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Research article

A trans-African migrant shows repeatable route choice in males and repeatable timing in females

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Migrant bird populations often show substantial variation in route choice and timing. Determining whether this population-level variation is driven by between-individual differences and/or flexibility within individuals is key to identifying drivers of migration patterns. 'Repeatability' (R, the proportion of population-level variation attributable to between-individual variation) has become a central metric for the relative consistency of individual behaviour. Individual repeatability in migratory route choice and timing is often reported to vary between seasonal and regional contexts and may also differ between demographic groups (e.g. sexes), but interpreting repeatability requires careful consideration of the underlying changes in between- and within-individual variation. We GPS-tracked repeat migrations for eight male and five female Eleonora's falcons *Falco eleonorae* and quantified the magnitude of within- and between-individual variation and the individual repeatability of their seasonal routes and timing at 100 km intervals all across Africa. We did this across both sexes, and then separately for males and females. We found greater between-individual variation in spring routes, albeit with substantial regional fluctuations in both seasons. The greatest between-individual variation in routes occurred during the spring desert-crossing, but this coincided with high within-individual variation, and thus only low repeatability of route choice. Route repeatability instead peaked (R = 0.6–0.8) through the Horn of Africa in spring, and during the rainforest-crossing in autumn. Variation and repeatability of timing was stable across regions, with generally higher between-individual variation and repeatability in spring. Sex-specific analyses suggest males exhibit higher route repeatability, while females exhibit stronger seasonal contrasts in timing repeatability. Such sex differences were unexpected, but overall, between-individual variation and repeatability in routes and timings appear greater where environmental and annual cycle constraints are weaker. Route repeatability is especially high where falcons show fidelity to stop-over sites, or individual barrier-crossing preferences. Individual routines may be acquired through early-life exploration-refinement.

Keywords: annual cycle, behavioural flexibility, individuality, migration, plasticity

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Introduction

For migrant birds not all roads lead to Rome, nor is there a Yellow Brick Road to lead them to an Emerald City. Instead, tracking studies often reveal marked spatial and temporal variation in migration patterns between and within populations, and even within individuals. Unravelling the extent to which population-level variation in migration routes and schedules is caused by consistent between-individual differences (e.g. innate or acquired habits) on the one hand, and within-individual variation on the other, is a key step towards understanding how extant migration patterns are formed, and how migrants cope with rapid environmental change (Alerstam et al. 2003, Carneiro et al. 2019, Åkesson and Helm 2020, Conklin et al. 2021). Accordingly, there is a growing effort to track individual migrants across multiple repeated migrations, and to partition population-level variation into between-individual and within-individual variation in seasonal routes and timing (Stanley et al. 2012, Conklin et al. 2013, Vardanis et al. 2016, Verhoeven et al. 2019).

Individual repeatability (R) can be defined as the proportion of population-level variation (the sum of within and between individual variation) attributed to between-individual variation, so that R > 0.5 indicates that most variation in a trait (e.g. behaviour) is driven by between-individual rather than within-individual differences. Repeatability has become a popular metric to test for 'consistency' in animal behaviour – i.e. whether behaviour varies less within than between individuals (Bell et al. 2009, Wilson 2018, Dochtermann and Royauté 2019), including migration (Vardanis et al. 2011, 2016, Franklin et al. 2022). The ecological interpretation of repeatability, however, also requires careful consideration of the underlying patterns in between-individual and within-individual variation (Wilson 2018, Dochtermann and Royauté 2019). For example, repeatability of spring arrival timing has been estimated at ~ 0.4 for species that arrive in their breeding areas over the span of a few weeks (e.g. pied flycatcher *Ficedula hypoleuca* (Both et al. 2016)) as well as of several months (e.g. black-tailed godwit *Limosa limosa* (Verhoeven et al. 2019)). So, between-individual differences have a comparable importance in driving arrival date variation in each of these two species. However, the greater magnitude of variation across all hierarchical levels suggests that godwits have a greater absolute potential to track phenological changes in their environment through natural selection, early-life learning (i.e. between-individual differences), and life-long flexibility.

Migratory traits typically show substantial within-individual variation and moderate individual repeatability compared to other life history traits (e.g. breeding traits) (Bell et al. 2009). A recent meta-analysis revealed on average moderate individual repeatability (R = 0.41, 95% CI = 0.3–0.5) in the timing of migratory events across 47 bird species (Franklin et al. 2022). Nevertheless, individual repeatability in route choice and timing vary greatly between studies, and within studies between migratory stages (range: < 0.1 – > 0.8, Both et al. 2016, Franklin et al. 2022). One reason for this could be that species are guided by different environmental cues which differ in their spatiotemporal predictability (Brown et al. 2021, Burnside et al. 2021). Geomagnetic inclination, celestial and daylight cues, for example, vary predictably across the globe between years (Åkesson and Helm 2020, Wynn et al. 2022), so that between-individual variation in responsiveness to such cues could result in high individual repeatability of routes and timings. High between-individual variation and repeatability of route choice (R > 0.6) is often associated with fidelity to individually distinct stop-over sites (Hasselquist et al. 2017, Sugasawa and Higuchi 2019). Conversely, repeatability of route choice may be reduced if between-individual variation is constrained by topography (e.g. coastlines, mountain ranges) (López-López et al. 2014, Vardanis et al. 2016), habitat availability (Vardanis et al. 2016, Hasselquist et al. 2017), or atmospheric circulation patterns (e.g. low-level jets, prevailing winds) (Wainwright et al. 2016, Shamoun-Baranes et al. 2017, Vansteelant et al. 2017, Van Doren and Horton 2018). And even when there is substantial between-individual variation in routes or timing, repeatability may still be low if individuals adjust their itineraries to annually variable foraging and weather conditions (Studds and Marra 2011, Conklin and Battley 2011, Burnside et al. 2021). Finally, the repeatability of migratory behaviour may differ between seasons and demographic groups depending on environmental and annual cycle constraints (Carneiro et al. 2019, Verhoeven et al. 2019, Franklin et al. 2022).

