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Author for correspondence:
Susanne Åkesson
e-mail: susanne.akesson@biol.lu.se

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Negotiating an ecological barrier: crossing the Sahara in relation to winds by common swifts

Susanne Åkesson, Giuseppe Bianco and Anders Hedenström

Centre for Animal Movement Research, Department of Biology, Lund University, Ecology Building, 223 62 Lund, Sweden

SÅ, 0000-0001-9039-2180; GB, 0000-0002-6144-2959; AH, 0000-0002-1757-0945

The Sahara Desert is one of the largest land-based barriers on the Earth, crossed twice each year by billions of birds on migration. Here we investigate how common swifts migrating between breeding sites in Sweden and wintering areas in sub-Saharan Africa perform the desert crossing with respect to route choice, winds, timing and speed of migration by analysing 72 geolocator tracks recording migration. The swifts cross western Sahara on a broad front in autumn, while in spring they seem to use three alternative routes across the Sahara, a western, a central and an eastern route across the Arabian Peninsula, with most birds using the western route. The swifts show slower migration and travel speeds, and make longer detours with more stops in autumn compared with spring. In spring, the stopover period in West Africa coincided with mostly favourable winds, but birds remained in the area, suggesting fuelling. The western route provided more tailwind assistance compared with the central route for our tracked swifts in spring, but not in autumn. The ultimate explanation for the evolution of a preferred western route is presumably a combination of matching rich foraging conditions (swarming insects) and favourable winds enabling fast spring migration.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

In the Palearctic–African migration system billions of birds have evolved to perform long migrations, including the crossing of ecological barriers like the Mediterranean Sea and the Saharan and Arabian deserts [1–3]. The migration routes used by bird migrants may have evolved as a response to the availability of suitable stopover sites, competition, topography and predominant wind regimes [4]. Barriers cause a substantial challenge to migrating birds, enforcing prolonged flights during crossing [5–7], or extended flights circumventing the barrier [8,9]. For migrating landbirds, the Sahara Desert and the Mediterranean Sea are considered a major barrier, requiring adaptations in terms of flight schedule [7,10–13], route selection (e.g. [14,15]) and the need for extensive fuelling [16–18]. Initially, landbird migrants were assumed to cross the Sahara Desert in one prolonged flight lasting several days, while later findings suggested an intermittent strategy with intermediate daytime stops and nocturnal flights (e.g. [7,10,11,19]). Nocturnal migrants may, however, opportunistically extend their flights into daytime, depending on the wind conditions encountered during the Sahara crossing [20]. However, depending on migration strategy and environmental conditions, substantial interspecific variation in fuelling, flight schedule and stopover behaviour have been observed in songbird migrants when crossing the Sahara [21].

Avian migrants are highly influenced by winds, which may vary from still air up to several times the airspeed of the birds themselves, and consequently, winds may change the potential flight range substantially [22]. Winds may, therefore, impose substantial energy and time costs or benefits, depending on

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how birds time their migratory flights relative to them [23–26]. Departing bird migrants have been shown to time their flight relative to situations with tailwind conditions (e.g. [27]), and to compensate for drift caused by winds during migratory flights (e.g. [28–31]).

If time of migration is an important objective the rate of fuelling should also be considered [32]. The best route for a bird migrant across a barrier whose objective is to achieve a fast overall migration should be one where the combined effects of food availability for fast fuelling and wind-assisted flights result in the fastest possible migration. In general, migration is slower in autumn than in spring, suggesting an elevated component of time minimization in spring compared with autumn [33]. A corollary from this is that in autumn we may expect migrants to time departures from stopover mainly with respect to the current tailwind assistance, while in spring, there should be an interaction between fuelling rate and winds. However, before a barrier there is a minimum expected stopover duration required to deposit enough fuel to cover the distance across the barrier [34]. Seasonally differing migration strategies may, therefore, lead to different routes, where a largely energy-selected autumn migration mainly depends on wind assistance on a broad front, while a time-selected spring migration that depends on the interplay between fuelling conditions and winds result in a narrow front along more specific routes. Further to this, latitudinal segregated populations often show shifted annual schedules with respect to timing of breeding and migration, where more northerly breeding birds migrate later than those breeding in the south [35]. Different populations may, therefore, be exposed to seasonally changing environmental conditions with respect to food availability and winds. Insectivore migrants breeding in the north can be expected to show some degree of time-selected autumn migration in order to emigrate from an area where the insect food source may decline rapidly.

The common swift (*Apus apus*) is an aerial insectivorous bird migrating between breeding areas in Europe and Asia and wintering areas in Africa south of the Sahara [15,18,36,37]. On migration, common swifts have been proposed to cross the central parts of the Sahara Desert on a broad front [18,37]. More recent trackings of common swifts breeding in south Sweden using miniature geolocators, revealed a substantial detour of migration routes both in spring and autumn by approximately 40–50%, indicating the birds avoid the Sahara Desert at its widest parts, with a preference to use a western route involving passage of the Iberian Peninsula in autumn and the use of a major stopover site in West Africa in spring [15]. An extreme aerial bird species such as the common swift, living the major part of its life on the wings [36,38–41], and showing extreme morphological and physiological adaptations to cost-efficient flight [42], should be constantly exposed to winds and expected to respond to winds in adaptive ways depending on season. Our study comprises latitudinal segregated populations, allowing us to test for differences in migration strategy related to time of season for migration.

We investigated if Swedish common swifts perform direct flights across the Sahara Desert in both spring and autumn, and if they cross the Sahara on broad or narrow fronts, respectively ([18]; cf. [15]). We explored the question of whether the spring stopover in West Africa [15] is related to favourable wind or fuelling conditions. We hypothesized that if winds are the reason for the use of this western route in spring, we expected the birds to time the departure relative to favourable wind conditions, and to show a higher speed of migration across the Sahara compared with birds selecting more easterly routes. We investigated whether the West African spring stopover is mainly related to the need to refuel before the barrier crossing, the birds should stay for a minimum duration after arriving there and remain in the area also under favourable wind conditions. To maximize the overall migration rate we predicted that common swifts should minimize the time spent at stopover and use routes providing the highest wind assistance. To answer these questions we have analysed a substantial number of tracks (72) concerning the migration of common swifts breeding in Sweden and recorded between 2009 and 2014 by miniature geolocators.

2. Material and methods

(a) Study sites and capture of birds

We equipped 157 adult common swifts with miniature geolocators (GLS; [15]), in six breeding populations in Sweden and recaptured 81 (51.6%) birds whose movements were recorded for 1 year during the study period 2009–2014. Out of these, we used GLS tracks from 72 individuals to evaluate the migration across the Sahara in autumn (70 tracks) and spring (70 tracks; table 1). Nine birds were excluded from this analysis due to battery failure at recapture or battery running out prematurely, not covering the full seasonal movement. The adult breeding swifts were captured at the nest location by mist nets arranged outside the nest entrance or by catching them in the nest [15]. The breeding locations were distributed across Sweden between the most northern location at Hakkas in Swedish Lapland (66.92° N), two in central Sweden (Falun 60.55° N; Östhammar 60.28° N) and three locations in south Sweden, Ås (56.24° N) near Ottenby at the island of Öland, Lund (55.71° N) and Skurup (55.47° N). Thereafter, the birds from different sites were combined into a north, central and south population, as outlined above, for further analyses. The recapture rate in particular years varied from 12.5% to 100% for the different sites, demonstrating some degree of variation, and also a high average recapture rate (51.5%) as compared to other, e.g. geolocator, studies (average recapture rate of 31% for great snipes *Gallinago media*, [43]). The total number of captured and recaptured individuals per study population and year are given in table 1.

We timed the attachment of geolocators to late breeding stages when the young were near to leaving the nest for migration departure or at a time when the adults were still active feeding the young (second half of the feeding period). The adult birds were later recaptured upon arrival or at the same stage of breeding the second year.

