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Evolution of chain migration in an aerial insectivorous bird, the common swift *Apus apus*

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Spectacular long-distance migration has evolved repeatedly in animals enabling exploration of resources separated in time and space. In birds, these patterns are largely driven by seasonality, cost of migration, and asymmetries in competition leading most often to leapfrog migration, where northern breeding populations winter furthest to the south. Here, we show that the highly aerial common swift *Apus apus*, spending the nonbreeding period on the wing, instead exhibits a rarely found chain migration pattern, where the most southern breeding populations in Europe migrate to wintering areas furthest to the south in Africa, whereas the northern populations winter to the north. The swifts concentrated in three major areas in sub-Saharan Africa during the nonbreeding period, with substantial overlap of nearby breeding populations. We found that the southern breeding swifts were larger, raised more young, and arrived to the wintering areas with higher seasonal variation in greenness (Normalized

Evolution 74-10: 2377–2391

Difference Vegetation Index) earlier than the northern breeding swifts. This unusual chain migration pattern in common swifts is largely driven by differential annual timing and we suggest it evolves by prior occupancy and dominance by size in the breeding quarters and by prior occupancy combined with diffuse competition in the winter.

KEY WORDS: **Annual timing, chain migration, common swift, diffuse competition, dominance by size, prior occupancy.**

Global seasonality and accompanying variation in food resources have led to repeated evolution of spectacular long-distance migration in many taxa (Alerstam et al. 2003). Competition for breeding and wintering sites has been regarded as an important driver leading to spatial segregation in avian migrants (e.g., Cox 1968; Lack 1968; Gauthreaux 1978, 1982). The cost of migration, seasonal variation in habitat quality, dominance, and asymmetric competition by size among individuals are assumed to be important factors governing the evolution of differential migration patterns (Salomonsen 1955; Lundberg and Alerstam 1986), including partial migration and residency (Lundberg 1988). The underlying factors for the evolution of differential migration in other animals such as fish, mammals, and insects may be similar (e.g., Fryxell and Sinclair 1988; Alerstam et al. 2003; Chapman et al. 2011), but empirical data from migratory systems covering larger spatial scales to test these assumptions are either still largely lacking (Chapman et al. 2011) or have not been evaluated in this way. Two characteristic migration patterns that have evolved in birds are leapfrog migration (Fig. 1A), for which the most northern breeding populations winter furthest to the south, and chain migration (Fig. 1B), where the most northern breeding populations winter furthest to the north (Salomonsen 1955; Newton 2008).

Two main scenarios for the evolution of differential migration based on competition have been evaluated in more detail for birds by Holmberg and Lundberg (1993), building on the ideal despotic distribution mediated by differences in arrival time between individuals (Fretwell and Lucas 1970; Fretwell 1972). Theory for ideal despotic distribution predicts that the quality of habitat controlled by territorial animals should vary depending on their competitive ability and the availability of resources. Because of interactions with dominant individuals through body size dominance, subdominants will distribute to make the best of a bad situation. This will lead to an ideal despotic distribution of individuals with unequal competitive ability due to differences in interference experienced (Sutherland and Parker 1985; Parker and Sutherland 1986). Two additional important assumptions relevant for the evolution of migration patterns are that the suitability of a site is dependent on type of parameters or activity considered (e.g., food abundance and predation pressure), which may vary with latitude, and that cost of migration may increase with migration distance (Holmgren and Lundberg 1993 and references therein).

By combining differential cost of migration expressed in relation to latitudinal suitability gradients for breeding and wintering, with either dominance through body size or dominance by prior occupancy, Holmgren and Lundberg (1993) evaluated alternative scenarios when a typical leapfrog (Fig. 1A) or chain migration pattern (Fig. 1B) may evolve. Leapfrog migration, where northern individuals migrate to the southernmost wintering areas (Fig. 1A), is common among passerines, raptors, waders, waterfowl, gulls, and seabirds (Salomonsen 1955; Lundberg and Alerstam 1986). Leapfrog migration predominantly evolves when migration costs are high in combination with prior occupancy or trait- (e.g., body size) related dominance (Lundberg and Alerstam 1986; Holmgren and Lundberg 1993; Figs. 2A, 2C, and 2F). Residency in one population on the other hand is expected to evolve when dominant individuals occupy the most suitable habitats in the south either by trait-related dominance or prior occupancy, and subdominants are forced to leapfrog on migration to occupy less suitable habitats (Figs. 2C and 2F). Chain migration, where individuals from the northernmost population also winter in the northernmost part of the winter range, has been observed more rarely than leapfrog migration in birds (Fig. 1B; references in Salomonsen 1955 and Newton 2008).