The Eleonora's falcon *Falco eleonorae* provides an interesting system to study how migratory conditions affect repeatability in route choice and timing because it is a colonial insular-breeding species with a relatively narrow non-breeding range in northern Madagascar (Kassara et al. 2017). As such, any between-individual variation in migration routes and schedules in a colony will not be biased by large individual differences in (non-)breeding destinations (Cresswell 2014, Brown et al. 2021, Kürten et al. 2022). Previous studies on this species have emphasized variable route choice among individuals (Gschweng et al. 2008, Hadjikyriakou et al. 2020), while others emphasized high within-individual variation in route choice, especially over ecological barriers (Mellone et al. 2011, 2013a). However, the relative importance of within- and between-individual variation in falcon routes and timing remains to be quantified formally. Our aim in this study was 1) to quantify between-individual variation, within-individual variation, and individual repeatability of route choice and timing in adult Eleonora's falcons across seasonal and regional contexts. Furthermore, 2) we asked whether between-individual variation was linked to differential migration strategies between sexes (i.e. are there sex differences in mean route choice and timing?) and 3) whether there are sex differences in between-individual variation, within-individual variation and individual repeatability of routes and schedules. Finally, 4) we assessed whether individual repeatability of route choice and timing were associated with stop-over behaviour by quantifying between- and within-individual overlap in stop-over areas and periods.

Eleonora's falcons cross diverse biomes and wind regimes on their trans-African journeys (López-López et al. 2010, Mellone et al. 2011, 2015, Hadjikyriakou et al. 2020, Vansteelant et al. 2021). Their rate of travel varies greatly between regional and seasonal contexts, which is largely due to landscape-dependent adjustments in daily travel time and orientation behaviour, with little to no individual repeatability or sex differences in travel rates (Vansteelant et al. 2021). We expect low repeatability in seasonal route choice, because even in areas with predictable wind regimes falcons are likely to face some inter-annual variation in wind speed and direction. A high tolerance for wind drift is also likely to increase within-individual route variation, especially over ecological barriers and through areas with strong winds (Mellone et al. 2011, Vansteelant et al. 2021). However, we also know that falcons use a broader migration corridor in spring when they face more supportive winds than in autumn (Vansteelant et al. 2021). We hypothesized that favourable winds allow for greater between-individual variation and repeatability in spring routes, whereas between-individual variation is more constrained along a path of least resistance through opposing autumn winds (Vansteelant et al. 2021).

Furthermore, falcons from our study population stopover in five distinct regions along their seasonal flyway and spend up to two months in pre-breeding areas in northwest Africa (Vansteelant et al. 2021). While Eleonora's falcons likely feed on a variety of large or abundant insects outside the breeding season, it is unclear to what extent they converge in (ephemeral) stop-over hot-spots, or repeatably use distinct stop-over sites. We hypothesized that local terrain knowledge may be more advantageous for falcons in regions where they spend more time, namely the Horn of Africa and the pre-breeding area, and that fidelity to individual stop-over sites may be associated with peaks in route repeatability through those areas. Due to the lack of extensive morphological and behavioural differences outside the breeding season, we did not expect sexes to differ in seasonal route choice and stop-over site use, nor in the repeatability of those behaviours.

The spring migration period in our study population is about twice as long as the autumn migration period (Vansteelant et al. 2021). The early arrival in their pre-breeding areas (Mellone et al. 2013b, Kassara et al. 2021, Vansteelant et al. 2021) may allow for substantial between-individual variation in spring timing, but also within-individual variation that may dampen individual repeatability in spring timing. Autumn departures may vary between individuals depending on their breeding success, but because falcons synchronize breeding with the migration of Afro-Palearctic passerine migrants, breeding failure owing to food shortages in certain years (Gangoso et al. 2020) may trigger colony-wide synchronized departure thus decreasing individual repeatability. Overall, we expect Eleonora's falcons to show low to moderate repeatability in seasonal departures, followed by a decrease in repeatability of timing as falcons flexibly adjust flight times to conditions en route.

Material and methods

Our study system is situated on Alegranza islet in the Chinijo archipelago of the Canary Islands (Fig. 1). We describe trapping and tagging methods, and methods for extracting migration data from the full tracking dataset in the Supporting information with full details in Vansteelant et al. (2021). Out of 19 falcons with migration data, five female and eight male falcons provided data across two to four migrations to assess how between- and within-individual variation shape population-level variation and individual repeatability in their routes and timing (Supporting information).

Testing for sex and individual differences in seasonal departure, arrival, trip duration and travel metrics

We first explored seasonal and sex differences in timing and trip-scale travel metrics by means of ANOVA models including all of the 19 falcons, but only using the first migration cycle we recorded for each bird to ensure independent measurements and a balanced dataset. We then restricted the data to the 13 falcons with multiple tracked journeys, and used linear mixed models (LMMs) to test for sex (fixed effect) and individual differences (random intercepts) in mean departure and arrival dates (using standardized day-of-year of departure/arrival as continuous response variables). We fitted analogous models to test for sex and individual differences in seasonal detour extent (ratio of cumulative travel distance to great-circle distance between start and end location), trip duration (number of days between departure and arrival), and the number of stop-over and travel days per trip (stopovers: daily distance < 100 km, corresponding to roughly three hours of directed flight per day).

Quantifying variation in route choice and schedules

Because flyways are often oriented in a north-south direction, variation in routes and timing is often quantified in terms of the longitudes and dates on which birds cross latitudinal thresholds. To measure variation along the zig-zagged flyway in our study population, we used a distance-based route-averaging approach (Brown et al. 2021). We first calculated the distance from each GPS fix to the colony and then resampled the hourly tracking data by taking the first fix in each interval of 100 km distance to the colony. We consider this to be an appropriate spatial resolution because falcons rarely exceed 100 km h^{-1} during travel so that we can expect to record at least one fix in each 100 km-interval in our hourly data. Next, we calculated individual-mean routes by averaging the latitudes and longitudes at which individual falcons crossed each 100 km interval on their repeated journeys (Supporting information). Analogously, we determined individual-mean schedules as the average day of year (DOY) on which the birds crossed each 100 km-interval. Individual-mean routes/schedules were then averaged across all birds to obtain a population-mean route and schedule, and across all males and females separately to obtain sex-mean routes and schedules (Supporting information).

