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Research article

Different migration patterns of Wahlberg's eagles *Hieraaetus wahlbergi* across Africa

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Intra-Africa movements of most African migratory birds remain an enigma. We describe the migrations of Wahlberg's eagle *Hieraaetus wahlbergi* using GPS-GSM transmitters on adult eagles in their South African (n = 3) and Kenyan (n = 7) breeding areas between 2018 and 2022. The dataset included 57 migratory tracks, 29 post-breeding and 28 pre-breeding. We found long-distance migrants (LDMs; from South Africa) and short-distance migrants (SDMs; from Kenya) using common non-breeding areas centered in the Sudans and Central African Republic. The timing of annual phases was similar, but LDMs departed on their pre-breeding migration on average later than SDMs (13 August versus 31 July) and arrived later on their breeding grounds (13 September versus 10 August). Conversely, the average departure date on the post-breeding migration was 4 April for SDM and 23 March for LDMs. LDMs spent significantly less time of the year than SDMs on breeding grounds (44 versus 57%), and slightly but not significantly more time (40 versus 38%) on non-breeding areas. The post-breeding migration distance was on average 3413.9 ± 170.9 km for LDMs and 491.9 ± 158.5 km for SDMs. At non-breeding areas, LDMs reached more northerly latitudes than SDMs, increasing the pre-breeding migration distance to 4495.9 ± 372.5 km for LDMs versus 1701.9 ± 167.3 for SDMs. Daily flight distances back to the breeding areas averaged 153.4 ± 130.3 km for LDMs and 167.4 ± 122.3 km for SDMs and to non-breeding areas were shorter for SDMs (124.8 ± 113.0 km) than LDMs (178.0 ± 134.4 km). Migration speed was similar across populations and for pre- and post-breeding migrations. LDMs used more stopover days than SDMs. We conclude that Wahlberg's eagles from different parts of Africa have adapted their migration to differences in timing of the breeding season, distance of travel, and resources in the landscapes encountered during migration.

Keywords: GPS-GSM tracking, Kenya, migration patterns, raptors, South Africa, stopover sites, Wahlberg's eagle

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Introduction

Satellite telemetry has established itself as a highly effective method of investigating the migration of migratory birds, including mortality rates (Klaassen et al. 2014, Oppel et al. 2015), main wintering areas (Limiñana et al. 2012, Terraube et al. 2012) and migration routes and strategies (Gschweng et al. 2008, Mellone et al. 2011, Phipps et al. 2019). Such studies have found that different patterns of migration are governed by differences in migration distance (Monti et al. 2018, Brown et al. 2021), fueling landscape (Fraser et al. 2017, Stanley et al. 2021), climate and weather conditions (Kölzsch et al. 2016, Vansteelant et al. 2017), the timing of breeding (Sergio et al. 2007, Rotics et al. 2018), and barriers (e.g. rainforests, deserts; Strandberg et al. 2009). While such relationships have been well studied in the Palearctic–African migration system, little is known about intra-African systems.

Migratory journeys are typically characterized by an alternation between flights, when distance is covered and energy consumed, and stopover periods when energy for the next flight stage is accumulated. Different stopover and flight strategies presumably have evolved as a consequence of trade-off relationships and constraints involving fuel deposition and flight performance (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Saino et al. 2010). The landscape that birds pass over during migration greatly influences their routes and flight strategies; Palearctic migrants often avoid ecological barriers such as deserts and large waterbodies or reduce the risk of passage (Newton 2023), by using a longer route around the barrier (Klaassen et al. 2010, Phipps et al. 2019), or by delaying migration until conditions become more suitable (Åkesson and Hedenström 2000). In addition to barriers, weather conditions are key in shaping migratory routes and affects a bird's decision to initiate migration and the course and pace of migration (Liechti 2006, Hedenström 2010). Contrary to Afro-Palearctic migrants, Afrotropical migrants in Sub-Saharan Africa face a general lack of landscape barriers, notably long-distance water crossings, and experience less severe weather conditions. In further contrast to Afro-Palearctic migrants, many Afrotropical birds undertake polarised migrations, with part of the population moving north, and part south of the tropics, which may be enabled by the spatial symmetry and large extent of savannas both north and south of the tropics (Hockey 2000). Also, the timing of breeding and migration are largely governed by rainfall in intra-African systems (Thiollay 1978, Jensen et al. 2006, 2008, Petersen et al. 2008, Iwajomo et al. 2018), and the common mode of migration among Afrotropical birds is movement from the tropics to more temperate areas to breed during the onset of the rainy season which triggers seasonal food resources (Benson 1982, Hockey 2000).

Migration strategies vary depending on the total distance traveled, and migratory birds can generally be categorized into short-distance migrants (SDMs) and long-distance migrants (LDMs), with their associated costs and benefits (van Noordwijk et al. 2006, Pulido 2007). Most studies that investigated differences in long versus short-distance migrations are complicated by inter-specific comparisons, which are influenced by the uncertainty over the role of morphology that influences migration strategies (La Sorte et al. 2013). Insight into the variation of migration patterns, including speed and stop-over frequency, is therefore best gathered within species that have populations of long-distance migrating and short-distance migrating individuals (Monti et al. 2018, Phipps et al. 2019). In general, LDMs are thought to achieve faster overall migration speed compared to SDMs (La Sorte et al. 2013); as the migration distance to be covered is larger, LDMs are supposed to suffer stronger constraints than SDMs, having limited leeway in their annual schedules to linger, particularly in pre-breeding migration (Nilsson et al. 2013). Studies in temperate species have shown that adjustments in stop-over time and frequency seem to act as a major determinant of seasonal difference in overall migration speed (the total distance covered divided by the total duration of travel, including time spent at stopovers; Nilsson et al. 2013). While some LDMs may be able to advance their departure date to arrive on time at destination, others must delay their departure for specific environmental conditions to arise (Duriez et al. 2009) and require a high travel speed with few or shorter stopovers to ensure a timely arrival on breeding areas (Alerstam 2003, Nilsson et al. 2013). SDMs, however, may travel more slowly and minimize energy expenditure by using more frequent stopovers (Strandberg et al. 2009). Thus far, these and other insights come from tracking studies on LDMs and SDMs in temperate-zone breeding species (Limiñana et al. 2012, Monti et al. 2018), contrasting with a general lack in tracking studies examining long- and short-distance migration patterns of intra-continental African migrants.