(b) Geolocation

For the first year (South Sweden; 2009–2010), we used eight archival Mk10 geolocators from the British Antarctic Survey (BAS), while for the remaining period we used 149 archival light loggers (Intigeo-W65B1) from Migrate Technology Inc. All geolocators (GLS) used were without a stalk. The light loggers were attached to the common swifts with a full body harness, with three loops around the neck and each wing, respectively [15]. The mass of the geolocators including harness, 0.8–1.3 g depending on the model, was never above 3% of the birds' body mass [15]. We had carefully evaluated the attachment method and monitored the effect on breeding birds in the initial study year (summer 2009) before attachment to birds in the same colony over winter (2009–2010). We did not observe any negative effects of attachment to the breeding performance, return rate and timing of migration [15]. In later years (2010–2014), we attached geolocators

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Table 1. Location of breeding areas, year of capture and number of trapped and recaptured common swifts attached with miniature geolocators (GLS) in three populations in Sweden (south, central and north) for which the Sahara crossing was recorded in autumn and spring.

population	site	latitude (N)	longitude (E)	year capture	logged (N)	year recaptured	recaptured (N)	recapture rate (%)	included	autumn routes (N)	spring routes (N)
north	Hakkas	66.92	21.55	2010	12	2011	7	58.3	6	5	6
north	Hakkas	66.92	21.55	2012	24	2013	13	54.2	12	11	12
central	Falun	60.55	15.78	2012	16	2013	4	25.0	4	4	4
central	Falun	60.55	15.78	2013	10	2014	5	50.0	3	3	2
central	Barkö	60.28	18.26	2009	2	2010	1	50.0	1	1	1
central	Barkö	60.28	18.26	2010	12	2011	7	58.3	6	6	6
central	Barkö	60.28	18.26	2012	7	2012	7	100.0	6	6	6
south	Ås	56.24	16.45	2011	14	2012	8	57.1	7	7	6
south	Ås	56.24	16.45	2012	17	2013	10	58.8	10	10	10
south	Lund	55.71	13.21	2010	13	2011	6	46.2	6	6	6
south	Lund	55.71	13.21	2011	11	2012	2	18.2	0	0	0
south	Lund	55.71	13.21	2012	8	2013	1	12.5	3	3	3
south	Lund	55.71	13.21	2013	2	2014	2	100.0	0	0	0
south	Skurup	55.47	13.50	2009	6	2010	5	83.3	5	5	5
south	Skurup	55.47	13.50	2010	3	2011	3	100.0	3	3	3
									72	70	70

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in the remaining colonies with the same attachment method. We found no negative effect on plumage or skin caused by the attachment of the geolocators on recaptured common swifts at recapture.

We used a linear correction function for our light-data correcting for clock drift using the program BASTrack, and extracted times for sunrise and sunset using a single light threshold of 2 by the program TransEdit for the initial year [44]. We observed minimal clock drift (0–2 min) during 1 year of data collection, and found no consistent pattern in the clock drift data. In the next step, we used the Bird-Tracker software to calculate latitude and longitude positions for all tracks [44], by inferring latitude from the length of the solar day/night and longitude from the time of local noon/midnight. For later models, we instead used the program Intiproc v. 1.03 provided by the manufacturer Migrate Technology Ltd (2012–2015), to perform the initial linear correction function for the clock drift, and extracting times for sunrise and sunset using the same light threshold as above (2). We used the critical sun angle corresponding to a light-level value of 2 on the arbitrary geolocator light scale (used by BAS and Migrate Technology Inc.) minimizing the difference in latitude between pre-and post-equinox (electronic supplementary material, figure S1), and at the same time minimizing the uncertainty in latitude close to the equinox for periods when the birds were stationary as defined by the estimations of longitude. We used 0.5° and 0.3° steps of critical sun angle extracted and evaluated across a range of sun angles (8–12 per bird) to define the one resulting in lowest difference in latitude between pre- and post-equinox periods (electronic supplementary material, figure S1). We used the 'Hill–Ekstrom' procedure [45] to evaluate which sun angle to use for a respective track and model of geolocator as outlined in [15]. The sun angles used varied between −3.0° to −5.0° and −6.0° to −7.0°, depending on geolocator model. Two relocations were recorded per day, except during a period around the equinox (March and September) period, because the latitude could not be accurately defined during this period. We excluded a five-week period around the autumn and spring equinoxes (two weeks before and three weeks after the autumn equinox and three weeks before and two weeks after the spring equinox) from analyses of trajectories, but used the longitude data to evaluate timing of movements. Owing to the clean light data (examples provided in the electronic supplementary material, figure S2), we could calculate a mean position for each day based on the two light measurements, and used those positions for further analyses of route choice and timing of movement patterns.

Archival light-level geolocators generate substantial errors when used on birds exploring forested habitat and as well as for seabirds in the open sea environment. The errors are influenced by geographical location, time of year, habitat and weather, and correspond to estimated values of 143 ± 62 km in forest (mean ± 95% CI; [46]) and 186 ± 114 km in the sea (mean ± s.d.; [47]) for latitude. Errors of longitude estimates in both cases have been shown to be lower 50 ± 34 km (mean ± 95% CI; [46]) and 85 ± 47 km (mean ± s.d.; [47]). Common swifts are expected to be continuously airborne during the non-breeding period [36,38,46], and during this time the light sensor on the geolocator receives continuous light exposure (electronic supplementary material, figure S2), and we may, therefore, expect lower errors than reported for forest dwelling birds as, for example, reported by Fudickar *et al.* [46]. More in-depth discussions on effects of location errors on evaluations of common swift geolocation data are found in Åkesson *et al.* [15], and how geolocation precision may be affected by environmental factors in Lisowski *et al.* [48].

(c) Evaluation of movement data

Here we have used GLS to evaluate the timing and speed of the Sahara passage in autumn and spring for common swifts, based on 1-day positions (two measurements per day). We have annotated the GLS data to pinpoint stopover areas and movement segments, when possible by evaluating a combination of latitude and longitudes, and during equinoxes only by using longitude (electronic supplementary material, figure S3). We considered a bird stationary, when the latitude and longitude positions showed limited variations around the mean, and flight sections when there was a substantial and directed change of latitude or longitude or both for several days. For tracks across the Sahara around equinoxes, the trajectory could not be presented, but only the time of movements relative to time spent resident given by the longitude alone. From each track we extracted the segment including the Sahara passage, based on the most southern stopover area identified just to the north of the Sahara Desert located in southern Europe or in northern Africa in autumn (electronic supplementary material, table S1), and the stopover area immediately south of the Sahara after the crossing in our analyses. The tracks were extracted in the same way for spring Sahara crossings. The segment of track defines the passage across the Sahara for an individual bird, and may include direct flights or a combination of time spent stationary, and periods of flight. For each individual, we calculated the mean winter latitude and longitude (November–February). For 10 birds (nine north population, one south), the passage occurred during the autumn equinox, for which we were unable to define locations of route or stopover areas during the passage, but could only note the occurrence and length of stopovers. We compared the migration and travel speeds in autumn for equinox and non-equinox birds from the northern population where most equinox birds were present and found no significant difference between the two groups (migration speed: $t = 0.35$, d.f. = 14, $p > 0.05$; travel speed: $t = 1.16$, d.f. = 14, $p > 0.05$, *t*-test), and therefore, we pooled birds from the two groups in further analyses of migration and travel speeds (as outlined below).

The movement trajectories have been used to calculate migration speed (km d^{-1}; movements including stopover time) and travel speed (speed of movement during travel days, km d^{-1}). Number of days at stopover and timing of movements have further been calculated for each (north, central and south) population. Locations of stopover areas were given as mean latitude and longitude positions for the time spent resident, and were presented if greater than or equal to 2 days were spent resident.

Departure directions from stopover areas north and south of the Sahara in autumn and spring, respectively, were calculated as the mean direction based on the initial three vectors based on 1-day average latitude and longitude positions, and calculated as the initial great circle route direction between nearby locations [49].