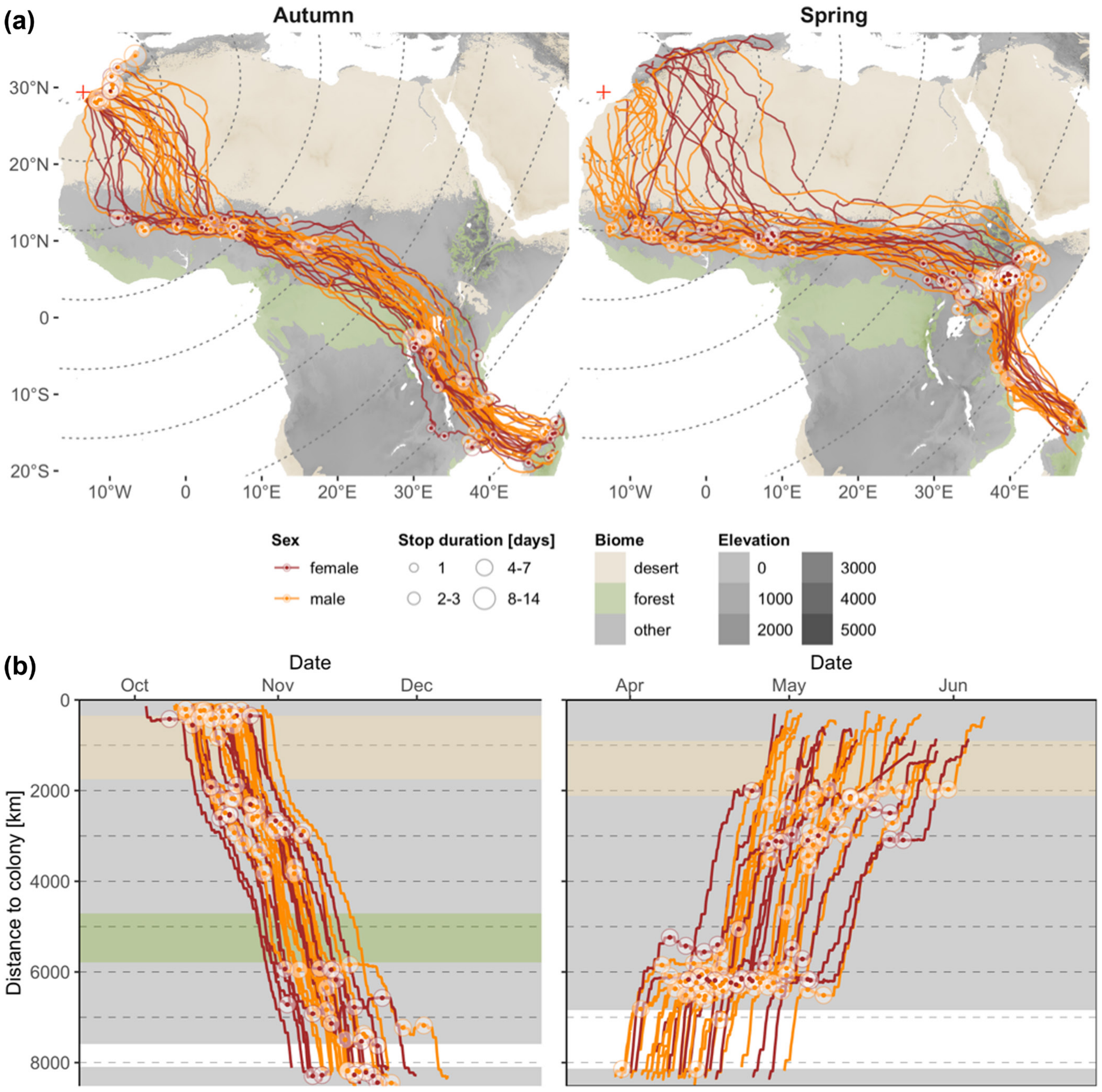

Figure 1. Seasonal migration (a) routes and (b) schedules of eight male and five female Eleonora's falcons that were GPS-tracked across at least two migration cycles each. (a) Red cross shows the position of the breeding colony on Alegranza, with dashed grey curves showing distance to the colony at 1000 km intervals. Biomes are coloured such as to highlight ecological barriers that falcons are known to avoid or to cross relatively fast (i.e. desert, seas/lakes and tropical humid forest), while grey areas predominantly consist of grass-, shrub- and woodland savannahs that may offer feeding opportunities to falcons. (b) Background shading corresponds to biome colours on the map, and is based on the mean distance to the colony at which falcons started and ended each of the major barrier-crossings in each season. (a and b) Note that the size of stop-over points is proportional to the duration of stop-overs on maps (a), but not on timing plots (b).

To determine the 'within-individual route variation' we calculated the average great-circle distance between the recorded trips and their respective individual-mean route in every 100 km-interval (Supporting information). To determine 'within-individual timing variation' we averaged the absolute time differences of each of the recorded trips to their respective individual-mean schedule in every 100 km-interval (Supporting information). Analogously, we calculated 'between-individual route variation' by averaging the distance from the individual-mean routes/schedules to the population-mean route (Supporting information), and 'between-individual timing variation' as the average absolute time difference from the individual-mean schedules to the population-mean schedule in each 100 km-interval (Supporting information). Overall population-level variation was calculated as the average spatial/temporal deviations from the recorded trips to the population-mean route/schedule. Between-individual variation was calculated across all birds (Supporting information) and for each sex separately (Supporting information) as the average deviations of the