The lack of knowledge of Afrotropical migration systems includes Afrotropical migratory raptors, a handful of which have long been known to have long- and short-distance migratory populations (Brown 1971, Thiollay 1978). To date, most information on intra-African migratory raptor movements have been obtained from year-round road surveys at different latitudes (Thiollay 1978, Buij et al. 2013a), and a few tracking studies (Meyburg et al. 1995, Garcia-Heras et al. 2019). Similar to Afro-Palearctic raptors, whose movements in Africa have been linked to spatiotemporal patterns in food abundance (Trierweiler et al. 2013, Hadjikyriakou et al. 2020), movements of African migratory raptors appear to be mainly linked to seasonal changes in food availability (Newton 1979). These changes are mostly governed by rainfall and subsequent drying of savannas, which influences the distribution and accessibility to trophic resources (e.g. termite alates, passerines; Thiollay 1978). Most intra-African raptor movements therefore appear to be closely tied to those of the Intertropical Convergence Zone, a latitudinal band of heavy rains that moves seasonally north and south across the continent (Thiollay 1978, 1989). Such seasonal movements have been best described in the West African tropics (Brown 1971, Thiollay 1978, Buij et al. 2013a), where various raptors perform short-distance migrations. These raptors track a

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wave of ephemeral food resources with the progressively later start of the rainy season north into the Sahel; as the rains cease, they move south again with foraging opportunities that arise from the drying, grazing, and burning of grassland savannas at more southerly latitudes. Long-distance migrations of African raptors are probably governed by similar processes, but less well understood, and little studied to date.

The Wahlberg's eagle *Hieraaetus wahlbergi* is Africa's most numerous eagle and the only African eagle that almost completely vacates its breeding areas seasonally, at least in a large part of its African distribution range (Ferguson-Lees and Christie 2001). The most detailed knowledge of the species' migration from breeding to nonbreeding areas thus far comes from two tracked adult females from the southern African breeding range (Meyburg et al. 1995), which spent their non-breeding season ca 3500 km further north in the Sudan and Sahelian savannas of Cameroon, Nigeria, and Chad. These Wahlberg's eagles breed in the southern summer and then migrate through the rainforest belt to areas north of the equator when the rains start there. At approximately the same time, the majority of Wahlberg's eagles breeding in East Africa migrate seasonally but probably over much shorter distances and without crossing dense equatorial forests, possibly to reach the same areas (Brown and Britton 1980, Lewis and Pomeroy 1989). However, there is no information to date on the non-breeding areas and the movement ecology and migratory strategies of the East African population.

In this paper, we investigate the annual migration cycle in two latitudinally separated breeding Wahlberg's eagle populations in Africa, contributing unique information on intra-African migration. We deployed GPS-GSM transmitters to track Wahlberg's eagles from their breeding areas in Kenya and South Africa, to examine their speed of migration, number of travel days spent traveling, distance covered, and stopover duration; and tested three main predictions. Our primary prediction concerns the distance and duration of migrations, which we expected would be greatest for the South African population which has to migrate furthest to the Sudan and Sahelian savannas north of the equator, while we expected that migration distance and duration would be shorter for the Kenyan population, assuming they use the same non-breeding areas. As they track food resources north into the Sahel during the non-breeding season, the departure on pre-breeding migration is at more northerly latitudes than the arrival from post-breeding migration (Meyburg et al. 1995); hence, we expected a longer travel distance and duration on pre-breeding than post-breeding migration. Our second prediction concerns the migration speed, daily distances traveled, and the use of stopovers. South African Wahlberg's eagles face greater time constraints and potentially large barriers unsuitable for foraging, such as the Central African forests, during their migration, whereas Kenyan eagles would be generally less affected by time restriction and able to forage in food-richer savannas on their migrations. We therefore expected eagles from South Africa to travel greater daily distances, and with proportionally fewer stopovers than those from Kenya, thus increasing their overall migration speed compared to the latter. Third, we expected that overall migration speed and daily distances covered were greater on the pre-breeding migrations back to breeding areas than on the outward migration, for both populations. This expectation was based on the premise that a higher overall migration speed with fewer stopovers during pre-breeding migration would ensure a timely arrival on breeding areas, thus preventing potential competitive exclusion at breeding areas. Lastly, given these expectations, we expected that the time spent on migration would be shorter for the Kenyan eagles, and longer for the South African eagles, which would lead to a proportionally longer stay at breeding and non-breeding grounds for the first.

Material and methods

Study areas

Birds were captured and fitted with GPS-GSM transmitters in the Maasai Mara ecosystem in southwestern Kenya (1°25'57.3"S and 35°07'46.4"E, ca 1400–1800 m a.s.l.) and in the lowveld region of South Africa (24°59'48.7"S and 31°42'22.0"E, ca 200–900 m a.s.l.). In Kenya, annual rainfall is typically between 700 and 900 mm, but up to 1300 mm in the northwest; there is a bimodal rainy season with peaks in November and April (Bartzke et al. 2018). The lowveld region of South Africa (24°S and 31°E, ca 200–900 m a.s.l.) has one rainy season from September until May, with 400–750 mm rainfall per annum.