(d) Wind analysis

The stopover locations before the Sahara crossing and the migration trajectories across the Sahara were annotated with the wind field components from the National Centers for Environmental Prediction (NCEP) [50] using the software R v. 3.2.3 [51] and the package *RNCEP* 1.0.7 [52]. Since GLS data do not provide information on the swifts' flight altitude, we analysed winds at six of the available pressure levels in the NCEP database (i.e. 1000, 925, 800, 700, 600 and 500 hPa) which cover the entire altitude span, approximately from 100 to 5500 m.a.s.l., where migratory birds have been observed. The conversion of pressure values to altitude was performed solving the equation for the standard atmosphere [53]. Wind components were interpolated in space from the original 2.5° × 2.5° grid using the inverse distance weighting method [52]. Interpolation in time occurred only for annotation at stopover arrival and departure time. Whereas, for the wind field condition during stopover and along the migration trajectories, the date and time interval of wind annotation were selected to be 6 h to match the NCEP database, and precisely to 00.00, 06.00, 12.00 and 18.00

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UTC time. We calculated the flow assistance FA as the tailwind component using $FA = y \cos \theta$, with y being the wind speed and θ the angular difference between the wind direction and the bird's direction of movement [54]. Prevalent winds at stopover sites were evaluated as the median of the entire period from stopover arrival and departure date and time. Before wind field annotation, migration trajectories were linearly interpolated in latitude and longitude every 6 h assuming constant ground speed between successive GLS positions, that is, assuming that the birds were constantly flying during day and night. The trajectories were successively smoothed using a local linear regression with a time window of 1 day using the Epanechnikov filter implemented in the *lpridge* 1.0–7 R package [55].[1] This procedure allowed us to transform the 1-day average GLS positions into a constant 6-hour sampled trajectory necessary to match the available wind database intervals (see above) and capture the local variation of the wind field during the Sahara crossing.

Birds that crossed the Sahara during the influence of the equinox (see above) were not used in the wind analysis. Moreover, 34 final positions at the end of the autumn crossing were excluded before the interpolation and wind analysis because for those tracks we could not exclude an extra stopover location before reaching the final destination of the crossing.

To study the effect of the winds along the migratory trajectories across the Sahara, for each location we calculated the wind contribution to the bird's flying speed as the air-to-ground speed ratio (AGR) following Alerstam [56] and Gill *et al.* [57]. The ground speed was the calculated speed from interpolated trajectories (see above) and the airspeed was the difference of such ground speed and the tailwind component as defined in the section above. With AGR < 1, the bird is receiving support from the winds, whereas AGR > 1 indicates that the wind is an impediment to the bird's movement relative to ground. We first calculated AGR values assuming that birds were flying at fix altitude for each of the six levels considered (electronic supplementary material, figure S4). The calculated AGR values in electronic supplementary material, figure S4 presented not only very large variation, especially considering all six levels together, but also potential good support from the winds (AGR values < 1) along the entire crossing in both seasons. Thus, we further calculated the AGR values under the assumption that at each trajectory's position the bird would choose the pressure level that provided the maximum wind support (minimal AGR; figure 3). In order to select the minimal AGR, the bird needed to change its altitude every 6 h to find the pressure level with the best wind support and it is then possible to use those values to predict the flying altitude that the bird should have followed to gain the maximum advantage (either time or energy) from the winds while crossing the Sahara Desert (electronic supplementary material, figure S5).

(e) Statistics

The departure directions were used to calculate basic circular statistics [58] for a group of birds including the mean angle of orientation (α), and the vector length (r) varying between 0 and 1, being inversely related to scatter. The Rayleigh test was used to calculate if the distribution was significantly different from random [58], while the Watson U^2-test was used to test if two distributions differed from each other [58]. The computer program Oriana 4.02 (see endnote 1), was used to calculate the circular statistics.

Differences in the proportion of detour between autumn and spring for individual birds was compared with matched-pairs t test, and differences between populations and routes (west of 0° longitude and east of 0° longitude for the central route was defined at the 30° N latitude in autumn) with respect to travel and migration speeds were compared with LMM (JMP 12.0.1; [59]). Linear mixed effects models were built with year and individual as random effects and population as a fixed factor, and with year and population as random effects and route as a fixed factor, respectively. Maps, plots and statistics on AGR and flying altitude were performed with R v. 3.2.3. The package *lme4* v. 1.1–12 [60] was used to build series of linear mixed effects models using individual and year as random effects and population and departure location as fixed effects. The p-values were obtained by likelihood ratio tests of the complete model against the model without the effect in question.

3. Results

(a) Stopover and wintering areas

The autumn stopover areas used before initiating the Sahara crossing were located across a range of longitudes (10° W to 20° E) from the western part of the Iberian Peninsula to the western coast of the Black Sea for our study populations (figure 1). From all swift populations approximately half of the individuals initiated the migration from the Iberian Peninsula, with the rest of the individuals making stopovers across a wider range of longitudes to the east (figure 1). Out of 70 tracks, only six individuals started the crossing from stopover areas located in North Africa in autumn.

The overall departure direction for all birds in autumn was southwest ($\alpha = 209.6°$, $r = 0.91$, $N = 54$, $p < 0.001$; electronic supplementary material, figure S6), with no difference in mean orientation between populations ($p > 0.05$ in all cases, Watson's U^2 test). The stopovers during the Sahara crossing in autumn were located across a more narrow range of longitudes to the west as compared to the starting longitudes north of the desert in autumn, resulting in somewhat different departure directions relative to longitude at previous stopover. For birds departing from central longitudes (0–10° E), the swifts moved to the west of south in autumn ($\alpha = 212.3°$, $r = 0.89$, $N = 22$, $p < 0.001$), as well as those at eastern longitudes (10–20° E; $\alpha = 214.3°$, $r = 0.96$, $N = 13$, $p < 0.001$), while departure directions from western stopovers at the Iberian Peninsula were more to the south (0–10° W; $\alpha = 193.1°$, $r = 0.87$, $N = 37$, $p < 0.001$). There was a significant difference in the mean angle of orientation for departure directions between the most western and eastern sites ($U^2 = 0.215$, d.f. = 13, d.f.2 = 37, $p < 0.05$, Watson's U^2 test), but not when these two sites were compared with the central group ($p > 0.05$ for both). Autumn stopovers in central Sahara were located from western coastal Mauritania and Senegal in the west to the border between Niger and Chad in the east (figure 1).

Common swifts breeding in Sweden explored wintering areas located in West Africa (Liberia) to the Congo Basin in the east, with extensive overlap between populations (figure 1), resulting in no longitudinal difference in wintering locations between the three populations in north, central and south Sweden ($F_{2,69} = 0.253$, $p = 0.777$; LLM, year and individual as random effects). The wintering areas extended over latitudes from 8.52° N to the north and 6.04° S to the south.

A large proportion of the common swifts initiated spring migration from an intermediate stopover area ($N = 29$) or their wintering location ($N = 23$) in Liberia, West Africa (figure 1), while the rest of the swifts ($N = 18$) started the migration from wintering (or stopover areas, $N = 4$) areas further to the east, located mainly in coastal Gabon and the

