

Research



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Animal behaviour

A circannual perspective on daily and total flight distances in a long-distance migratory raptor, the Montagu's harrier, *Circus pygargus*

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Long-distance migrants are particularly recognized for the distances covered on migration, yet little is known about the distances they cover during the rest of the year. GPS-tracks of 29 Montagu's harriers from breeding areas in France, The Netherlands and Denmark showed that harriers fly between 35 653 and 88 049 km yr⁻¹, of which on average only 28.5% is on migration. Mean daily distances during migration were 296 km d⁻¹ in autumn and 252 km d⁻¹ in spring. Surprisingly, males' daily distances during breeding (217 km d⁻¹) were close to those during migration, whereas breeding females moved significantly less (101 km d⁻¹) than males. In terms of flight distance, the breeding season seemed nearly as demanding as migration periods for males. During the six winter months, both sexes moved less (114 and 128 km d⁻¹ for females and males, respectively) than during migration. Harriers therefore covered shorter daily distances during winter which might allow birds to compensate for the more demanding phases of migration and breeding.

1. Background

Migratory lifestyles are considered to have evolved under the premise that benefits of breeding in high-quality seasonal habitats more than outweigh the costs associated with making migratory journeys [1–3]. However, costs and benefits of migration remain poorly understood, partly because we have little knowledge of the relative costs of migration compared with other phases of the annual cycle [4–6]. It has been argued that migration is particularly costly since travel distances are relatively large [5,6], yet most birds also