GPS-GSM tracking

We used GPS-GSM transmitters to track ten Wahlberg's eagles: five adult males and five adult females (Supporting information). The adults were trapped and tagged near their nests (< 500 m) in South Africa and Kenya between March 2018 and December 2020. Birds were sexed based on their breeding behavior (females lay and incubate the egg) and weight (male weight: 1070–1230 g, females: 1330–1557 g). We used a noosed bal-chatri trap baited with live mice or young chickens to trap the adult eagles. The birds were fitted with two types of solar-powered GPS-GSM transmitters using backpack harnesses made of Teflon™-like ribbon. We used four 20 g GPS-GSM Ornitela transmitters and six 27 g solar-powered backpack transmitters by madebytheo. The madebytheo transmitters collected GPS location data throughout the full 24-h period on a dynamic sampling schedule with time intervals ranging from 30 s to 1 h between locations, depending on the speed of movement and angle of the transmitter to the ground (Hatfield et al. 2024). Time intervals shortened as continuous accelerometer movement energy (20 Hz) increased and transmitter tilt angle exceeded 70°. In cloudy weather conditions, these solar-powered transmitters reverted to collecting four locations per day at 6-h intervals (05:00, 11:00, 17:00, and 23:00). The Ornitela transmitters collected data at frequencies of between one GPS location per second to one per hour. Transmitter casings had rounded

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edges with durable neoprene padding on the bottom and no external antenna. The devices and harnesses weighed approximately 25–32 g, which was below 3% of the body weight of all tagged eagles. We fitted the harnesses with a weak link that allows all straps to be released simultaneously, to ensure that the devices fall off after ca 4–5 years to prevent long-term impacts on the birds. All data were sampled at one point per hour per individual before any calculations. Then any further subsetting was from that dataset.

Phases in the annual cycle and migration components

The annual cycle was examined for both populations, which were distinguished as SDMs or LDMs based on existing long-distance (i.e. over 3000 km) migration tracks of eagles from southern Africa and migration tracks less than half that distance of those from East Africa (Table 1). We defined the different phases of the annual cycle as follows: 1) the migration period was the period during which the birds moved > 50 km per day in a direction north (post-breeding migration) or south (pre-breeding migration). Directed movements were defined as the average daily direction $<=-135^{\circ}$ or $>=110^{\circ}$ to define the transition between non-breeding season and pre-breeding migration. The average daily direction $<=135^{\circ}$ and $>=-135^{\circ}$ defined the transition between the breeding season and post-breeding migration. The start of migration was defined as the last GPS position at the breeding site and the end of migration as the first GPS position at the non-breeding area. 2) The breeding season was distinguished from migration movements by local movements in the breeding area, i.e. where the bird was nesting in one or more years, not exceeding linear movements in a single direction of > 50 km per day. 3) The non-breeding season started with the crossing of a latitude based on breakpoint regression and ended by the first GPS position of linear movement in the direction of the breeding areas. The transition between post-breeding migration and non-breeding was based on breakpoint regression analysis using the ‘segmented’ package in R (Muggeo 2008). We fixed the number of breakpoints to 1 and only used movement data greater than 1 degree latitude, for both populations, to not include small-scale movements at the start of migration. Such directed movement hit latitudes of 2.8°N for SDMs and 4.4°N for LDMs (Supporting information); the red line in the Supporting information indicates the latitude where the northerly directed movements slow down. Therefore, all locations north of 2.8° for SDMs and 4.4° for LDMs were considered movements carried out at non-breeding areas. Stopovers during migration were defined as days during migration where the total movements were < 25 km (c.f. Strandberg et al. 2008). We defined migration speed as the total distance divided by number of days to complete migration, including stopovers. The total duration of migration (i.e. number of days to complete migration) and percentage time spent on migration included stopover days, whereas travel days were defined as 24-h periods during which > 25 km were traveled during migration, i.e. excluding stopover days. We defined the daily distance traveled as kilometers moved per day for days when eagles were migrating, i.e. flying in the migratory direction, using one random point per day per individual. The total migration distance was defined as the total distance between consecutive locations from the start to the end point of migration, and calculated using one random point per day per individual. We used one location per day to eliminate small movements and to allow for consistency across all individuals, as this was the frequency of points available for all individuals.

Data analysis

We evaluated the effects of population, SDM or LDM, on the proportion of time spent in their breeding versus non-breeding areas (a) and components of pre- and post-breeding migrations (b–f) and. Migration components included (b) proportion of time spent on migration, (c) the number of travel days (excluding stopover days), (d) total migration distance, (e) daily distance traveled, and (f) migration speed, for a total of six models explained below.

All data processing and analyses were done in Program R (www.r-project.org). We used generalized linear and linear

Table 1. Population-level migratory flights, average (μ ± SD) number of migration trips (i.e. number of trips between breeding and nonbreeding areas, and vice versa), number of adult birds, average departure and arrival dates, the number of traveling days, stopover days, stopovers, average migratory distance, average daily distance, and average number of days to complete migration for short-distance migrant (SDM) and long-distance migrant (LDM) populations of Wahlberg’s eagles (2018–2022).

	SDM		LDM	
	Pre-breeding migration	Post-breeding migration	Pre-breeding migration	Post-breeding migration
n (migration trips)	2.6 ± 1.3	2.6 ± 1.3	3.3 ± 0.6	3.7 ± 0.6
n (birds)	7	7	3	3
Departure date (days)	31 July	4 April	13 August	23 March
Arrival date (days)	10 August	8 April	13 September	11 April
Traveling days (days)	10.2 ± 2.3	3.9 ± 2.9	30.2 ± 5.1	19.2 ± 5.4
Stopover days (days)	1.1 ± 0.4	0	1.5 ± 1.1	2.6 ± 4.2
Number of stopovers	1	0	4 ± 1	2.0 ± 1.0
Average migratory distance (km)	1701.9 ± 167.3	491.9 ± 158.5	4495.9 ± 372.5	3413.9 ± 170.9
Average daily distance (km)	167.4 ± 122.3	124.8 ± 113.0	153.0 ± 130.3	178.0 ± 134.4
Total duration to complete migration (days)	9.7 ± 1.9	3.9 ± 2.9	24.7 ± 5.6	15.5 ± 2.7

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mixed-effect models ('glmmTMB' package; Brooks et al. 2017) to evaluate the effect of population (categorical: SDM versus LDM) and migration (pre- or post-breeding) on the migratory components mentioned above as well as on percent of time on breeding areas versus non-breeding areas. We included 'individual' as a random effect, for all models except model (d), the inclusion of a random effect created convergence issues. Additionally, 'migration' (pre- versus post-breeding), 'season' (breeding versus non-breeding), 'population' and their interaction were included as fixed effects. A beta distribution with logit link was used for the proportion of time spent within breeding versus non-breeding (a) and proportion of time spent on post- and pre- breeding migration (b). A Gaussian distribution was used for model (c–f) with a square-root transformation for model (f). We used one-way ANOVA to test for significant differences between populations of the most northerly latitude reached; due to limited sample size, we grouped years and individuals together per population. 'DHARMa' (Hartig 2022) was used for all model diagnostics. This package uses simulations to create interpretable residuals of mixed models. It includes the Kolmogorov–Smirnov goodness of fit test, an outlier test, and a dispersion test. Outliers are points outside the simulation envelope. Lastly, we ran a multiple comparison post hoc Tukey test to assess the significance of the effect of the interaction between population and migration on each component of interest. Wahlberg's eagles from Kenya had zero stopover days during their post-breeding migration, causing the model to be unidentifiable. Therefore, we report only summary statistics (i.e. the number of stopover days and the number of days spent on stopovers) for both populations (Table 1). All summary statistics (Table 1) are presented as μ ± SD, while modeled output in text are μ and se, unless stated otherwise.