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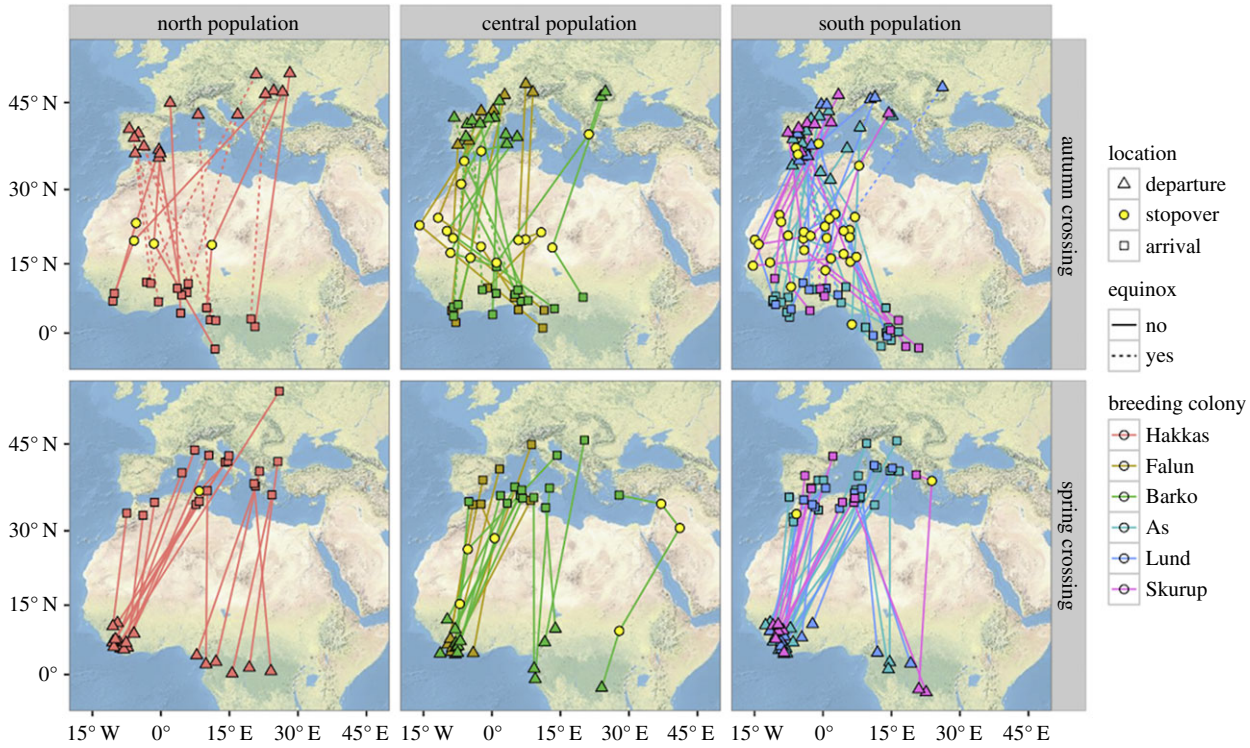

Figure 1. Map of stopover areas before initiating migration across the Sahara Desert (triangles), stopover areas on passage (filled yellow circles) and stopover or final wintering areas at arrival after crossing the barrier (squares), for different populations of common swifts breeding in north, central and south Sweden as recorded for spring and autumn by miniature geolocators. Solid lines are connecting routes for birds recorded outside equinox periods, while dashed lines connect starting and endpoints for swifts passing the Sahara during the equinox period. Lines connecting departure, stopover and arrival events simplify the assumed migratory pathway of the birds.

Congo Basin (figure 1). The mean departure direction for all birds during spring migration was near due north ($\alpha = 1.8^\circ$, $r = 0.94$, $N = 70$, $p < 0.001$; electronic supplementary material, figure S4). The mean initial departure directions from Liberia ($\alpha = 4.2^\circ$, $r = 0.95$, $N = 53$, $p < 0.001$) as compared to that from the Congo Basin ($\alpha = 353.8^\circ$, $r = 0.94$, $N = 17$, $p < 0.001$) was not significantly different from each other ($U^2 = 0.089$, d.f. = 17, d.f.2 = 53, $p > 0.05$, Watson's U^2 test). We could identify a dominating western migration route across the Sahara in spring (0–15° W longitude), used by swifts staging mainly in Liberia prior to the crossing and a central route used by birds leaving directly from wintering and stopover areas in the Congo Basin (0–20° E longitude). A more eastern route used during crossing starting from the Congo Basin and thereafter crossing the Arabian Peninsula (20–40° E longitude) was used by only one bird from the central breeding population (electronic supplementary material, figure S7).

(b) Timing of migration

On average, the central and south populations arrived first to the stopover areas in the Mediterranean region in autumn, in late July and early August (mean arrival dates (±s.d.): 18 August ± 9.7 (south); 17 August ± 11 (central)), while the northern birds arrived about one week later (mean ± s.d.: 25 August ± 7.1), resulting in a significant difference in arrival time between populations ($F_{2,69} = 5.714$, $p = 0.0050$; LLM, year and individual as random effects). On average, the swifts spent approximately two weeks at the stopovers in southern Europe before initiating the Mediterranean–Sahara crossing (mean stopover duration (days ± s.d.); south: 15.9 ± 11, central: 14.2 ± 11.1, north: 16.4 ± 9), with no difference between populations in stopover duration ($F_{2,69} = 1.135$, $p = 0.327$; LLM, year and individual as random effects). Therefore, there was a difference in departure date between the populations ($F_{2,67} = 4.293$, $p = 0.0176$; LLM, year and individual as random effects), with the most northern population departing latest. The swifts arrived to their initial stopover area south of the Sahara after a substantial time in autumn (table 2), suggesting the passage involved one or more periods of residency. We found a significant difference between populations in arrival time south of the Sahara in autumn, with birds from the central population arriving first and the southern population arriving last ($F_{2,65} = 6.261$, $p = 0.0033$; LLM, year as random effect). Swifts from the southern population used around one week (6–8 days) more to cross the Sahara as compared to the central and northern populations (table 2). We, did not find any significant variation between populations in timing of departure in spring (mean departure date: 11 May (south), 9 May (central) and 12 May (north); table 2) ($F_{2,67} = 1.678$, $p = 0.194$; LLM, year and individual as random effect). All individuals departed between 26 April at the earliest and 28 May at the latest.

(c) Speed of migration

In all populations, most individuals crossing the Sahara in autumn did so by intermittent flights and stops (figure 1), and the total crossing time, therefore, lasted longer in autumn (range: 4.0–72.8 days) as compared to spring (range: 2.0–13.7 days; table 4), with the fastest passage noted for the central population (median crossing duration 22.3 days), with intermediate crossing times for the northern population (25.6 days) and the longest crossing for the southern population (29.5 days; table 4) in autumn. The time difference was

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Table 2. Timing of departure and arrival (mean ± s.d., range) after crossing the Sahara in autumn and spring for three populations of common swifts breeding in south, central and north Sweden as recorded by GLS.

season	population	*N*	mean departure date (±s.d.)	range of departure dates	mean arrival date (±s.d.)	range of arrival dates
autumn	north	16	03 Sep (±9.7)	19 Aug–24 Sep	28 Sep (±13.3)	30 Aug–14 Oct
autumn	central	20	26 Aug (±14.5)	02 Aug–22 Sep	24 Sep (±17.9)	22 Aug–17 Oct
autumn	south	34	27 Aug (±12.3)	06 Aug–22 Sep	02 Oct (±14.1)	25 Aug–30 Oct
spring	north	18	12 May (±6.6)	03 May–28 May	17 May (±5.7)	09 May–31 May
spring	central	19	09 May (±6.3)	26 Apr–20 May	14 May (±5.5)	03 May–28 May
spring	south	33	11 May (±4.2)	03 May–22 May	16 May (±4.5)	05 May–28 May

Table 3. Mean distance (±s.d., *N*, Min, Max) of Sahara crossing in autumn and spring, and the detour calculated relative to a great circle distance between the starting and endpoint for the populations of common swifts breeding in north, central and south Sweden passing Sahara on migration and recorded by geolocation.

		distance Sahara crossing (km)					detour					
season	population	mean	s.d.	*N*	min	max	mean	s.d.	*N*	min	max	detour %
autumn	north	4790	1119	18	3152	7314	1.19	0.12	7	1.00	1.36	18.5
	central	4133	573	20	2824	5177	1.46	0.38	17	0.99	2.37	46.3
	south	4122	632	33	2962	5210	1.61	0.51	26	1.03	2.86	61.2
spring	north	4371	838	18	2599	6577	1.08	0.06	18	1.00	1.23	8.2
	central	3730	601	19	2713	4787	1.19	0.20	19	1.01	1.65	18.5
	south	3746	602	33	2787	5146	1.16	0.17	33	0.83	1.78	15.9

statistically significant between populations ($F_{1,68} = 4.091$, $p = 0.047$; LLM, year as random effect).