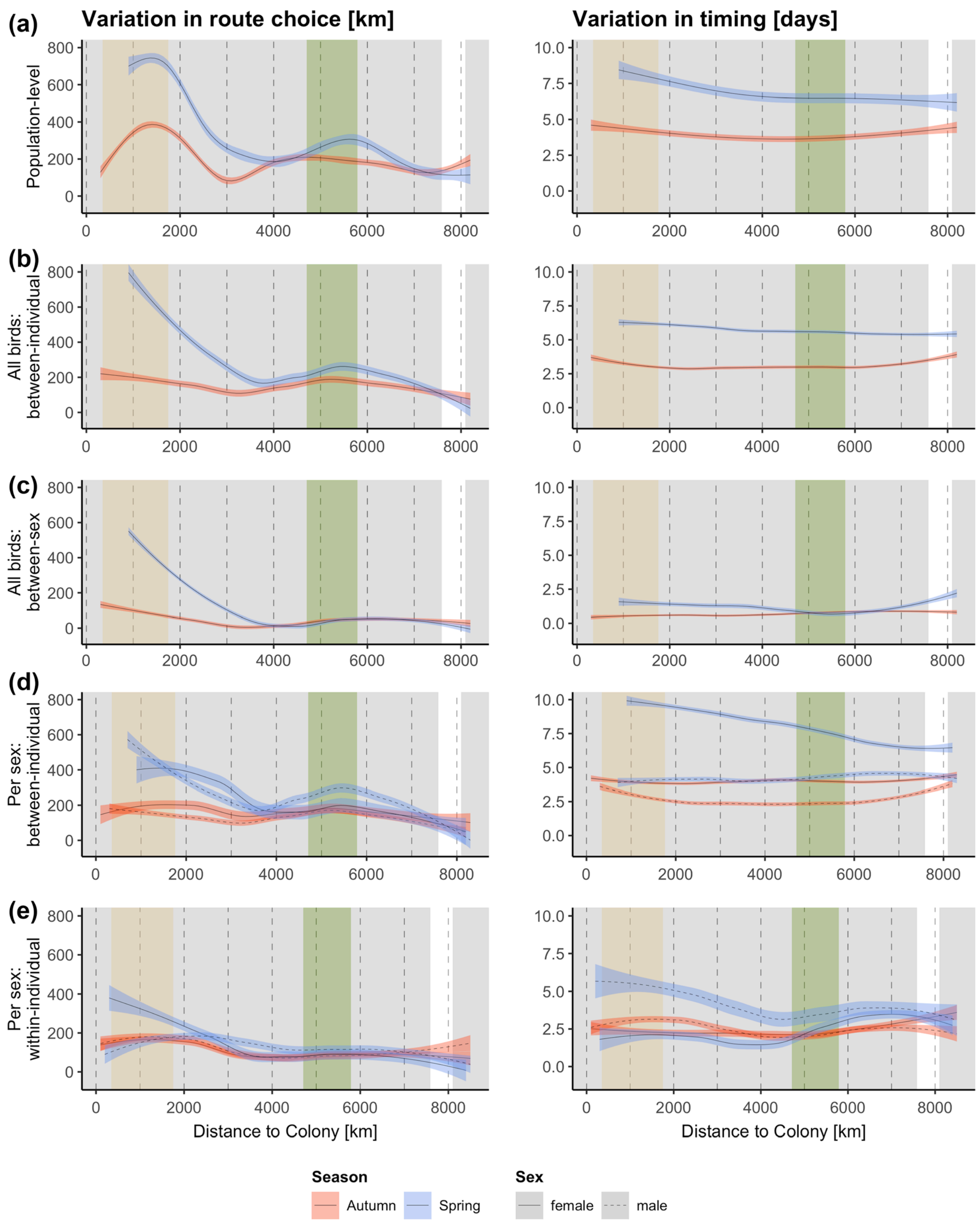

Figure 2. Seasonal and regional patterns in the (a) overall variation, (b) between-individual variation, (c) between-sex variation, (d) between-individual variation within each sex and (e) within-individual variation in migratory route choice (left) and timing (right). Graphs show route and timing variation smoothed across three bins of 100 km distance to the colony across all birds (a)–(c) or for each sex separately (d)–(e). Vertical dashed lines correspond to intervals of 1000 km distance to the colony also shown on maps, with shaded areas indicating the approximate location of autumn barrier-crossings (Fig. 1b for barrier-crossing thresholds in spring).

individual-mean routes/schedules to the corresponding sex-mean routes/schedules. Between-sex variation was calculated by averaging the deviations of the sex-mean routes/schedules to the population-mean route/schedule (Supporting information). We then applied a standard loess-smoothing to visualize how variation in routes and timing change throughout the falcons' seasonal flyway at population level, between sexes, between individuals (across all birds and separately per sex) and within individuals (per sex) (Fig. 2).

Repeatability of routes and schedules

We used a mixed linear modelling approach to estimate repeatability in route choice and timing at every 100 km interval in each season at the population-level, and for each sex separately. Repeatability (R) was estimated as the proportion of population-level variance explained by between-individual (i.e. group) variance (V_G) over the sum of between-individual and residual (V_R; i.e. within-individual) variance: $R = V_G/(V_G + V_R)$. To test for repeatability in routes and timing, we must consider not only the magnitude but also the direction in which the recorded tracks deviate from the reference route and schedule. Therefore, we arbitrarily attribute negative signs to spatial deviations if the recorded trips were located to the south or west of the reference route, and to temporal deviations if tracks crossed the 100 km intervals earlier than the reference track.

To quantify repeatability across all birds, spatial and temporal deviations from the population-mean were modelled as a function of sex (fixed effect) while allowing for randomly varying intercepts per individual. In an early stage of our analyses, we also allowed for randomly varying intercepts per year, but we found little to no evidence for substantial annual effects in either route choice and timing, and so opted not to include year effects in our models to reduce model complexity. Repeatability at individual level and per sex was then quantified as the proportion of the variation explained by sex and individual effects, respectively. Next, we quantified individual repeatability separately for males and females by modelling the spatial and temporal deviations from the sex-mean routes/schedules as a function of only random effects (individual). Using the rptR package (www.r-project.org, Stoffel et al. 2017), the significance of individual repeatability was estimated using a likelihood ratio test, and confidence intervals (CI) for repeatability estimates were obtained by bootstrapping models across 1000 iterations (Sugasawa and Higuchi 2019, Verhoeven et al. 2019). For interpreting results, it is important to recognise that repeatability estimates often come out as statistically significant even when the CI is very broad and/or deviates only slightly from 0. Therefore, we attribute greater 'ecological relevance' to repeatability estimates whose lower CI deviates more from 0 across multiple 100 km-intervals.

Spatial and temporal overlap of stop-overs within and between individuals

Falcons from our study population engage in seasonal loop migrations, stopping-over in five distinct geographical clusters: northwest Africa (22–36°N, 16–3°W,), the western Sahel (15°W–20°E, 7–15°N), and the East-African plains in autumn (18–1°S, 25–45°E) and the Horn of Africa (4°S–13°N, 25–45°E) and the western Sahel in spring (Supporting information). After their arrival to northwest Africa in April–May, falcons spent about 1–2 months on the mainland and making short excursions to the colony, before finally resettling on territories in June–July (Supporting information). After exploring a range of possible thresholds, we defined the final return to the colony as the first day after which falcons visited Alegranza daily for at least seven consecutive days. We chose this seven-day threshold because at lower thresholds, the return to the colony was often estimated too early, for example in the case of individuals that spent a few days on the Canary Islands, but still returned to pre-breeding sites in northwest Africa for long periods before finally settling on their territories. To assess between individual differences and within-individual consistency of stop-over areas and periods we defined stop-over/pre-breeding periods as the time periods between the first and last stop-over day of a falcon within the aforementioned latitudinal and longitudinal boundaries encompassing each region. Stop-over and pre-breeding areas were calculated as 90% bivariate normal kernels per cluster, based only on the locations recorded during stop-over days, using the adhabitatHR package (Calenge 2006). Falcons did not make any other localized stop-overs over distances of 1000–2000 km between each of these regions (Fig. 1, Supporting information).