Results

Of the 10 adult Wahlberg's eagles GPS-GSM-tracked from their breeding areas in South Africa and Kenya (Fig. 1), nine were tracked over multiple (2–5) pre- and post-breeding migrations (Table 1; see the Supporting information for individual averages). For all analyses, we included only complete seasonal tracks. The dataset included 57 migratory tracks: 29 pre-breeding and 28 post-breeding migration tracks (Table 1). All diagnostic tests were not significant at p of 0.01 indicating good model fit, except for the daily distance model, which

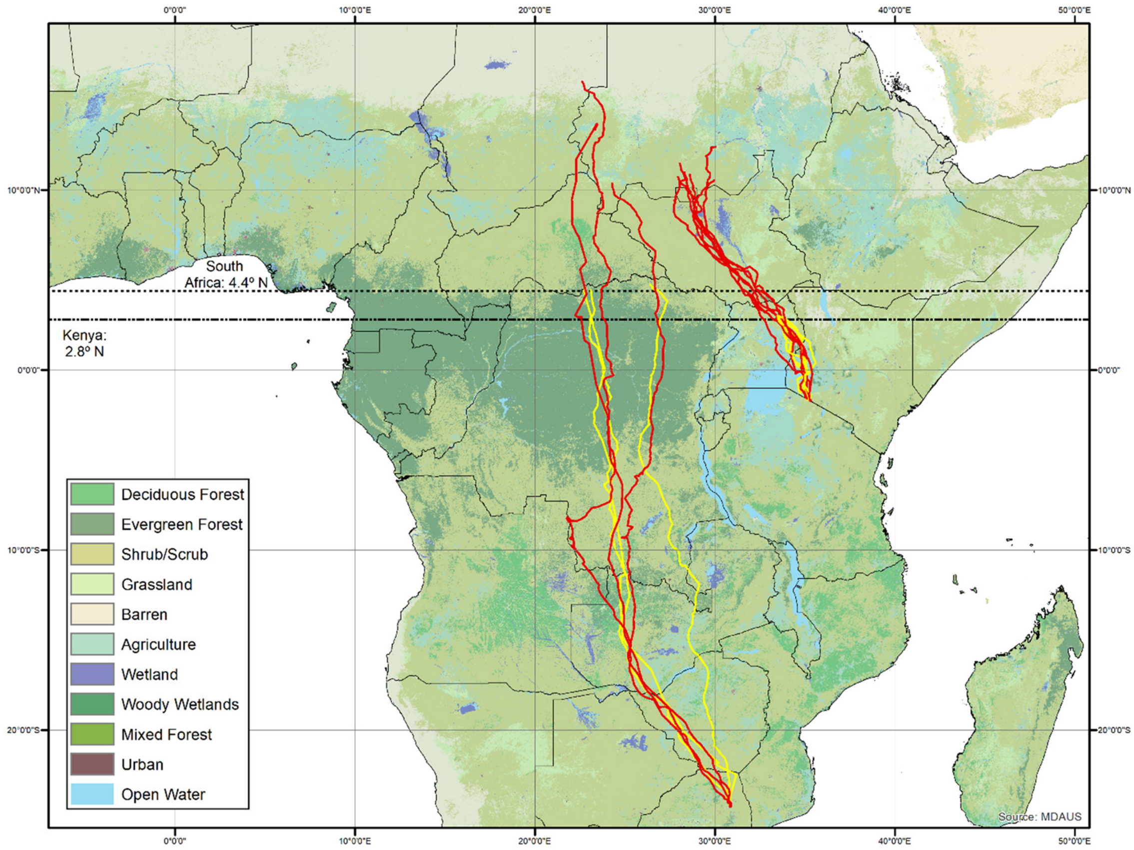

Figure 1. GPS tracks of 10 adult Wahlberg's eagles between 2018 and 2022 during their migration, based on 1 point/hour. Red = pre-breeding migration; yellow = post-breeding migration. Land cover background data from GeoPortal (https://www.africageoportal.com/maps/africa::africa-land-cover/about). Horizontal lines indicate the 4.4°N and 2.8°N lines where non-breeding areas start for the long-distance and short-distance migrants, respectively.

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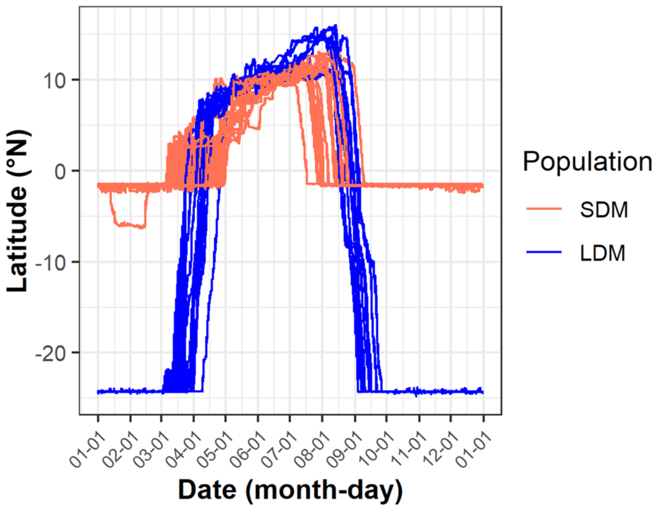

Figure 2. Latitude plotted against date at 1 point/hour/individual, for 10 adult Wahlberg's eagles between 2018 and 2022. The transition between migration north and non-breeding (blue vertical line) was defined as a 13 latitude of 2.8°N for short-distance migrants and 4.4°N for long-distance migrants.

showed a slight significant deviation in two of the three tests (Supporting information). Eagles moved progressively further north after arriving on their main non-breeding areas in Sudan, South Sudan, Central African Republic, Uganda, and Chad (Fig. 2; Supporting information). In doing so, the LDMs reached more northerly latitudes in the non-breeding areas than the SDMs; the most northerly reached latitude across migrations was 13.93°N ± 2.08°N for the LDMs versus 11.93°N ± 0.78°N for the SDMs (one-way ANOVA; $F(2,27) = 1188.6$, $p < 0.001$).