The typical chain migration pattern may evolve under two main scenarios, as predicted by Holmgren and Lundberg (1993), where dominant individuals monopolize resources, achieved either through trait-related dominance (Parker and Sutherland 1986; Sutherland and Parker 1985; Fig. 2B) or prior occupancy (Fretwell and Lucas 1970; Fretwell 1972; Figs. 2D and 2E). According to the first scenario of resource monopolization, chain

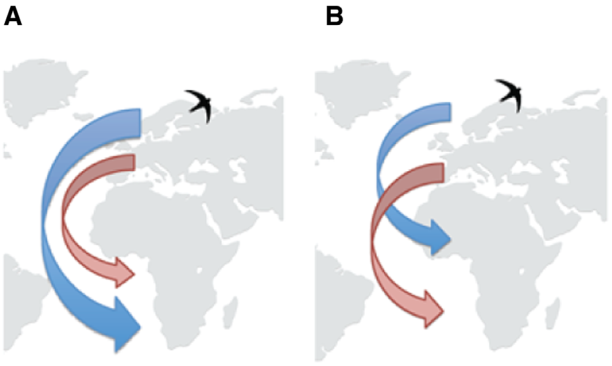

Figure 1. Schematic view of predicted typical migration patterns. (A) Leapfrog migration pattern and (B) chain migration pattern.