To quantify spatial overlap in migratory stop-overs and pre-breeding areas we calculated the Bhattacharyya affinity (BA, 0–1) between each pair of stop-over areas within each cluster. We then averaged BA values across all unique pairwise comparisons within each individual per geographical cluster as a measure of within-individual spatial similarity. Analogously, for each individual we calculated the average BA relative to other individuals to obtain between-individual spatial similarity estimates.

To calculate temporal overlap between stop-over periods we calculated the proportion of matching days in the combined stop-over date range for each pairwise comparison within each geographical cluster. Analogous to spatial similarity estimates, temporal overlap estimates were then averaged within and between individuals. We then used ANOVA to test for differences in the within- and between-individual spatial similarity and temporal overlap of stop-overs between the five stop-over clusters and the pre-breeding area. Finally, we repeated the above procedure for males and females separately, and then used t-tests to compare similarity and overlap metrics between sexes within each of the six areas.

Results

Sex and individual differences in seasonal departure, arrival, trip duration and travel metrics

We did not find any significant differences in departure and arrival timing, trip duration, and stop-over days across all four combinations of sex and season (Supporting information).

Falcons travelled longer routes, detouring more from the great-circle route between their seasonal destinations in spring than in autumn (with seasonal differences being less pronounced among females due to one 'outlier' female with protracted detours in autumn). Despite this, falcons completed spring migration in the same number of travel days as their shorter autumn migration routes (Supporting information).

The lack of sex differences in seasonal timing and travel rates was further corroborated by season-specific LMMs based on individuals with repeated migrations (Supporting information, repeatability values indicated that sex never explained more than 10% of variation in any of the performance metrics in either season). These models showed with high certainty that autumn stop-over duration was highly repeatable (R > 0.5, p = 0.01, Supporting information). Furthermore, models indicated moderate individual repeatability (R > 0.4) in autumn arrival, spring departure and spring stop-over duration, although these results were not statistically significant (p = 0.5–0.6, Supporting information).

Variation and repeatability in route choice

Falcons showed large regional fluctuations in route variation at all levels, with generally higher population-level and between-individual variation in spring than in autumn (Fig. 2a–b). Population-level route variation clearly peaked over the desert in both seasons, albeit with much greater magnitude in spring (Fig. 2a). The autumn migration corridor widened between 4000 and 6000 km from the colony (Fig. 2a), corresponding to the passage of the equatorial rain forest belt (Fig. 1) and narrowed again towards the passage of the Mozambique Channel. In spring, the falcons' migration corridor widened between 5000 and 7000 km from the colony (Fig. 2a), corresponding to the passage through the Horn of Africa and the following longitudinal flights over the eastern Sahel-Sudan zone (Fig. 1).

In general, fluctuations in population-level route variation (Fig. 2a) seemed to be associated with fluctuations in between-individual variation (Fig. 2b) more than within-individual variation (Fig. 2e, but note large increase of within-individual

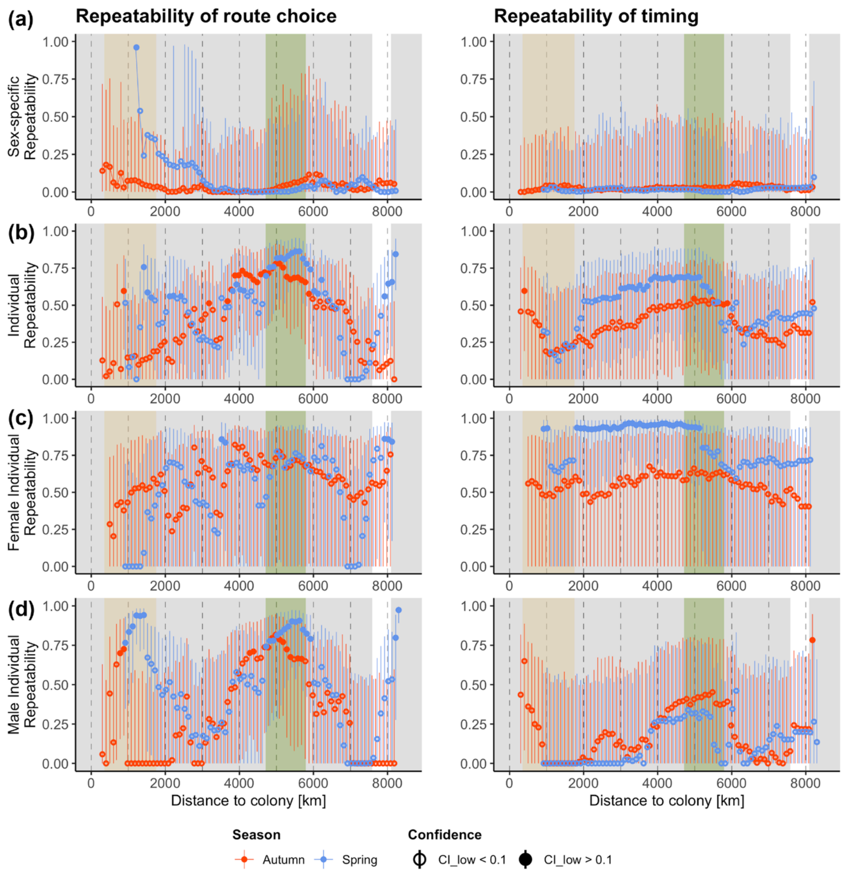

Figure 3. Repeatability in Eleonora's falcon route choice (left) and timing (right) at the level of (a) sexes and (b) individuals and at individual level modelled separately for (c) females and (d) males. Repeatability (points) was estimated using a single mixed effects model across all birds (a)–(b) or using a separate model for each sex, with random intercepts per individuals (c)–(d). In all graphs whiskers show 95% confidence intervals (CI) for repeatability estimates. We attribute greater ecological relevance to significant repeatability estimates if the lower end of CI clearly deviates from zero (CI_low > 0.1, solid points), and especially if such a signal persists across a considerable distance (e.g. individual repeatability in route choice between 4000–6000 km from the colony in both seasons). Open points indicate repeatability estimates for which lower end of CI does not exceed 0.1.

route variation of females over the desert in spring). Between-individual variation seemed to be caused in part by sex differences in route choice over the desert, with particularly large differences in spring desert-crossings (Fig. 1, 2c), but not elsewhere. Indeed, when calculated separately for males and females, the seasonal difference in between-individual variation in trans-Saharan routes was much smaller, though still substantial (Fig. 2d). Furthermore, the spring peak in between-individual variation between 5000–7000 km from the colony was due to large between-individual variation in route choice of males, more than females.