The spring passage was mostly performed by fast and direct flights across the Sahara, lasting 2–15 days, and only rarely did a bird use a brief stop (only individuals from the south and central populations did so; figure 1). There was no significant difference between populations in number of days used to cross the Sahara in spring ($F_{2,69} = 1.630$, $p = 0.206$; LLM, with year and individual as random effects). When comparing the migration speeds including both travel and stopover for individuals tracked both seasons, the speed in spring was faster (mean migration speed = 857.3 km d^{-1}) as compared to in autumn (281.5 km d^{-1}, mean difference = 575.8 km d^{-1}; $t = 14.23$, d.f. = 68, $p < 0.0001$, matched-pairs *t*-test). Travel time (days with movements excluding time spent at stopovers) was higher in autumn (median number of travel days = 11.7–15.5) compared with spring (median travel days = 4.4–5.6; table 4). As a result individuals tracked during both seasons showed significantly higher travel speeds excluding time at stopover in autumn as compared to spring (median speed spring = 890.5 km d^{-1}, autumn = 447.6 km d^{-1}, mean difference = 442.8 km d^{-1}; $t = 10.80$, d.f. = 68, $p < 0.0001$, matched-pairs *t*-test).

(d) Migration routes in autumn and spring

On average the migration routes followed by common swifts across the Sahara are longer in autumn as compared to spring (table 3), leading to significantly longer detours calculated relative to a great circle route distance (mean detour: 16.5% in spring and 50.1% in autumn). The largest difference in detour between autumn and spring was found in the southern breeding population (mean detour: 61.2% in autumn and 15.9% in spring), and the smallest difference between the two seasons was found for the northern population (mean detour: 18.5% in autumn and 8.2% in spring; table 3). For individuals tracked both seasons and for which the detour could be estimated (migration not overlapping with equinox), we found a significant difference in detour length between autumn and spring (mean detour spring = 1.16, autumn = 1.50, mean difference = −0.33, s.e. = 0.061; $t = -5.40$, d.f. = 47, $p < 0.001$, matched-pairs *t*-test). On the population level, we found significantly longer detours in autumn as compared to spring for the south (mean detour spring = 1.15, autumn = 1.61, mean difference = −0.46, s.e. = 0.088; $t = -5.23$, d.f. = 25, $p < 0.001$, matched-pairs *t*-test) and central (mean detour spring = 1.21, autumn = 1.46, mean difference = −0.25, s.e. = 0.099; $t = -2.53$, d.f. = 15, $p < 0.05$, matched-pairs *t*-test), but not for the northern population (mean detour spring = 1.12, autumn = 1.19, mean difference = −0.064, s.e. = 0.069; $t = -0.93$, d.f. = 5, $p > 0.05$, matched-pairs *t*-test), although the sample size for the latter was small due to equinox problems.

(e) Movements in relation to winds

The wind conditions on arrival at the stopover sites before the Sahara crossing were favourable both in autumn and in spring

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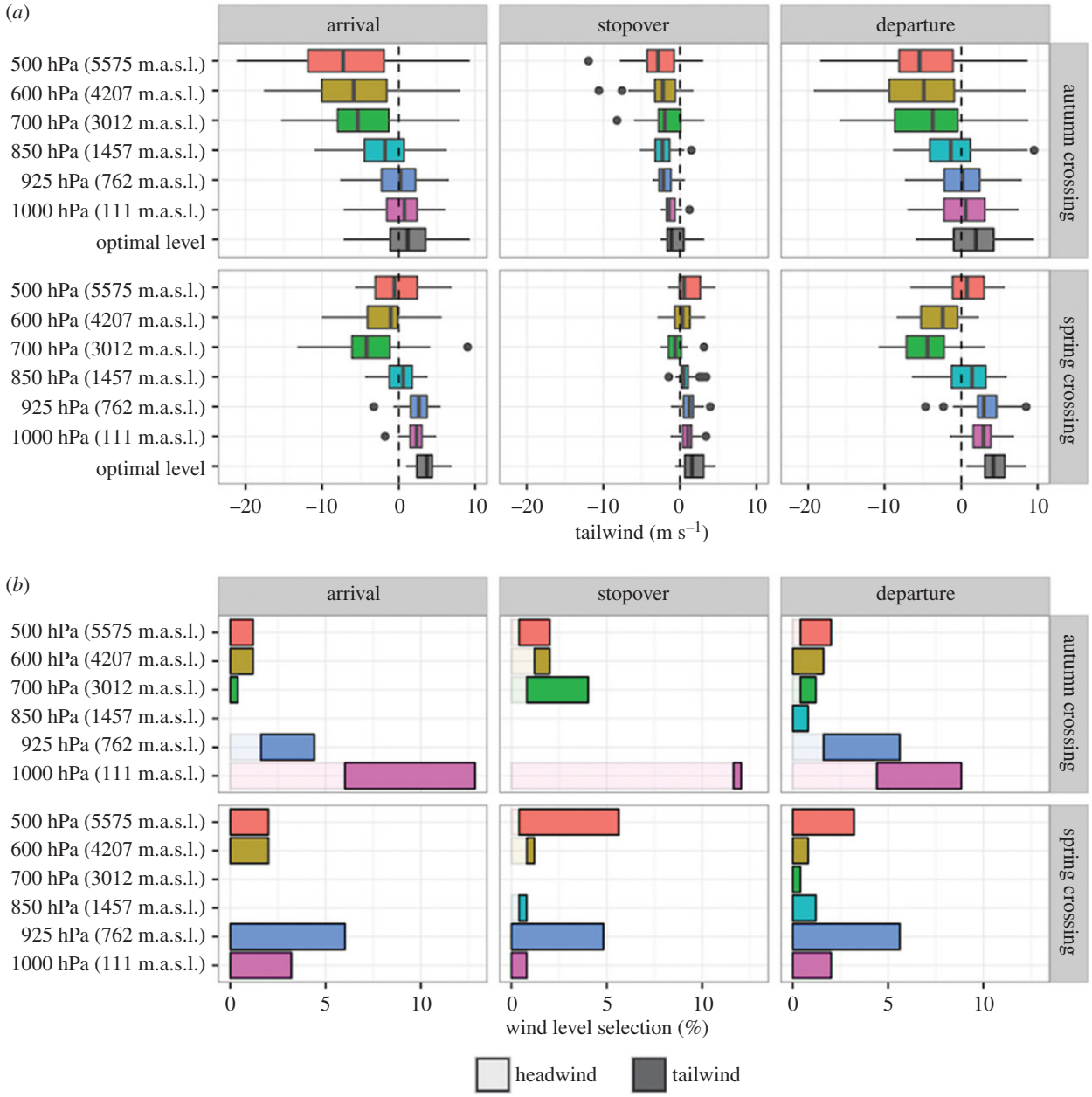

Figure 2. Wind support on arrival at during stopover (median of the entire duration) and at departure from the stopover site before the Sahara crossing during both autumn and spring migration. (*a*) The boxplot of the birds' tailwind component for each pressure level (and corresponding altitude) and for the *optimal level*, that is the resultant tailwind if each bird was able to select the pressure level that provided the best wind condition along its own departure directions (presented in electronic supplementary material, figure S4). (*b*) The pressure layers that provided the *optimal level* included in upper panel. When the winds are not favourable, that is no tailwind opportunity available, the birds are forced to depart with the wind that provided with the lowest headwind (negative values in (*a*); shaded colour in (*b*)). To exclude birds that started the spring migration crossing from the wintering area, we included in the analysis only birds departing after a stopover duration not longer than 30 days (autumn $n = 54$, spring $n = 33$).

(figure 2). Indeed, the mean tailwind component at the *optimal level* (based on the most favourable wind condition for each bird) was in both cases positive (mean ± s.d.: 1.3 ± 3.6 m s^{-1} and 3.8 ± 2.1 m s^{-1} in autumn and spring, respectively), indicating that it was a favourable situation for the birds to immediately continue on migration across the Sahara when arriving at the stopover site immediately preceding the Sahara crossing.