Timing and duration of annual phases

The overall timing of annual phases was similar between SDMs and LDMs (Fig. 3), but the LDMs departed on average later (average departure date: 13 August) on their pre-breeding migration than the SDMs (average departure date: 31 July), with considerable differences in mean start and end dates of migration (i.e. over a month) between individual SDMs, but not in LDMs (Supporting information). Conversely, the departure date on the post-breeding migration was on average later for the SDM (4 April) than the LDMs (23 March). Average arrival dates on breeding areas were 10 August and 13 September, respectively, for SDMs and LDMs, and 8 and 11 April, respectively, on non-breeding areas.

On average (μ, SE) SDMs spent significantly more time of the year on the breeding areas than the LDMs, 56.7, 0.04 versus 43.9, 0.02%, respectively; while LDMs spent slightly (but not significantly) more time on the non-breeding areas than the SDMs, 40.3, 0.04, and 37.9, 0.03%, respectively. The proportion of time on breeding and non-breeding areas was significantly different for SDMs, but not so for LDMs (Fig. 4a). SDMs and LDMs both spent significantly more time on their pre-breeding than on their post-breeding migration, and LDMs spent more time on pre- and post-breeding migration than SDMs (Fig. 4b). The LDMs spent 6.5, 0.01% of the year on post-breeding migration while the SDMs spent 1.7, 0.002%; the LDMs spent 9.3, 0.01% of the year on pre-breeding migration, compared to 3.6, 0.004% by the SDMs.

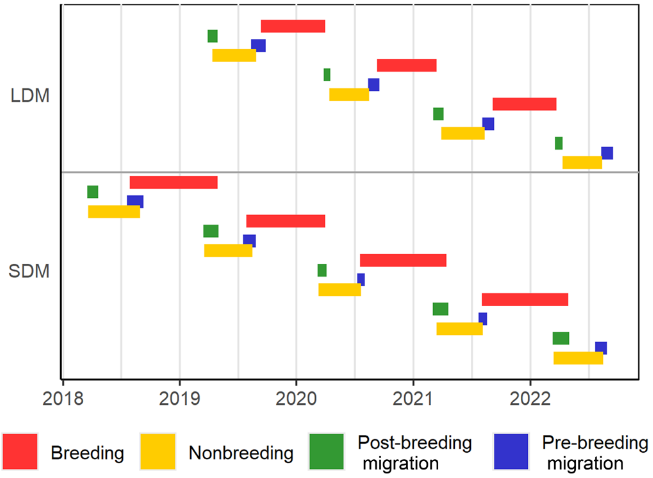

Figure 3. Timing of migratory phases during the annual cycle for 10 adult Wahlberg's eagles (7 short-distance migrants, SDMs; 3 long-distance migrants, LDMs) tracked in 2018–2022. The earliest start date and latest end date of any individual within each population was used to delineate the four phases.

All combinations of migratory season and population showed significantly different effects on the number of travel days, excluding stopover days (Fig. 4c). SDMs spent significantly more days traveling during pre- than post-breeding. Similarly, the LDMs spent significantly more days (~ 10) traveling during pre- than post-breeding migration (Fig. 4c).

Migratory distance, daily distance covered, and overall migration speed

On average, the post-breeding migration distance was 3413.9, 62.7 km for the LDMs and 491.9, 50.4 km for the SDMs. As eagles of both populations gradually moved further north over the course of the non-breeding season, their return pre-breeding migration was significantly longer than their post-breeding migration; 4495.9, 65.7 km for the LDMs versus 1701.9, 49.0 km for the SDMs (Fig. 5a).

The daily distance traveled during the post-breeding migration for the LDMs was significantly longer than for the SDMs' post-breeding migration (Fig. 5b). LDMs traveled on average the longest daily distances during their post-breeding migration, while LDMs and SDMs moved similar daily distances during pre-breeding migration. The longest daily flight distance was recorded on 20 September 2019 for LDM female F5014, which covered a total of 657 km from northwestern Zambia to Matebeleland, north Zimbabwe.

Migration speed was on average 187.2 km per day, 14.2 km per day for LDMs during post-breeding migration and 151.3 km per day, 14.1 km per day during pre-breeding