Across all birds, we found that sex differences explained most of the variation in trans-Saharan route choice during spring (i.e. a strong increase in repeatability from 2000 to 1000 km from the colony), but nowhere else (Fig. 3a). Individual differences explained substantial amounts of the remaining variation in route choice between 4000–6000 km from the colony in both seasons (Fig. 3b, $0.5 < R$ 0.8 across several 1000 km with lower end of CI > 0.25). Note that peak repeatability estimates were quite similar in both seasons despite the greater between-individual variation in spring (Fig. 2b), due to within-individual variation also being larger in spring. In autumn, the broad desert-crossing corridor (Supporting information) was associated with slightly increased within- as well as between-individual variation, and no repeatable route choice (Fig. 2b, d, 3b). Individual route repeatability remained low as falcons converged through a narrow corridor over the western Sahel, gradually increased as falcons diverged along repeatable routes across the tropical rainforest belt (Fig. 2b, 3), and finally reduced again as they converged into the Strait of Mozambique (Fig. 3b). In spring, falcons started out from highly repeatable positions on Madagascar, but route repeatability quickly dropped over the Indian Ocean. After they reached mainland Africa at about 7000 km from the colony, individual repeatability sharply increased again as birds took distinct routes through the Horn of Africa and the eastern Sahel, and converged again in a narrow latitudinal band over the western Sahel. Individual repeatability increased again over the desert, but with very broad CI deviating only slightly from 0.

Sex-specific analyses showed that the pronounced regional fluctuations in individual repeatability of route choice were due almost entirely to males, including a much stronger signal for individually repeatable route choice over the desert by males in spring (Fig. 3d). Females, on the other hand, showed a noisier signal, with generally moderate to high route repeatability estimates, but very broad CI that hardly deviated from 0 (Fig. 3c). Although females showed particularly large between-individual variation in spring desert-crossings – larger than males (Fig. 2d) – female route choice was not repeatable here due to the great within-individual variation in their easterly desert-crossing routes (Fig. 1, 2e, Supporting information).

Variation and repeatability in seasonal timing

Variation in the timing of falcon migrations was in the order of days to weeks. Compared to the variation in routes, population-level and between-individual variation in timing showed a markedly more stable signal throughout each season (Fig. 2a–b, right), with substantially greater variation at both levels in spring than in autumn. Within individuals, males showed particularly high variation in spring timing (Fig. 2e). There was a mild but notable increase in population-level variation in timing from about 3000 km from the colony towards the end of spring migration (Fig. 2a), which could be associated with an increase in within-individual variation (Fig. 2e).

Greater between-individual variation in spring was not associated with greater between-sex variation (Fig. 2b–c). In fact, timing hardly varied between sexes in either season (Fig. 2c), and between-individual timing variation was greater in spring than autumn for both sexes (Fig. 2d). However, within each season females showed greater between-individual variation in timing than males, and the seasonal difference in between-individual variation was greater for females than for males (Fig. 2d). In addition, males showed much greater within-individual variation in spring than in autumn, and compared to females in either season.

Consistent with the weak variation we found in timing between sexes, we found no evidence for sex-specific repeatability in timing (Fig. 3a, right). In autumn, individual repeatability in timing ranged from low to moderate, with the strongest evidence for significant repeatability between 4000–6000 km from the colony, where the lower ends of CI deviated moderately but quite consistently from 0. In spring, we found moderate to strong and significant individual repeatability in timing ($R = 0.5$–0.7, Fig. 3b-right) between 2000 and 6000 km from the colony.

Sex-specific analyses showed that the pronounced seasonal difference in the individual repeatability of timing was due entirely to females, which showed moderate ($R > 0.45$–0.5) to very high ($R = 0.9$, Fig. 3c-right) repeatability in autumn and spring, respectively. By contrast, and despite the fact that males also showed seasonal contrasts in between-individual variation of timing, males showed low (even $R = 0$) repeatability in both seasons (Fig. 3d-right).

Stop-over site use and between- and within-individual overlap in stop-over areas and periods

The consistency with which falcons stopped-over varied greatly between the five migratory stop-over clusters and the pre-breeding area (Fig. 4). The most regularly used migratory stop-over area was the Horn of Africa during spring migration, where 10 of 13 individuals stopped on all their recorded trips (Fig. 4a), and where stop-overs lasted marginally longer than in other areas (Supporting information). In general, within-individual overlap in stop-over areas was greater in spring than in autumn, and within each season greater in areas closer to the colony (Fig. 4). Females showed greater between-individual overlap in stop-over areas than males in the Horn of Africa in spring, and vice versa over the Sahel in spring (Supporting information). Females generally showed lower between-individual overlap in stop-over periods than