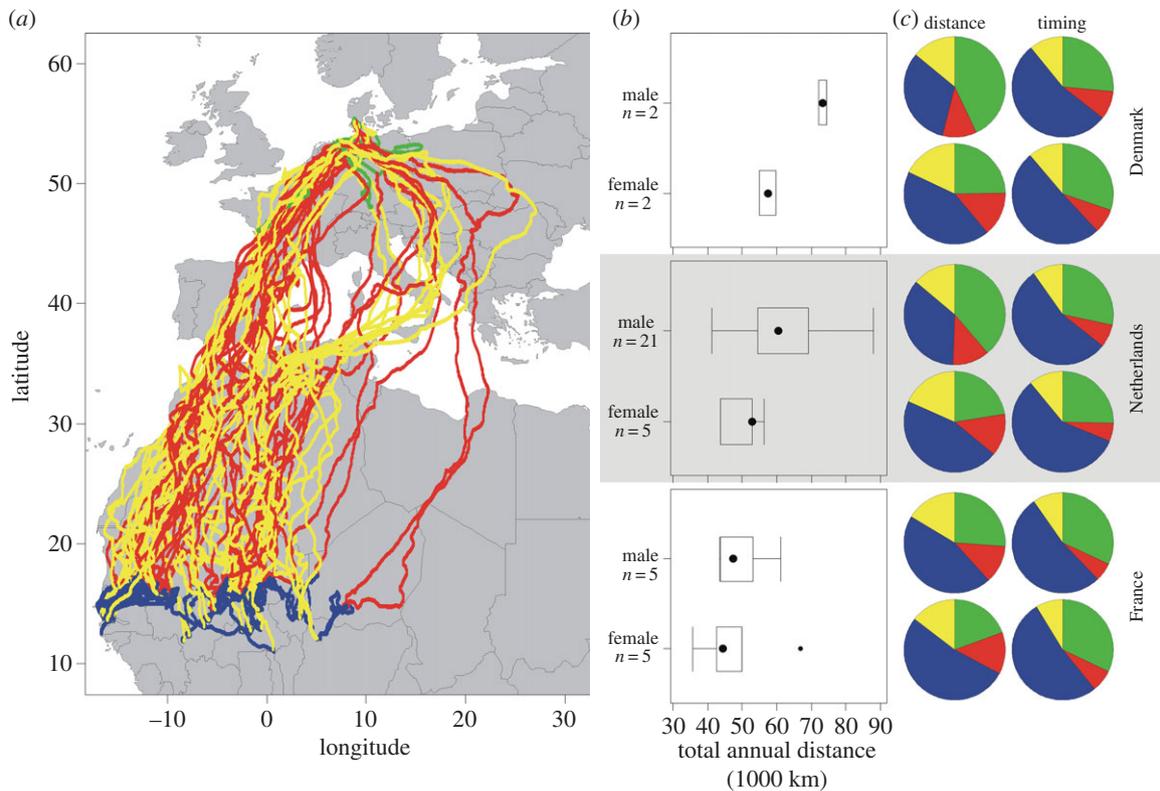


Figure 1. (a) Map showing all tracks with colours indicating annual cycle phases (green = breeding, red = autumn migration, blue = winter, yellow = spring migration). (b) Total annual distance flown by female and male Montagu's harriers from France, The Netherlands and Denmark during 1 year. Number of tracks per sex is given besides boxplots. (c) Pie charts depicting fraction of distance and time per annual cycle phase separated for populations and sexes. For individuals with repeated journeys the average value was used. Colours as in (a).

move substantial distances within the breeding and wintering seasons to gather food for themselves and their young. Thus, movements during stationary periods may contribute considerably to the total annual distance covered by birds. How the distance covered during stationary periods scales to migration distance is however largely unknown.

Montagu's harriers (*Circus pygargus*) are long-distance migratory raptors with a southwest-Palaeartic breeding and Afrotropical/Indomalayan wintering distribution [7]. Migration distance is shorter for more southerly breeding populations, whereas distances travelled in winter and during breeding might depend on habitat quality and food availability [8,9]. Montagu's harriers forage on the wing, and therefore might cover long distances also during stationary periods [10].

Here we aim at comparing the daily and total flight distances as proxies of energy expenditure during the main phases of the annual life cycle for both sexes of this long-distance migrant, replicated for three breeding populations, using 40 complete annual cycles of 29 Montagu's harriers followed by GPS-trackers.

2. Material and methods

(a) GPS-tracking data

We collected data for 40 complete annual cycles (from 1 July until 30 June the following year) of 9 female and 20 male Montagu's harriers tracked by means of UvA-BiTS GPS-trackers (www.uva-bits.nl, [11]) between 2009 and 2016. Seven individuals were tracked during 2 and two individuals during 3 years. Birds originated from breeding areas in Denmark ($N = 3$), The Netherlands (18)

and France (8). GPS-trackers were mounted using a Teflon ribbon harness and programmed to collect GPS-positions at intervals of 5 min ($N = 7$ tracks), 10 min (12), 15 min (16), or 30 min (5) during daytime and a maximum of once per hour at night during migration and winter. During breeding, higher frequencies were obtained (most common interval was 5 min, but additional bursts of high-resolution data (3 s) were collected) but tracks were subsampled to the most common interval for the whole year. Data were checked for outliers visually on a map and points for which instantaneous or trajectory speed was higher than 30 m s^{-1} were deleted (453 fixes deleted, 1 134 664 fixes remained for analyses). Using a map of the recorded positions, daily tracks were assigned annual cycle phases (breeding, autumn migration, wintering, spring migration; figure 1). Pre- and post-migratory movements [12] were assigned to the nearest stationary period (pre-autumn ($N = 8$) and post-spring ($N = 4$) to breeding, post-autumn ($N = 16$) to winter). Daily distance was calculated by adding the distances between consecutive positions using function *distMeeus* from R package *geosphere* v. 1.5–5 [13]. Cumulative distance for each annual cycle phase was the sum of all daily distances within the phase and total annual distance was the sum of all daily distances within the whole year.