The prevalent winds during stopover after day 1 in autumn were mainly directed towards the northeast (electronic supplementary material, figure S8), which is in the opposite direction to the expected departure direction of the birds (electronic supplementary material, figure S6). As a consequence, even if the swifts were selecting the pressure level with the optimal wind support (*optimal level* in figure 2*a*), the resultant mean tailwind component resulted in negative values (-0.6 ± 2.5 m s^{-1}), and thus not favourable winds for departure. The fact that autumn departures occurred with mainly positive tailwinds (1.9 ± 3.7 m s^{-1}, figure 2), supports the fact that birds were waiting for more favourable (or less disadvantageous) winds before initiating the Sahara crossing when leaving the European and North African stopover sites.

The wind conditions during the stopover in spring were different to that in autumn, such that the winds were mainly favourable for crossing the Sahara by movements to the north throughout spring stopovers (mean *optimal level* tailwind ± s.d.: 1.9 ± 1.5 m s^{-1}). Furthermore, the wind speeds at the time of departure during spring were high (4.3 ± 2.0 m s^{-1}), but not different from the winds on arrival

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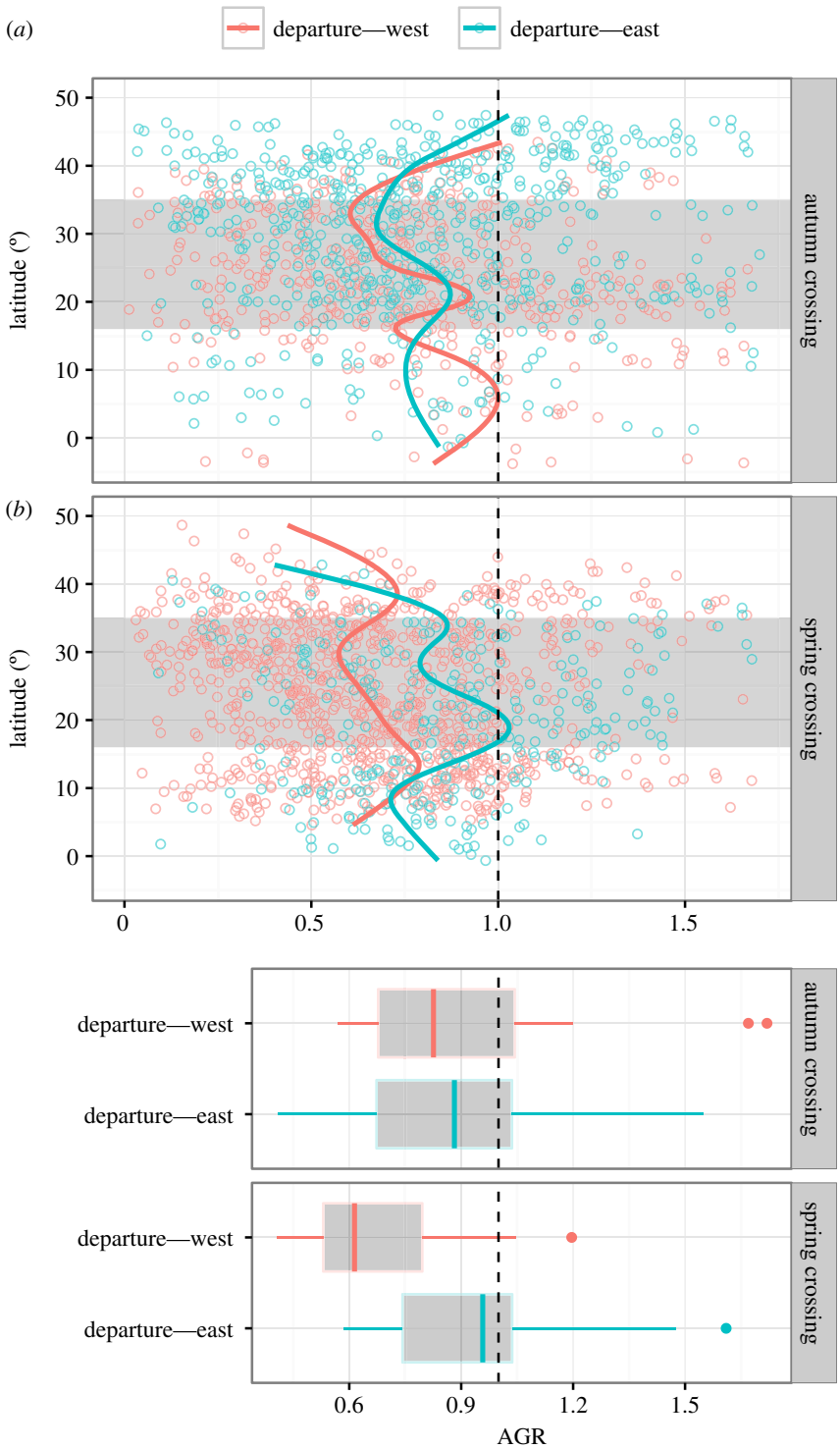

Figure 3. Air-to-ground speed ratio (AGR) for two groups of birds departing from different locations (west and east, respectively) before the Sahara crossing in both the autumn and spring migrations (AGR $<$ 1 represents wind support; AGR $>$ 1 represents wind impediment). (*a*) As function of latitude the AGR at the pressure level that provided the highest wind assistance (see text; AGR for all pressure levels in electronic supplementary material, figure S7). Dots are AGR for all locations, solid lines are local polynomial regression fitting and the shaded grey area represents the extension of the Sahara Desert (16–35° N). (*b*) The boxplot of the mean AGR for each individual (autumn $n = 21$ and $n = 23$, spring $n = 53$ and $n = 17$, for west and east departure locations, respectively) during the Sahara crossing (i.e. while crossing the shaded area in the upper panel). Statistical tests between departing locations has been performed using linear mixed effects models to account for repeated measures of the same individuals and year of sampling (see text for details).

at the same stopover site ($W = 207$, d.f. $= 32$, $p = 0.195$, Wilcoxon signed-rank test).

For both autumn and spring, and in all three groups (arrival, stopover and departure), the most favourable winds were either below 800 m (pressure levels of 1000 and 925 hPa) or above 5000 m (500 hPa) (figure 2*b*). The selection of those winds at the extremes of the studied pressure interval occurred both when winds were not favourable, as was the case in the autumn stopover when the winds were mainly blowing in the opposite direction to the expected departure direction (see above), and also in all other scenarios when the birds could choose a pressure level with favourable wind support (figure 2).

The study of the AGR along the migratory trajectories showed variable wind support along the latitudinal gradient and for winds at different pressure levels (electronic

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supplementary material, figure S6). Indeed, the optimal AGR would have been obtained only if the birds were able to select different altitudes during the crossing (electronic supplementary material, figure S5). If such a strategy was followed by the birds, in both autumn and spring crossing the Sahara would have been possible with wind support (AGR < 1, figure 3). The likelihood ratio tests of the models including population as a fixed factor against the simplified models showed no effect of population in the predicted optimal flying altitude ($\chi^2 = 0.753$, d.f. = 2, $p = 0.686$ and $\chi^2 = 0.160$, d.f. = 2, $p = 0.923$ for autumn and spring, respectively). Furthermore, there was no difference in the predicted optimal flying altitude (and the relative gain from the winds) in the autumn for birds departing from different longitudes ($\chi^2 = 0.557$, d.f. = 1, $p = 0.455$) (electronic supplementary material, figure S5 and figure 3, respectively). During the crossing of the Sahara in spring, the swifts would have benefitted the most by flying at higher altitudes if departing from the western stopover location ($\chi^2 = 38.05$, d.f. = 1, $p < 0.001$; mean ± s.e.: 3531 ± 111 m.a.s.l.) as compared to departures from the more eastern locations, where the highest gain from winds would have been met at lower altitudes (1874 ± 225 m.a.s.l.; cf. also electronic supplementary material, figure S5). In fact, by following the differential optimal level routes the swifts following the western route would have gained significantly more wind support as compared to the eastern (central) route (AGR ± s.e.: 0.66 ± 0.03 west, 0.98 ± 0.06 east) ($\chi^2 = 23.50$, d.f. = 1, $p < 0.001$; figure 3).