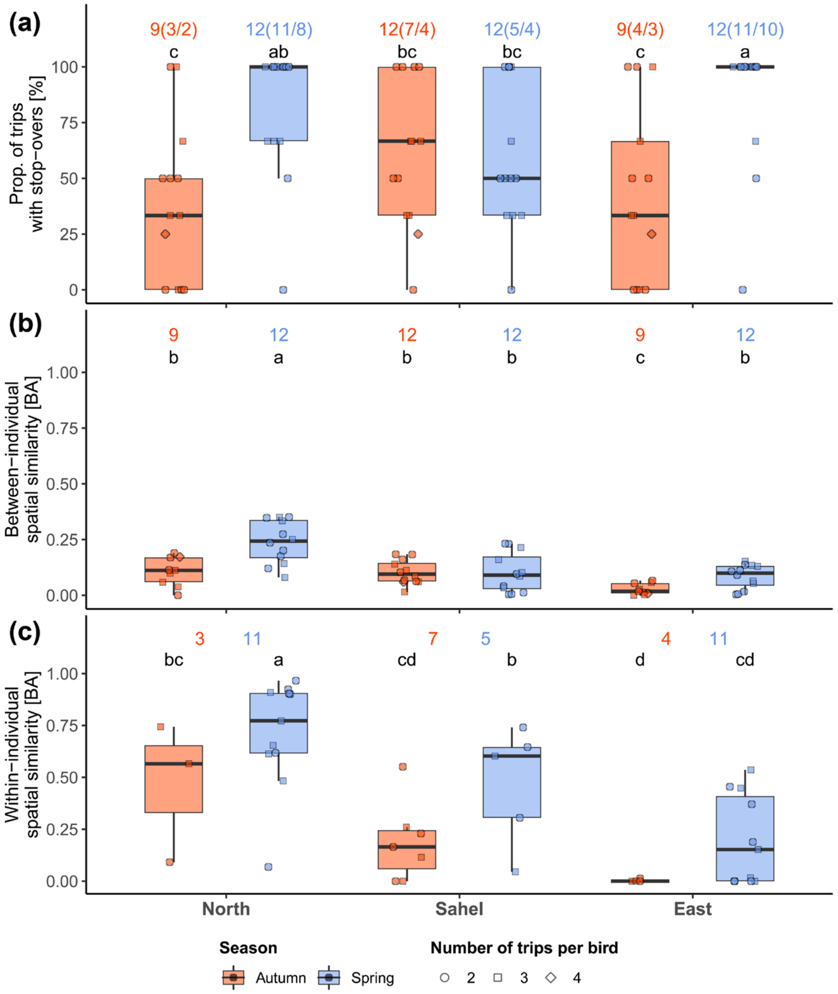

Figure 4. (a) Individual use of stop-overs, and (b) between-individual spatial similarity and (c) within-individual spatial similarity of seasonal stop-overs in northwest Africa, the western Sahel and East Africa, respectively. (a) Coloured labels 'x(y/z)' indicate sample sizes, with 'x' being the number of falcons that stopped-over during at least one migration (i.e. the sample size for between-individual comparisons in b), 'y' being the number of falcons that stopped-over during at least two migrations (i.e. the sample size for within-individual comparisons in c), and 'z' being the number of falcons that stopped-over on all of their recorded journeys. Black letters are Tukey grouping factors, whereby distinct labels indicate significant differences ($p < 0.05$) in mean stop-over use and spatial overlap between the six seasonal stop-over regions.

males in all areas except in SE Africa in autumn (Supporting information). A more detailed summary of stop-over analyses is provided in the Supporting information

Discussion

By tracking individual falcons over repeated migrations, we aimed to determine how changes in within- and between-individual variation shape patterns of individual repeatability in route choice and timing across regional and seasonal contexts. In our study system, falcons use a relatively small breeding and wintering range (Gangoso et al. 2015, Kassara et al. 2017), yet their trans-African migration corridor is hundreds to several thousand kilometres wide in places, and their seasonal migration window spans up to two months (Vansteelant et al. 2021). Our results show that this tremendous population-level variation is associated with complex patterns of between- and within-individual variation, and thus repeatability, in migration routes and timings, and that the repeatability of behaviour also differs between the sexes. Admittedly, our results are based on a small sample of individuals with repeated tracks ($n = 13$). Therefore we focus on particularly large regional, seasonal and sex-specific differences in the variability and repeatability of routes and timings.

Individual repeatability of route choice varied depending on seasonal and regional contexts, which we believe is largely due to differences in the falcons' orientation behaviour across different landscapes and seasonal wind regimes (Vansteelant et al. 2021). For example, our results corroborate our hypothesis that the migration corridor is narrower in autumn than spring due to lower between-individual variation in route choice. This was expected because opposing winds constrain falcons along the path of least resistance towards the Strait of Mozambique and into Madagascar during autumn, whereas supportive spring wind fields allow for greater diversification of routes between individuals (Vansteelant et al. 2021). By contrast to route choice, seasonal migration timing showed more stable population-level and between-individual variation across distinct regions. We also found that the broader spring migration window was associated with greater between-individual variation and repeatability in spring than in the shorter autumn migration period. This was expected because falcons have a protracted pre-breeding period (Mellone et al. 2013b, Vansteelant et al. 2021), suggesting they face only weak timing constraints in spring, whereas in autumn we might expect more synchronised departures between individuals depending on annual breeding conditions at the colony (Gangoso et al. 2020).

Sex differences in seasonal migrations, and individual repeatability

As expected, we found little differences in average route choice and timing between the sexes. The only exception was that female falcons tended to cross the desert along more easterly routes than males in spring, seemingly due to unanticipated sex differences in pre-breeding site selection. More specifically, males, who choose territories and nest sites in this species (Walter 1979, Gangoso et al. 2015), were observed to make a quick visit to the breeding colony before settling in pre-breeding areas, likely explaining why they crossed the desert further west, while females returned to pre-breeding areas in mainland nortwest Africa by taking a more direct route. In addition, males more often made stop-overs in nortwest Africa in autumn, which we suspect is due to the males' greater chick-provisioning effort in summer, limiting their ability to lay down energy reserves for migration before leaving the colony (Gangoso and Figuerola 2019, Gangoso et al. 2020).

Perhaps our most striking finding is that sexes contributed differently to patterns of individual repeatability of routes and timing. Regional peaks in individual route repeatability were exhibited mostly by males, whereas seasonal patterns in the repeatability of timing were exhibited most strongly by females. While numerous tracking studies have looked for differences in the mean timing of migration between sexes, few studies have investigated whether the variation and repeatability in timing or other migration traits differs between sexes. Those that did found that females showed more repeatable timing than males in both Icelandic whimbrels *Numenius phaeopus islandicus* (Carneiro et al. 2019) and Scopoli's shearwaters *Calonectris diomedea* (Müller et al. 2014), while the mean timing only differed between sexes in the latter species.