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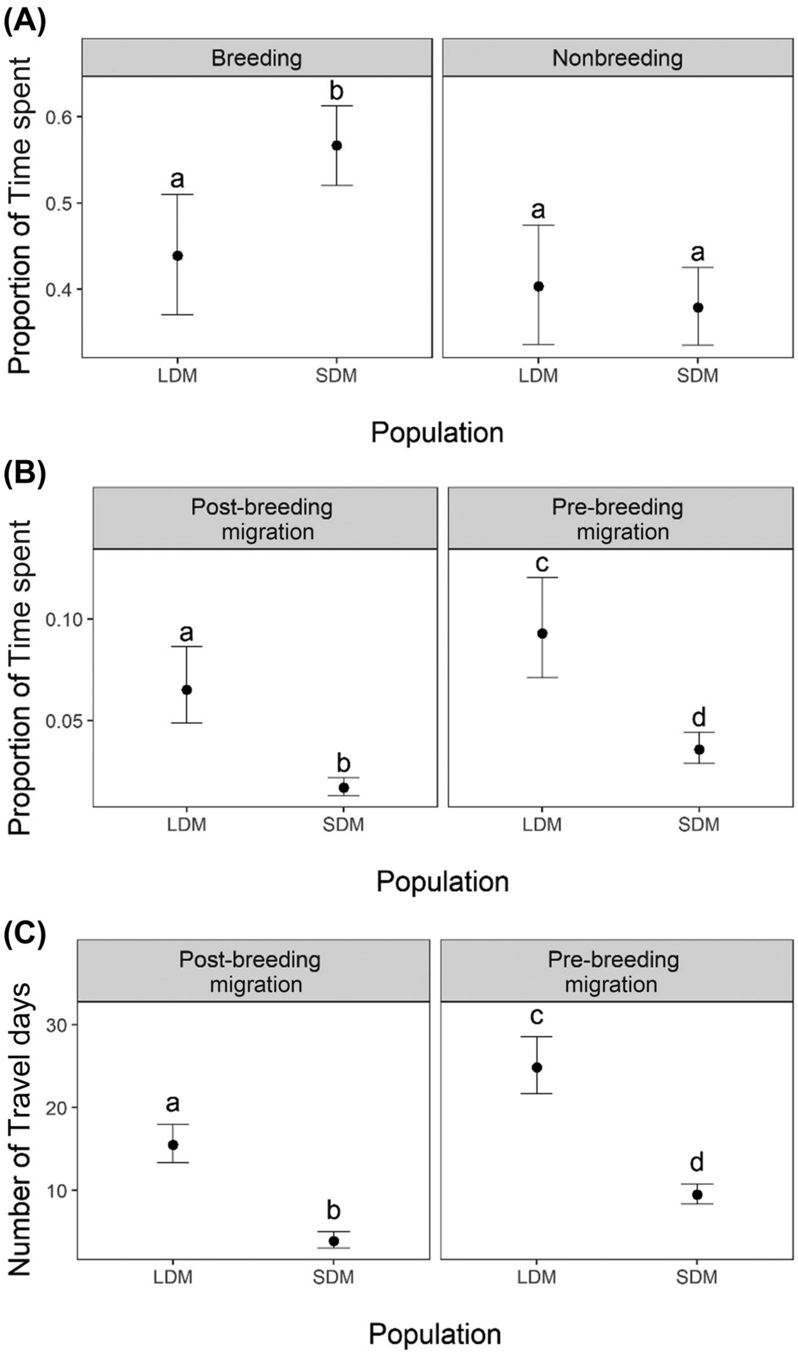

Figure 4. The effect of population for 10 adult Wahlberg's eagles (7 short-distance migrants, SDMs; 3 long-distance migrants, LDMs) tracked in 2018–2022 on (A) the proportion of time spent on breeding versus non-breeding areas, (B) the proportion of time spent on post- and pre-breeding migrations, and (C) the number of travel days on post- and pre-breeding migrations. Error bars represent the standard errors. Significant differences are indicated with letters.

migration. For SDMs it was 160.7 km per day, 11.4 km per day and 172.0 km per day, 11.1 km per day during post- and pre-breeding migration, respectively (Fig. 5c). The migration speed during post-breeding migration for the SDMs was at the same speed as their pre-breeding migration, and not different from either migration for the LDMs.

Stopover duration

The LDM population spent 2.6 ± 4.2 stopover days on their post-breeding migration, while the SDM population did not stopover at all during their post-breeding migration. On their pre-breeding migration the LDM population spent on

