ longer daily flight time in Africa (Klaassen et al. 2008). In the Montagu's harrier the difference in time budgets between regions was smaller in that harriers flew only 0.8 h less per day in Europe compared to Africa, resulting in daily flight distances being

Table 1. Summary of daily time budgets for travel days of Montagu's harriers, per region and per season (in hours). Provided are means \pm standard deviations.

	Autumn		Spring	
	Europe	Africa	Europe	Africa
Foraging	1.8 \pm 1.5	1.4 \pm 1.3	2.4 \pm 1.7	2.0 \pm 1.5
Interruption for foraging	0.71 \pm 0.68	0.62 \pm 0.63	0.57 \pm 0.60	0.60 \pm 0.58
Interruption for resting	0.45 \pm 0.45	0.63 \pm 0.63	0.39 \pm 0.35	0.48 \pm 0.45
Short interruptions	0.37 \pm 0.38	0.40 \pm 0.32	0.43 \pm 0.41	0.40 \pm 0.32
Travelling (flying)	8.6 \pm 3.2	9.4 \pm 2.8	8.7 \pm 3.0	9.0 \pm 2.8
Resting	12.1 \pm 2.9	11.5 \pm 2.1	11.5 \pm 2.5	11.6 \pm 2.5

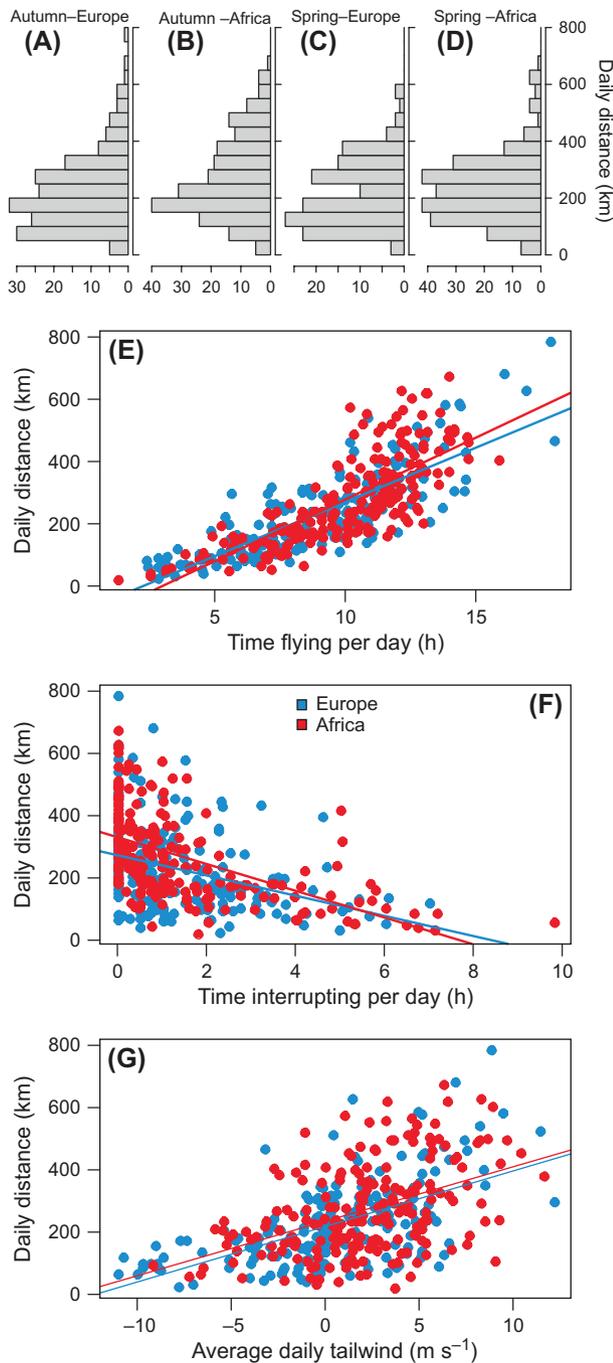


Figure 6. Travel performance of migrating Montagu's harriers for different regions and seasons. Upper histograms show the frequency distribution of daily travel distances for regions and seasons (A–D). The lower panels show the effects of number of time flying per day (E), time making interruptions per day (F), and average tailwind during the day (G), on daily travel distance, for autumn migration. See Supplementary material Appendix 1 for additional correlations with weather, including the same correlations for spring migration.

42 km shorter in Europe compared to Africa. Daily variation in travel performance in the harriers is instead explained by daily variation in time budgets, caused by daily variation in wind. Thus, in Montagu's harriers, wind conditions rather than the landscape/season seem to shape travel performance.

Obviously, it is now the challenge to describe daily travel routines for a range of migrants in order to allow for more comprehensive interspecific comparisons.

It should be stressed that the comparison between Montagu's harriers and ospreys remains incomplete as for ospreys effects of wind on time budgets have not yet been analysed (Klaassen et al. 2008). In addition, in the osprey study only the autumn migration was considered (Klaassen et al. 2008). For Montagu's harriers, time budgets for spring migration were very similar to time budgets for autumn migration, with almost identical flight and interruption hours. Thus, contrary to our expectation, fly-and-forage migration was as pronounced in spring as in autumn. One subtle difference between the seasons was that in contrast to autumn, no correlation was found between wind conditions and the timing of the end of the daily travel in spring, but why the birds respond differently to winds in spring compared to autumn remains unknown. Daily travel distance during spring migration was slightly shorter than in autumn, which can be explained by less favourable wind conditions in spring (Vansteelant et al. 2015), rather than differences in their daily travel routines.

For the analysis of time budgets in this paper we discarded the occasional overnight flights over the Mediterranean Sea as under these circumstances harriers are forced to continue their flights (rather than having the choice to end the flight). However, it is worthwhile to mention the distances travelled during these flights as they provide an indication about the potential capacity of daily travel distances in Montagu's harriers. Average flight distance during sea crossings including a nocturnal flight was 917 km (458 km d⁻¹), and the maximum distance was 1488 km (744 km d⁻¹). These distances are considerably longer than the average daily flight distances over land (217–270 km d⁻¹, Fig. 6). Sea crossings including a nocturnal night are not extremely uncommon in Montagu's harriers (in this study about 3% of all flights), and might be more common than was estimated from satellite telemetry (Trierweiler et al. 2014). In addition, two overnight flights over land were recorded.

Outlook

One of the fascinating aspects of bird migration is the variability in migratory behaviours between and within species, populations and individuals (Alerstam 2011). It seems that almost every species tells a slightly different story, adding new information to the grand picture of bird migration ecology. The specific 'novelty' of the current study is the similarity in daily travel routines among regions and between seasons in the Montagu's harrier. In particular, the contrast with the strong regional variation in time budgets observed for the osprey was unexpected. It is tempting to suggest that the differences in daily time budgets reflect the differences in the species' feeding ecology, with the Montagu's harrier being a food generalist of open landscapes and the osprey a food specialist, and therefore highly dependent on lakes and other water bodies. Although variation in migration behaviour between species and populations sometimes makes it difficult to make general statements about how migration exactly works, we argue that this variation is highly interesting, in particular as it is informative about

factors shaping migratory behaviour. We are in this respect living in an exciting time as the recent and ongoing advances in tracking technologies mean that many species are now tracked for the first time, providing an unprecedented wealth of tracking data for interspecific comparisons.

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Supplementary material (Appendix JAV-01362 at <www.avianbiology.org/appendix/jav-01362>). Appendix 1–2.