(b) Interval bias correction

Adding straight-line distances between GPS-positions underestimates true distance travelled depending on sampling interval and tortuosity of the movement path [14,15]. To correct for this effect, we subsampled high-resolution tracks (1200 fixes per hour) to intervals of 600, 300, 150, 75, 37.5, 18.75, 12, 6, 4, 3 and 2 fixes per hour (for an example see electronic supplementary material, figure S1). High-resolution data were regularly collected during breeding, but rarely during migration and winter owing to limited memory storage. In total, we accumulated 16.5 h for autumn migration, 11.5 h for spring migration,

11 h for winter and 14 h for breeding from tracks of Dutch male Montagu's harriers. By recalculating straight-line distances between GPS-positions for each subsampled dataset we calculated proportional accuracy (ratio of apparent to true distance travelled) using the original 1200 fixes per hour distance as reference (electronic supplementary material, figure S2). Daily distance was then corrected according to sampling interval of the track and annual cycle phase by multiplying with a correction factor (mean (range) breeding: 4.08 (2.73–7.79), autumn migration: 1.32 (1.24–1.36), winter: 3.30 (2.56–3.99), spring migration: 1.35 (1.27–1.43)). Correction factors are higher during stationary periods owing to more tortuous movements compared with directed flights during migration (cf. electronic supplementary material, figure S1). This correction might overestimate distances for females during breeding (incubation) and for birds moving between sites in winter or on stopover days.

(c) Statistical analyses

In order to test for differences between the sexes and populations regarding total annual distance, daily distance, and cumulative distance, we used linear mixed models (LMMs) with function *lme* from package *nlme* v. 3.1–127 [16] in R v. 3.3.0 [17]. In all models we included *individual* as random effect and *population* and *sex* as fixed effects. In the annual cycle phase-specific estimates we also included *phase* and the interaction terms *phase:sex* and *phase:population* as fixed effects. This resulted from comparing models with all possible combinations of interaction terms using the Akaike information criterion (AIC). Multi-comparison post-hoc tests were performed to evaluate differences between populations and annual cycle periods using R-function *testInteractions* from package *phia* v. 0.2–1 [18]. Estimates were calculated using R-function *allEffects* from package *effects* v. 3.1–2 [19].

3. Results and discussion

Montagu's harriers travelled on average 57 841 km (range 35 653–88 049 km) per year. Males travelled about 20% more than females (table 1a, figure 1; mean values: males 61 071 km, females 50 305 km), mainly because males covered longer daily distances during the breeding season compared with females (217 and 101 km day⁻¹, respectively; table 1b, figure 2; cf. electronic supplementary material, figure S3 for individual time-series). This difference results from males provisioning the incubating female and both chicks and female during the first weeks after hatching [10]. Interestingly, despite female Montagu's harriers being substantially larger (370 versus 260 g), and therefore needing more food, we found no significant difference in winter flight distance (table 1b, figure 2; mean values: males 114 km d⁻¹, females 128 km d⁻¹). This might either indicate that food availability in general is not limiting or hint towards differential prey choice of the sexes during winter.

French birds travelled less than Dutch and Danish birds (table 1a, figure 1; post-hoc test in electronic supplementary material, table S2a), mainly because French males flew less during breeding (table 1b, figure 2; mean values: F 92, NL 211, DK 217 km day⁻¹) and not due to their shorter migration routes. It remains to be investigated whether this is caused by varying habitat quality and food availability.

Whereas 17% of the year was allocated to migration, birds covered 28.5% of their annual distance during this period (figures 1 and 2; females 31%, males 26%). Migration is often seen as an exceptional investment, but interestingly,

Table 1. Results of analyses of variance of LMMs on (a) total annual distance, (b) mean daily distance and (c) cumulative distance of male and female Montagu's harriers from France ($N = 10$), The Netherlands ($N = 26$) and Denmark ($N = 4$ tracks). All models included *individual* as random effect and *population* (F, NL and DK) and *sex* (female, male) as fixed effects. In (b) and (c) we also tested *phase* (breeding, autumn migration, winter, spring migration) and all (two- and three-way) interaction terms. Models were compared using the Akaike information criterion (AIC) and output of the model with the lowest AIC is shown. All estimates can be found in the electronic supplementary material, table S1.