(f) Migration routes across the Sahara

We found that there was no difference in time spent on migration (including days at stopover) between the western and central route (west and east of 0° longitude at 30° N latitude, respectively) in autumn (migration days west route: median = 29.6 days, $N = 56$, range: 6.0–72.8 days; central route: median = 22.1 days, $N = 14$, range: 4.0–61.6 days; $F_{1,68} = 0.226$, $p = 0.636$, LMM), and not for travel days (including only days at travel) (travel days west route: median = 14.6 days, $N = 56$, range: 5.0–48.4 days; travel days central route median = 22.1 days, $N = 14$, range: 4.0–61.6 days; $F_{1,66} = 1.43$, $p = 0.236$, year as random effect). In spring, the swifts did not spend much time at stopovers, and we found no difference in the number of days spent on migration or travel between the western and central route (migration days: west route : median = 5.5, $N = 54$, range = 2.0–10.3; migration days: central route : median = 6.0, $N = 17$, range = 3.6–13.7; $F_{1,68} = 1.117$, $p = 0.294$, LMM; travel days west route: median = 5.0, $N = 54$, range = 2.0–10.0; travel days central route: median = 5.6, $N = 17$, range = 3.6–13.7; $F_{1,68} = 1.68$, $p = 0.199$, LMM, year as random effect).

We compared the mean migration and travel speeds for swifts crossing the Sahara by a western and a central route (definition above), and found a significant difference between the two groups in autumn for travel speed (west route: median = 328.4 km d^{-1}, $N = 56$, range = 108.8–1417.2 km d^{-1}; central route: median = 551.9 km d^{-1}, $N = 14$, range = 91.5–1241.2 km d^{-1}; $F_{1,68} = 3.956$, $p = 0.0507$, LMM, year as random effect), but not for migration speed (west route: median = 188.4 km d^{-1}, $N = 56$, range = 61.0–1084.3 km d^{-1}; central route: median = 205.2 km d^{-1}, $N = 14$, range = 83.8–1241.2 km d^{-1}; $F_{1,68} = 1.526$, $p = 0.221$, LMM, year as random effect). In spring, there was no difference in migration or travel speed between the western and central routes (migration speed west route: median = 766.1, $N = 54$, range = 399.1–1869.7 km d^{-1}, central route: median = 912.4, $N = 17$, range = 465.2–1184.7; $F_{1,64} = 0.133$, $p = 0.716$, LMM; travel speed west route: median = 785.7 km d^{-1}, $N = 54$, range = 561.4–1869.7 km d^{-1}; travel speed central route: median = 917.2 km d^{-1}, $N = 17$, range = 465.2–1184.7 km d^{-1}; $F_{1,66} = 0.0666$, $p = 0.797$, LMM, all with year as random effect). The highest speeds of travel occurred for birds migrating via the most western route in spring (range: 561.4–1869.7 km d^{-1}; with the highest speeds exceeding the maximum travel speed predicted by the birds own air speed during 24 h of flight (flight range approximately 900–1000 km d^{-1}, based on radar measurements of air speeds of common swifts on migration of 10.6 m s^{-1}; [61]), which suggests occasions with substantial tailwind assistance along the route when departing from the most western part of Africa (i.e. Liberia) in spring.

4. Discussion

(a) Population differences

We found differences in timing of migration between populations mainly in autumn, where the southern breeding populations arrived at the stopovers in south Europe before the two more northern populations. However, the time spent at the stopover of approximately two weeks was similar between the populations suggesting similar needs to prepare for the crossing by fuelling for all populations. We also found differences in the departure timing and time used to cross the Sahara between populations, where the most northern populations departed the latest, but used the shortest time to cross the Sahara, such that individuals from the most southern population were the last to arrive to the initial wintering areas south of the Sahara. There was large spatial overlap in stopover and wintering areas used between populations, and in spring the swifts from different populations departed without any time difference from the stopover areas in West Africa and the Congo basin, suggesting that decisions related to fuelling conditions and wind assistance were timed relative to local conditions at the stopover sites, where West Africa attracted most of the birds.

(b) Routes and migration strategy

How migratory birds cross the Sahara during migration has received much attention over the years, rendering a number of hypotheses about adaptive behaviours to save energy, perform the crossing in relation to winds, to avoid increased turbulence and extreme daytime temperatures and to avoid the risk of dehydration (e.g. [1,11,13,19,62–65]). From initially expecting continuous flights across the Sahara [1], more recent studies have suggested that songbirds predominantly fly at night and rest in shadow on the ground during the daytime (e.g. [10,11,13,19]) to preserve water and energy [19,63,64,66]. However, in spring, birds may extend the flight period to also include part of the daytime hours [7,13], in order to save time and energy. Previous studies indicate that without tailwind assistance, crossing may not be possible because the fuel levels measured in birds caught prior to departure were not sufficient [12,67]. However, at least some passerine migrants may stop to refuel at

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oasis and thereby manage the crossing on initial limited reserves [68]. In contrast with Moreau's [2] original suggestion that the grounded birds in the Sahara are fallouts, birds with large fuel stores were subsequently shown to land in the desert during the daytime and await better flight conditions at night-time [10,69,70]. Others have argued that detours may save energy, because of the reduced cost of carrying the extra fuel load needed to cross the barrier, which in turn lead to flights that circumvent the barrier to different degrees, supporting the evolution of migration routes to avoid rather than cross barriers [9]. Despite all these potential challenges, billions of birds each year cross the Sahara Desert [3].

Common swifts, expected to be constantly on the wing [38,41] (A Hedenström, G Norevik, K Warfinge, A Andersson, J Bäckman, S Åkesson 2016, unpublished data), avoid stopping and resting during migration, and therefore, most likely use a continuous flight strategy during the Sahara crossing as compared to songbirds [11,13,19]. In our previous work, including tracks of six migrating common swifts, we found a preference for a western route across the Sahara in autumn. In spring, there was a strong tendency to use the coastal areas in West Africa (i.e. Liberia) to stopover prior to the return migration across the Sahara [15]. This pattern re-emerged in the current study, where we found that Swedish common swifts from three latitudinally different populations migrate south to southwest on a broad front across Western Sahara in autumn. We could further establish a preference in autumn to initiate the Sahara crossing from stopover sites located on the Iberian Peninsula, as well as a strong tendency to use the Liberian stopover also in spring in the majority of our tracked swifts (52 of 70). The individual swifts remained at the stopover for a few days up to one month, suggesting a migration strategy including fuelling at stopovers, rather than a continuous fly-and-forage strategy. Both stopovers in autumn and spring were needed for fuelling, as individual swifts remained in the area for a few days up to four weeks (range: 1.5–32 days). Expected fuelling was supported by the fact that the swifts arrived at the autumn stopovers on days when the winds were favourable for continued migration across the Sahara (with tailwind-assisted flights towards south to southwest), but in spite of this the birds interrupted migration (figure 2). During the stopover the wind assistance along the preferred migration direction decreased for the remaining period and had stayed negative throughout the stopover. At the time of departure, the winds had changed to provide positive wind assistance in the preferred migration direction towards south to southwest (figure 2). This pattern suggests the reason for this initial stopover was not influenced by winds, but was due to the need to store fuel before continuing on migration across the Sahara. We may, thus, expect a capacity by common swifts to perform a significant flight across the Sahara. Extensive fuelling in southern Europe before departure on the autumn migration has been observed in the barn swallow, *Hirundo rustica*, another species adapted to aerial foraging [71].