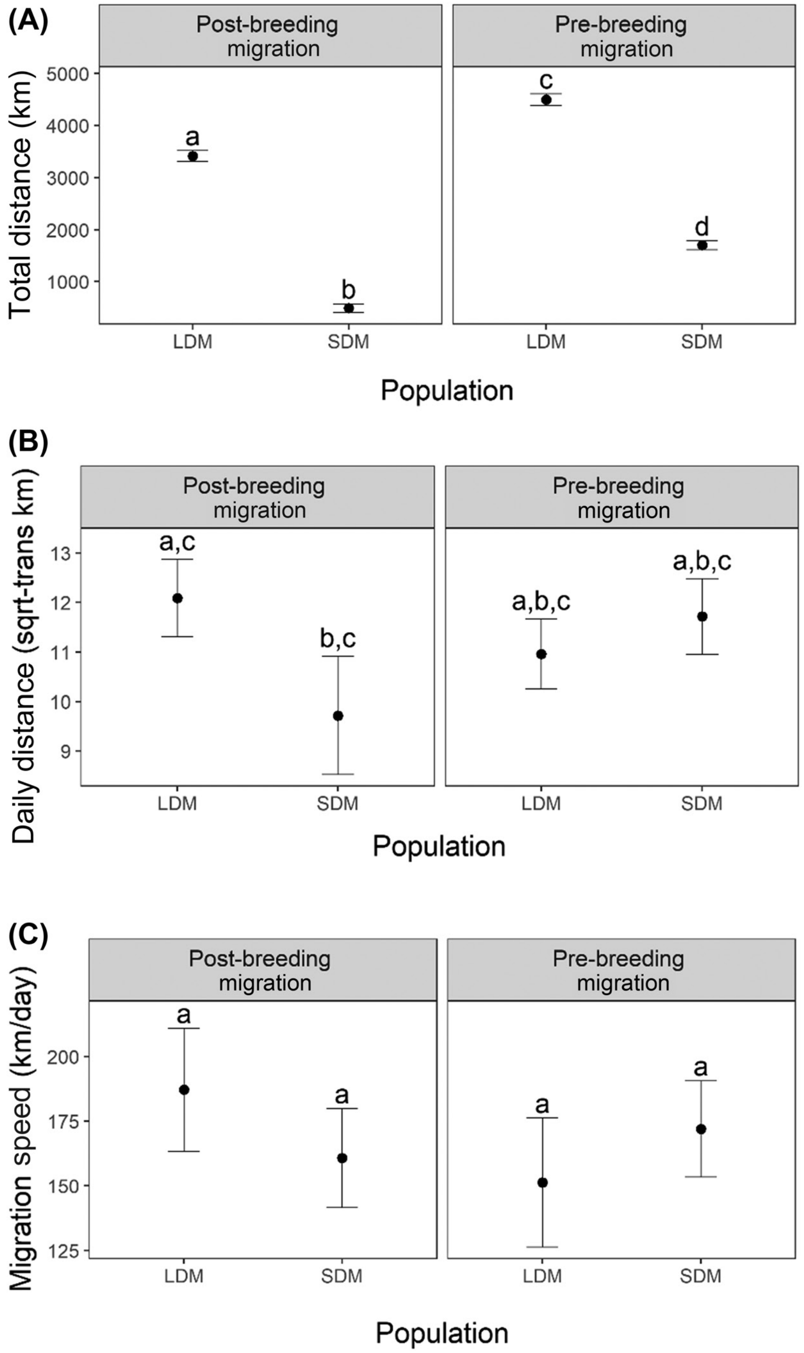

Figure 5. The effect of population for 10 adult Wahlberg's eagles (7 short-distance migrants, SDMs; 3 long-distance migrants, LDMs) tracked in 2018–2022 on (A) the total migratory distance on post- and pre-breeding migrations, (B) the square root transformed daily distance (in kilometers) on post- and pre-breeding migrations, and (C) on overall migration speed on post- and pre-breeding migrations. Error bars represent the standard errors. Significant differences are indicated with letters.

average 1.5 ± 1.1 stopover days versus 1.1 ± 0.4 days for the SDM population (Table 1).

Discussion

Using GPS-GSM tracking on adult Wahlberg's eagles in South and East Africa, we describe for the first time differences in migration patterns of two distinct breeding populations of this Afrotropical migratory raptor. We showed that breeding populations from both regions converge in the same non-breeding areas north of the equator, which necessitates a much longer migration distance in the LDMs from South Africa than the SDMs from Kenya. We found that LDMs depart on average 12 days earlier and travel almost seven times the distance, compared to the SDMs from Kenya, to reach

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their joint non-breeding areas mainly in the Sudans, Central African Republic, Uganda, and Chad. Overall migration speeds were similar across populations during post-breeding migrations, but LDMs covered greater daily distances than SDMs and stopped over on a few days before reaching the non-breeding areas, whereas SDMs did not stop over during their brief post-breeding migration. As such, the SDMs spent a few days traveling to the non-breeding areas north of the equator, whereas LDMs took about three weeks to reach the same areas at around the same time, yet slightly further north. After reaching their non-breeding areas, the eagles gradually moved further north into the Sahel as the non-breeding season progressed. This gradual northward movements of Wahlberg's eagles on their non-breeding grounds is most likely linked to food resources triggered by the northward shifting Intertropical Convergence Zone (Thiollay 1978) and shows parallels with northward rainy season movements from other (seasonally) insectivorous intra-African migrants, such as the scissor-tailed kite *Chelictinia riocourii*, grasshopper buzzard *Butastur rufipennis* (Thiollay 1978, Buij and Croes 2014), Abdim's stork *Ciconia abdimii* (Jensen et al. 2006, Petersen et al. 2008), Abyssinian roller *Coracias abyssinicus* and African grey hornbill *Tockus nasutus* (Jensen et al. 2008).

The longer daily travel distances, use of stopovers, and more northerly arrival on their non-breeding grounds of LDMs compared to SDMs is likely a consequence of differences in feeding opportunities linked to the landscapes along the two main migration routes. After only a few days of post-breeding migration, SDMs reach a flush of prey associated with rainfall over northern Uganda's savannas, which lowers the need for stopovers during their migration. Conversely, LDMs fly over drying savannas with lower food availability at the end of the rains in southern Africa during their post-breeding migration, which may explain the LDMs' use of stopovers while maximizing daily distances covered. Unlike the SDMs, LDMs subsequently need to cross the equatorial rainforests on their way north, which also offer little in terms of accessible food resources. Avoidance of rainforests during migration has also been reported for Eurasian hobbies, which minimize their flight distance across the equatorial forest, concentrating in a corridor where the more open habitat may be more suitable for traveling and foraging, and traveling with increased speed where they are forced to cross rainforest (Strandberg et al. 2009). In contrast to these Palearctic falcons, Wahlberg's eagles do not feed on the wing as they track rain-triggered insect resources, but are known to avoid dense equatorial forest as they hunt vertebrates or forage for alate termites and ants on the ground (Ferguson-Lees and Christie 2001). This explains why the LDMs only slow down once they reach the wet savannas north of the rainforest belt; at about the same time when the SDMs arrive at ephemeral food resources further east, but at lower latitudes. These results suggest that the migratory behaviour of the Wahlberg's eagle is flexible and adapted to landscapes and feeding opportunities along the route, notably the presence of different habitats that offer different degrees of seasonal feeding opportunities. Indeed, across the distribution range Wahlberg's eagle populations appear to exhibit varying degrees of LDM, SDM, and sedentarism. In West Africa, birds migrate seasonally but at short distances of ~1100 km, tracking seasonal rains north into the Sahel after breeding in Sudanese savannas (Thiollay 1978, Buij and Croes 2014), whereas in Ethiopia, birds appear to be sedentary year-round (Ash and Atkins 2009). Such a variety of migration patterns is well described in temperate-zone raptors (Bildstein 2006), but more research is required to fully understand patterns of sedentarism and migration in Wahlberg's eagles and other Afrotropical migratory raptors, and how they may be adaptive under prevailing conditions.

When returning to breeding areas, SDMs and LDMs covered similar daily distances and at a similar overall migration speed. Because SDMs departed to their breeding areas on average two weeks before the LDMs, and SDMs averaged a much shorter pre-breeding migration distance than LDMs (1702 versus 4496 km), they arrived on their breeding areas approximately one month earlier than LDMs. In general, LDMs are expected to linger less and have a higher overall migration speed than SDMs, particularly during pre-breeding migration (La Sorte et al. 2013, Nilsson et al. 2013), with LDMs generally spending less time on stopovers than SDMs (Kölzsch et al. 2016, Monti et al. 2018, Schmaljohann 2018). Contrary to expectations, the LDM population of Wahlberg's eagle did not have a higher overall migration speed than SDMs. Rather, LDMs spent proportionally more time on stopovers than SDMs, as they needed to forage to refuel during their much longer travel distance to breeding grounds.