Repeatability of route choice

There was a notable peak in individual route repeatability between 4000–6000 km in both seasons. In autumn, this peak was due in part to two individuals (one male, one female) that directly crossed the tropical rainforest on consecutive journeys, but also due to differences in routes among individuals that detour around this barrier (Supporting information). This is the only stage of the autumn migration where falcons face weak winds, allowing for a temporary diversification of routes between individuals until between-individual variation gradually decreased again through adverse autumn winds over southeast Africa, and through the Mozambique Channel (Vansteelant et al. 2021). The midway peak in between-individual route variation and route repeatability during spring was associated with the passage through the Greater Horn of Africa, where falcons from all across the breeding range stop-over in spring (Mellone et al. 2013a, Hadjikyriakou et al. 2020, Vansteelant et al. 2021). Following a sharp reduction in route repeatability over the ocean in spring (due to within-individual flexibility in over-water route choice; c.f. Mellone et al. 2011), falcons diverged along repeatable routes again over mainland Africa. This is partly due to two individuals (one male, one female) that consistently took the GCR back to the Canary Islands across East Africa, while all other individuals detoured 500–1000 km to stop-over for roughly a week in the Horn of Africa (Vansteelant et al. 2021). In addition, individuals from our study population appeared to consistently use individual stop-over areas within this region. This supports the notion that learnt stop-over sites act as anchoring points that lead to repeatable route choice, as has been found in other species (Hasselquist et al. 2017, Sugasawa and Higuchi 2019). However, more work is needed to determine to what extent falcons with different breeding origins use overlapping stop-over areas within the Horn of Africa, as they do in the species' restricted Malagasy non-breeding range (Kassara et al. 2017).

We are unsure about why route repeatability differs between sexes. However, higher route repeatability of males through the Horn of Africa is associated with less overlap in stop-over areas among individual males than females, which again affirms the notion that stop-over site fidelity increases individual repeatability in route choice. The females' lower route repeatability over the desert in spring, despite comparable between-individual variation in both sexes, was due to a particularly high within-individual flexibility in female routes (Supporting information). One male that also returned over the central Sahara in spring showed similar flexibility as females, with desert-crossing routes hundreds of kilometres apart. This suggests that sex differences in within-individual route variation are not driven by innate sex differences per se. Instead, falcons that cross the desert along more eastern routes in spring may simply have more 'room' to adjust routes to variable wind conditions between trips. Similarly, female Scopoli's shearwaters show less repeatable migration distances (a proxy for route choice) than males, and this seems to be related to differential non-breeding site selection between sexes, with females having more room to alternate routes out of their non-breeding areas depending on variable wind conditions (Müller et al. 2014).

Repeatability of timing

Many long-distance migrants show moderate repeatability in migration timing. However, it is uncommon for adults to show greater population-level and between-individual variation in timing during spring than autumn migration. Verhoeven et al. (2019) found greater between-individual variation in spring migration timing of adult black-tailed godwits than we found for Eleonora's falcons, particularly during the first stage of their migration, with up to 4–5 months difference in the timing of individual migrations from west African non-breeding grounds to south Iberian staging sites. Thereafter, godwits greatly reduce between-individual variation in spring timing, and eventually arrive to breeding areas over the course of ~ five weeks. That is still greater than observed in most other migrants (Verhoeven et al. 2019), and similar to what we found for Eleonora's falcons. In contrast to godwits, however, the migration schedule of Eleonora's falcons did not tighten as birds approached their (pre)-breeding areas. That between-individual variation in timing did not decrease along the flyway is likely due to the long pre-breeding period that buffers against carry-over effects of spring arrival dates onto breeding. By contrast, the relatively narrow autumn migration window is most likely due to falcons departing shortly after breeding (Mellone et al. 2013b, Kassara et al. 2021, Vansteelant et al. 2021). Autumn departures could thereby vary more between years than between individuals due to annual variation in climate-driven food availability and breeding success on the Canary Islands (Gangoso et al. 2020).

Interestingly, repeatability of spring timing was greater mid-way migration, than at the start or end. Females in particular showed extremely high repeatability in timing of trans-Sahelian flights ($R > 0.9$), due to a sharp drop in within-individual flexibility of timing after passing through the Horn of Africa, until making irregular stop-overs prior to the final desert-crossing. This suggests that their departures from Madagascar are mediated by more variable cues than departures from the Horn of Africa. Departures from Madagascar might be mediated by the northward shift of the Inter-Tropical Front that signals the end of the wet season in northern Madagascar and the onset of spring rains in the Horn of Africa and the Sahel (Moreau 1972, Mellone et al. 2013a, Vansteelant et al. 2021), as well as the availability of supportive winds to cross the Indian Ocean (Alerstam 2011, Shamoun-Baranes et al. 2017).

Implications for migratory development

Although repeatability is often considered to present the upper bound of heritability of behavioural traits (Bell et al. 2009, Vardanis et al. 2016, Dochtermann and Royauté 2019) it is important to recognise that high repeatability in behaviours like route choice and timing need not result from innate differences. An alternative possibility is that early-life experiences lead to the establishment of differential migratory habits between individuals. In fact, cross-sectional studies suggest that Eleonora's falcons do not establish adult migration routines until after their first autumn and spring migrations (Gschweng et al. 2008, Mellone et al. 2013a, Hadjikyriakou et al. 2020). Therefore, differential route choice between individuals may emerge from exploration-refinement learning, which appears to be a common developmental pathway in long-lived birds (Sergio et al. 2014, Campioni et al. 2019, Loonstra et al. 2020), and has also been hypothesized to shape large between-individual differences in timing of some species (e.g. godwits, Verhoeven et al. 2019).

Despite substantial differences in route choice between individuals in our study, previous work based on the same data revealed little to no individual differences in the seasonal travel metrics of Eleonora's falcons (Vansteelant et al. 2021). This suggests that the individual differences we found in terms of route choice and timing do not result in differential travel performance between falcons, and are unlikely to have any carry-over effects on breeding success. However, our study is biased to breeding adults, and may underestimate the full range of between-individual variation that can arise from exploration-refinement learning in this species. Longitudinal tracking from fledging to adulthood would allow a deeper understanding of how individual migration routines develop with age and experience, and how innate factors such as sex mediate this development.

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Author contributions

Wouter M. G. Vansteelant: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Laura Gangoso**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Duarte S. Viana**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Judy Z. Shamoun-Baranes**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Jordi Figuerola**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Raw tracking data are stored in the UvA-BiTS database (www.uva-bits.nl). Pre-processed data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1rn8pk0zp (Vansteelant et al. 2023).

The code for reproducing our analyses is provided through the Github directory of WMGV (https://github.com/Wouter-Vansteelant/Vansteelant-etal-2023-JAvianBiol). The code automatically installs all required packages and the Dryad and Github repositories contain readme-files with instructions for obtaining open access third party data.

Supporting information

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

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