Our study, however, shows that the swifts in autumn perform the migration across the Sahara by periods of flight, and periods of residency across a wide area in central and southern Sahara, lasting on average two weeks up to 2 months. At this time of year when the swifts arrive to these latitudes, in late August to early October, the Inter-Tropical Convergence Zone, which generates latitudinal variations in rainfall in Tropical Africa, is located at its northernmost latitudinal range, likely providing good foraging conditions in the Sahel zone for insectivorous birds [72]. Many bird migrants have been shown to remain in this zone during the initial part of their wintering in Africa, where they may moult and after some weeks of residency continue to wintering sites further south (e.g. [73,74]). It seems that common swifts also follow this pattern of movement, with initial stops in south Sahara and the Sahel zone, followed by continued migration to wintering areas just north and south of the equator (8° N–6° S; [15]).

(c) Migration and travel speeds

The migration and travel speeds across the Sahara in autumn were considerably slower than in spring, further underlining a seasonally different migration strategy during barrier crossing for the common swift. The spring passage was fast, with a minimal detour relative to the shortest-distance route (i.e. great circle route), and lasted on average only 5.5 days for all our swifts, with no difference in speed related to population or route selected (western or central), although the highest speeds were observed during spring along the western route. With an airspeed of 10.6 m s^{-1} [61], a direct flight of 3700 km would take about 4 days in continuous flight, suggesting that the spring crossing of the Sahara is more or less a direct flight by most swifts. A few individuals reached speeds about twice the expected airspeed (table 4), which means these birds enjoyed tailwind assistance of a similar strength to their own airspeed throughout their flight. Prolonged migration flights in spring extending into daytime hours have been reported also for songbird migrants, both in radar [13] and tracking [7] studies across western Sahara, suggesting favourable flight conditions relative to winds and an urge to perform migration by minimizing the time of the crossing. The rapid flight across the Sahara implies that common swifts migrate both during the night and daytime in spring.

(d) Migration in relation to winds

Our swifts experienced positive wind assistance during spring migration, with especially good conditions for birds selecting the western route rather than the central and eastern routes. In fact our evaluations of migration departures and route selection relative to winds suggest that the swifts following the western route in spring have the chance to exploit more favourable wind conditions compared with birds crossing the Sahara at locations near to the Congo Basin in Central Africa along a central route. Combined with the situation at departure the winds also provide tailwind assistance along the entire route for our tracked swifts (figure 3), which makes wind assistance in combination with presumed favourable fuelling conditions at the location in Liberia a likely explanation to the evolution of this typical migration pattern in North-European common swifts [15]. Previous work has pointed out important migration routes across the Sahara that may evolve in response to predominant trade-wind patterns, suggesting that a southwestern route in autumn across southwest Europe and thereafter across the Sahara may evolve, if good foraging conditions are provided prior to the barrier crossing in the Iberian Peninsula or northwest Africa [12]. Another study, which evaluated the stability of wind patterns over time on a global scale, identified a number of energetically favourable routes across the Sahara, where flight would be supported by predominant tailwind

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Table 4. Median number of days spent on migration (including stopover periods) and travel (excluding stopovers) across the Sahara in spring and autumn, and speed of passage (migration and travel speed, km d^{-1}) for different populations of common swifts breeding in north, central and south Sweden.

		autumn					spring				
population		migration days	travel days	*N* stops	migration speed (km d^{-1})	travel speed (km d^{-1})	migration days	travel days	*N* stops	migration speed (km d^{-1})	travel speed (km d^{-1})
north	median	25.6	11.7	1	199.5	411.0	5.3	5.3	0	803.1	803.1
	N	16	16	16	16	16	18	18	18	18	18
	min	4.0	4.0	0	83.3	91.5	2.5	2.5	0	642.2	642.2
	max	49.0	43.3	2	1241.1	1241.1	8.4	8.4	0	1556.2	1556.2
central	median	22.3	13.0	1	235.8	408.1	4.8	4.4	0	912.4	985.2
	N	20	20	20	20	20	19	19	19	19	19
	min	9.0	5.0	0	93.9	108.8	2.6	2.6	0	560.6	604.4
	max	72.8	48.4	2	882.8	1305.0	10.0	10.0	2	1668.7	1668.7
south	median	29.5	15.5	1	186.4	324.8	5.6	5.6	0	751.0	762.8
	N	34	34	34	34	34	34	34	34	34	34
	min	8.0	6.4	0	61.0	117.5	2.0	2.0	0	399.1	465.2
	max	71.1	39.2	3	1084.3	1417.2	13.7	13.7	1	1869.7	1869.7

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conditions, which may lead to prolonged routes relative to great circle routes, but shorter travel times [75]. The optimal wind-assistance routes, may further lead to differential flight altitudes. In our study, we could predict at which flight altitudes the swifts should fly to maximize the wind assistance at any given time. This analysis showed that birds following the spring route across western Sahara should fly at higher altitudes than those following the central route. Our analyses also showed that birds following an optimal route relative to winds, would select lower flight altitudes in autumn than in spring. We could not confirm this differential altitude choice connected to geographical region in spring or between the two seasons in our study as the geolocation data did not provide flight altitudes. However, these predictions based on our analyses can be tested in the future using suitable tracking technology. That migratory birds may use different altitudes between seasons is supported by tracking radar studies at an inland oasis and desert areas in west Sahara [76], where in fact the tracking of songbird migrants showed this predicted differential altitude selection in autumn and spring.

We considered the assistance provided by the winds calculating the tailwind component both at the stopover sites and along the Sahara crossing. However, most wind conditions also include a side wind component that birds should account for to efficiently use the wind flow to save time and energy to progress along the preferred direction of movement [30,56,77]. There are different more sophisticated ways for calculating flow assistance but all require additional assumptions on the degree of wind compensation in the form of changes in the bird's heading and speed, either air- or ground speed depending of the strategy considered, which would increase the complexity of the analysis [54]. Indeed, one of the approaches proposed to disentangle the differences between the different possible assumptions is to use a flow assistance individual based model to simulate the trajectories that an animal would exhibit in the real world if it acted according to the rules of a specific preferred direction of movement, that is a compass direction, combined to one of the possible flow assistance strategies ([54], see also [78]). Future studies on swift migration should integrate observations and modelling to shed light also on compass mechanisms used in flight and to what extent swifts can deal with side winds by compensation in the numerical models of movement strategies, including the possibility to change altitude rather than speed or heading to use more profitable winds.

5. Conclusion

We confirm that the common swifts crossing the Sahara in autumn and spring use different migration strategies between seasons, showing more stops and longer migration and travel times in autumn as compared to spring. We found timing differences between populations in autumn, but not in spring and higher travel speeds for swifts crossing the Sahara by a central route in autumn. Our data suggest the swifts are sensitive to winds and depart in winds providing immediate support as well as positive wind support later on during the flight across an ecological barrier. The time spent at stopover as well as the timing of departures from stopover areas suggest that the swifts explore stopover sites presumably to fuel before the crossing, both in autumn (Iberian Peninsula and South Europe) and in spring (Liberia and Congo Basin). The evolution of a preferred western route used by European common swifts in spring, are supported by a combination of timing favourable fuelling conditions related to high insect abundance and favourable supporting winds across the Sahara crossing. Future studies will reveal at what flight altitudes the common swifts explore tailwind conditions for the Sahara crossing in autumn and spring as well as between the three major flyways across the Sahara in spring.

Ethics. Ethical permission to attach geolocators to common swifts was given by Malmö-Lunds djurförsöksetiska nämnd (M112-09, M470-12). Permission to trap and ring common swifts in Sweden was given by the Swedish Environmental Protection Agency and the Swedish Ringing Office at the Natural History Museum in Stockholm (licence no. 440) to S.Å.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. S.Å. designed the study, collected, prepared and annotated the GLS data for analyses, evaluated routes, timing of movements and speed data, performed statistical analyses and wrote the initial draft of the manuscript. G.B. prepared the data and performed the wind analyses, performed statistical analyses and wrote parts of the manuscript. A.H. collected GLS data, discussed the outline and contributed to the writing of the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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Endnote

[1]Kovach Computing Services 1994–2013. Oriana 4.02.

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