Wahlberg's eagles from different breeding areas appear to time their arrival on breeding grounds in accordance with regional rainy seasons that peak at different times of the year. Across their distribution range, Wahlberg's eagles appear to time their breeding cycle with the rains so that fledging occurs at a time of maximum food availability, well into the rainy season and at times of high plant growth (Newton 1979). The LDMs from South Africa's lowveld lay their eggs mostly in September–October (Steyn 1983, Chittenden et al. 2016, Tate unpubl.), whereas SDMs from the Kenyan population lay earlier on average, in late August and early September (Smeenk 1974, Lemein Par unpubl.). Average rainfall increases from October in both breeding areas, but in Kenya there is an extended and bimodal rainy season from October to May, whereas rainfall in South Africa peaks in December–February and declines thereafter. As such, Wahlberg's eagles in Kenya are timing chick fledging during the first rainy peak in December/January, several months before peak plant growth (Ojwang 2015), whereas those in South Africa time fledging during the rainy peak in January/February when plant growth peaks (Mathieu et al. 2019). We conclude that the later start of the breeding season in South Africa allows LDM Wahlberg's eagles to move further north into the Sahel, and depart later from their non-breeding areas, while traveling at similar speeds and stopping over to forage more often en route to their breeding areas, compared to their SDM counterparts.

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We found that the LDMs leap-frog the SDMs, arriving at higher latitudes although not sharing overlapping migration routes, but rather parallel (so-called 'parallel leap-frog migration'; sensu Boulet and Norris 2006). A leap-frog migration pattern of LDMs and SDMs has also been found in temperate migratory birds, including various raptors (Schmutz et al. 1991, Kerlinger 2008, Craighead et al. 2016). This is most common among species whose populations are spread over a wide range of latitudes (Kerlinger 2008), and may be the result of competition as the earlier arrivals push the later arrivals further north. In the case of Wahlberg's eagles and other intra-African migrants, the ubiquitous but ephemeral food resources that are triggered by rains in the non-breeding areas (e.g. termite alates, quelea; Thiollay 1978) make competition a less likely explanation for the observed leap-frog pattern. Rather, tracking the seasonal rains into more northerly latitudes is possibly more profitable for LDMs than SDMs, as LDMs have a longer, more energetically demanding pre-breeding migration and SDMs need an earlier start to the breeding season.

As raptor research in the tropics lags behind efforts made in temperate regions (Buechley et al. 2019), so is the migration of Afrotropical raptors relatively understudied in comparison to Afro-Palearctic raptors. The only Palearctic migratory raptor in the *Hieraaetus* genus is booted eagle *H. pennatus*, which is relatively similar to Wahlberg's eagle in morphology and diet, and has migratory populations from Europe spending the northern winter in Sub-Saharan Africa (Ferguson-Lees and Christie 2001). A comparison between booted eagles and LDM Wahlberg's eagles, which have a similar migration distance, highlights disparities and similarities in terms of migration strategies, apart from the difference in migration direction. First, migration speed for the booted eagles that breed in Spain varied between on average 107 km day^{-1} during pre-breeding versus 147 km day-1 during post-breeding migration (Mellone et al. 2015), which is somewhat slower than the overall pre-breeding (151 km day-1) and post-breeding (187 km day-1) migration speeds obtained for the LDM populations of Wahlberg's eagle. The higher post-breeding migration speed of booted eagles compared to pre-breeding migration might be related to the need to arrive early on defended winter territories; alternatively, it has been proposed that deteriorating food resources at the end of the northern winter may force booted eagles out of their winter grounds, which then migrate slowly to prevent loss of energy reserves before breeding, delaying arrival on breeding grounds to avoid suboptimal resource conditions in early spring (Mellone et al. 2015). In fact, booted eagles on pre-breeding migration may stop for several to more than 10 days or longer in the Sahara Desert (Mellone et al. 2023), possibly to take advantage of foraging opportunities provided by migratory songbirds. Although differences were not significant, the LDM Wahlberg's eagles tended to move at greater speeds and covering greater daily travel distances during post- than pre-breeding migrations, similar to booted eagles. Whereas booted eagles may be forced out of their Sahelian non-breeding areas with plummeting food resources at the end of the northern winter, LDMs may profit from lingering there as productivity peaks at the end of their non-breeding period; departing later than SDMs, with more stopover days, and resulting in a one month' later arrival on their southern African breeding grounds, which also points to optimization of energy reserves to time arrival with a later start to the breeding season there. At present, we have no evidence for defended winter territories in Wahlberg's eagles which would make a relatively high post-breeding speed beneficial, but we suspect a timely arrival on non-breeding grounds with the rain-triggered food flush may be beneficial for replenishment of energy reserves.

We presented the first detailed analysis of movements during the annual cycle of intra-African migratory Wahlberg's eagles in different parts of their range, and showed different migratory patterns that match the differences in migration distance, fueling landscape on the way, and differences in the onset of regional rainfall and breeding. Further information is needed to evaluate the ecological aspects that drive the variation in migration patterns across the distribution range of Wahlberg's eagle, including from populations that migrate even shorter distances in West Africa, where seasonal migration of Afrotropical raptors is more pronounced than elsewhere in Africa. Such studies coupled with field work would also aim to better understand the role of rainfall in driving the annual cycle of Wahlberg's eagles, as this may be the most significant driver of their prey population densities. At present, there are indications that Wahlberg's eagles are experiencing population declines across Africa, amounting to a median 74% decline within three generation lengths (Shaw et al. 2024). Such declines may be driven by factors during breeding, migration, or when the birds are in the Central African savannas. The timing of arrival on breeding territories and over-wintering grounds is likely to be a key determinant of reproductive success and survivorship, and migratory phenology and population dynamics of African raptors are quite likely to be affected by changing rainfall (Wichmann et al. 2003, Buij et al. 2013b). Future work needs to question how changing rainfall patterns may affect migration phenology and population dynamics of Wahlberg's eagle and other intra-African migrants.

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handling, and tagging were approved by the Endangered Wildlife Trust Animal Ethics Committee, ethics no. EWTEC2018_002.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ffbg79d47 (Buij et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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