variable	edf	F-value	p-value
(a) total annual distance (km) (LMM, figure 1, estimates electronic supplementary material table S1)			
intercept	25	966.94	<0.001
sex	25	6.46	0.02
population	25	3.84	0.04
(b) mean daily distance (km) (LMM, figure 2a, estimates electronic supplementary material table S1)			
intercept	119	1337.3	<0.001
phase	119	71.85	<0.001
sex	25	2.71	0.11
population	25	2.4	0.11
phase × sex	119	10.55	<0.001
phase × population	119	2.56	0.02
(c) cumulative distance (km) (LMM, figure 2c, estimates electronic supplementary material table S1)			
intercept	119	894.16	<0.001
phase	119	112.79	<0.001
sex	25	6.13	0.02
population	25	3.39	0.05
phase × sex	119	18.08	<0.001
phase × population	119	2.67	0.02

males reached nearly similar daily distances during breeding as during migration. When comparing these daily distances to seasonal variation in mortality rates derived from satellite telemetry [5], it is striking that daily mortality rates during breeding (0.0012) are considerably lower than during autumn (0.0023) or spring migration (0.0052). Therefore, high mortality rates during migration are unlikely to be related to endurance of long-distance flight *per se*. Instead, it was suggested that high mortality rates during migration were related to unfavourable conditions encountered during migration and, possibly, to carry-over effects of demanding breeding seasons [5]. During the six winter months, Montagu's harriers fly relatively short daily distances and mortality is at its lowest (0.0006 [5]). Studies on other migratory species confirm that the wintering period seems to be the least demanding as survival rates are comparatively high [20,21]. Still, deteriorating environmental conditions in the course of the Sahelian winter force harriers to increase foraging time, and thereby daily distance travelled, and cause delays in spring departure for individuals wintering at the driest sites [8].

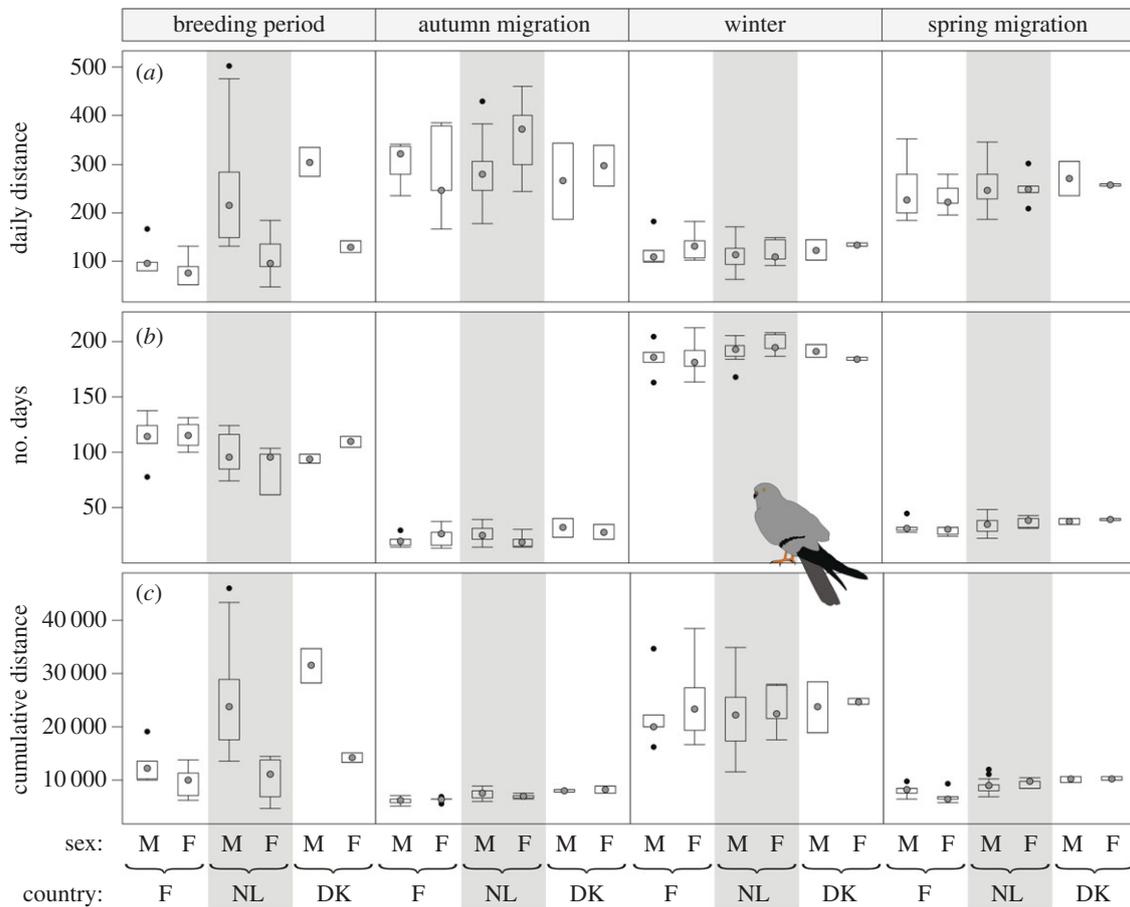


Figure 2. (a) Mean daily distance (km), (b) number of days and (c) cumulative distance (km) during the four main annual cycle periods for male and female Montagu's harriers originating from breeding populations in France, The Netherlands and Denmark. Boxplots show between-individual variance using the mean value per individual. For sample sizes see figure 1. (Online version in colour.)

How general is the pattern of long-distance migrants flying daily distances during migration nearly similar to those during other annual cycle periods? We consider it likely that species hunting on the wing, like swallows, swifts, seabirds and many raptors, may cover similar distances during stationary and migratory periods, whereas for birds foraging on the ground or in the foliage, migration may indeed be outstanding in terms of daily flight distances. It is important to mention that recording interval strongly affects estimated distance and thus high-frequency tracks are required [15,22]. Earlier reports on daily travel distances of Montagu's harriers using satellite tracking data (autumn 175 km d^{-1} , spring 166 km d^{-1} [9]) or lower resolution GPS-tracking data (autumn 205 km d^{-1} , spring 182 km d^{-1} [23]) were indeed 28–35% lower than our corrected calculations using high-resolution tracks (autumn 296 km d^{-1} , spring 252 km d^{-1}).

To place migration into a life-history perspective, we consider it essential to compare the investment with that in other life cycle phases, as performed here for harriers using distance as a proxy for energy expenditure. Our main findings show that daily distances of breeding males are almost comparable to daily distances flown during migration, but that winter is less demanding. However, we need to investigate at what cost this comes, and whether effects carry over to survival, reproductive success and even population dynamics. This might become more important with further intensification of agricultural landscapes making breeding even more

demanding owing to decreasing habitat quality and food availability.

Ethics. Tracking was approved by local ethical committees: University of Groningen, The Netherlands (permits 5869B and 6429B), the Natural History Museum of Denmark, and CRBFO Muséum National d'Histoire Naturelle for France (permit 1308).

Data accessibility. Data are available from the Dryad Digital Repository: doi:10.5061/dryad.84jk0 [24].

Authors' contributions. Fieldwork: A.E.S., R.H.G.K., I.H.S., A.V. Data-analysis and processing: A.E.S., W.B., C.B. Local project coordination: V.B., H.H. Drafting manuscript: A.E.S., C.B. All authors helped edit and revise the manuscript, gave final approval for publication and agreed to be held accountable for the content therein.

Competing interests. We have no competing interests.

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