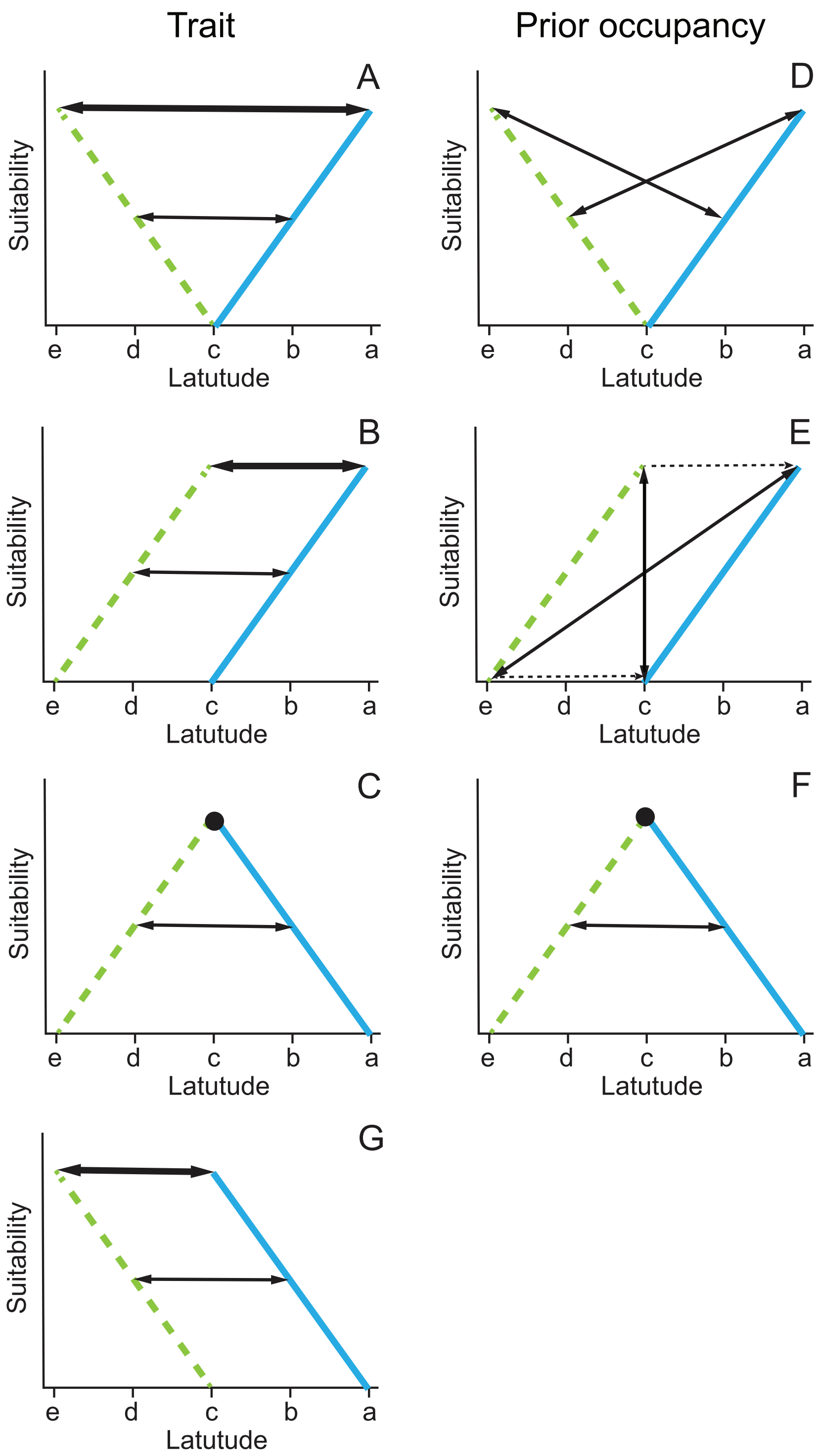

Figure 2. Illustrations of suitability gradients as a function of latitude with migration cost included for different evolutionary scenarios, under which chain or leapfrog migration may evolve. Solid (blue) lines refer to breeding suitability (sites a-c), whereas broken (green) lines refer to winter suitability gradients (sites c-e). Filled (black) circle refer to resident population. Panels A-F refer to scenarios outlined in Holmgren and Lundberg (1993), with panels A-C referring to trait-related dominance, and panels D-F prior occupancy-related dominance. Leapfrog migration evolves under panels A, C, E, and F, whereas chain migration evolves under panels B and D. Panel G is a new situation considered here where dominance due to body size leads to chain migration. In panel G, dominant (large) birds will exclude subdominant (small) birds from the best breeding site (c), and after breeding they will migrate to the most favorable (e) site for wintering (upper arrow). Subdominants will be forced to adopt the b-d route (lower arrow), hence chain migration arise. Latitude a-e varies from north to south. For further information, see main text, and Holmgren and Lundberg (1993).

migration will evolve if breeding and wintering period suitability gradients increase toward the north in combination with trait-related dominance. In the second scenario of competitive exclusion through prior occupancy, chain migration will evolve when the suitability gradients during breeding season increase toward north and wintering suitability increases toward south (Holmgren and Lundberg 1993; Fig. 2D). An unstable situation may evolve when suitability in breeding and wintering areas is parallel, leading to individuals following a loop pattern between seasons (Fig. 2E; Holmgren and Lundberg 1993). A new situation leading to chain migration (Fig. 2G) occurs when breeding and wintering period suitability gradients increase toward the south in combination with trait-related dominance. Based on individual movement data from different populations across the breeding range and information on spatial suitability gradients in the breeding and nonbreeding ranges, the assumptions behind the alternative scenarios can be evaluated. Here, we used tracking data from common swifts *Apus apus* to do so.

The common swift shows extraordinary adaptations for an aerial life style, including high aspect ratio wings, streamlined body, energy-saving flap-gliding flight, and likely also sleep while on the wing at night (Lack 1956; Lockley 1970; Weitnauer 1975; Bäckman and Alerstam 2001; Lentink et al. 2007; Henningsson et al. 2008; Åkesson et al. 2012; Muijres et al. 2012; Dokter et al. 2013; Sachs 2017), allowing for practically continuous flight during the nonbreeding period (Hedenström et al. 2016). Their migration routes and wintering areas were, until recently, largely unknown (Perrins 2005; Fransson et al. 2008; cf. Åkesson et al. 2012). The migration patterns observed are the result of both inherited differences and those that arise between individuals through their distinctive ontogenetic experiences (Åkesson et al. 2012, 2016; Wellbrock et al. 2017; Åkesson and Helm 2020).

We recorded the migration of 102 individual common swifts from 11 populations (grouped by country or region) across extensive parts of the European breeding range using geolocators (Åkesson et al. 2012, 2016). We used data from tracked individual common swifts, morphological measurements, and clutch sizes collected across the breeding range to characterize and interpret putative ecological factors that may lead to either leapfrog or chain migration pattern in this species, as outlined above. We assumed that competitive dominance by body size and/or prior occupancy could lead to dominant individuals being able to monopolize the most favorable habitats for breeding and wintering (Lucas and Fretwell 1970; Fretwell 1972), which in combination with relevant suitability gradients during breeding and winter seasons may lead to specific migration patterns. We hypothesized that the strongest competition for resources in aerial insectivorous swifts is met during breeding (i.e., nest sites; Lack 1956), and that flying insects as food cannot be directly monopolized by swifts, but when locally exploited may lead to diffuse competition (Pianka 1974). Because swifts are highly mobile and may have difficulties to monopolize resources outside the breeding season, we expected that dominant individuals will occupy the most favorable breeding sites and that winter distribution is a consequence of prior occupancy contingent on which population can get to the most favorable wintering areas first.

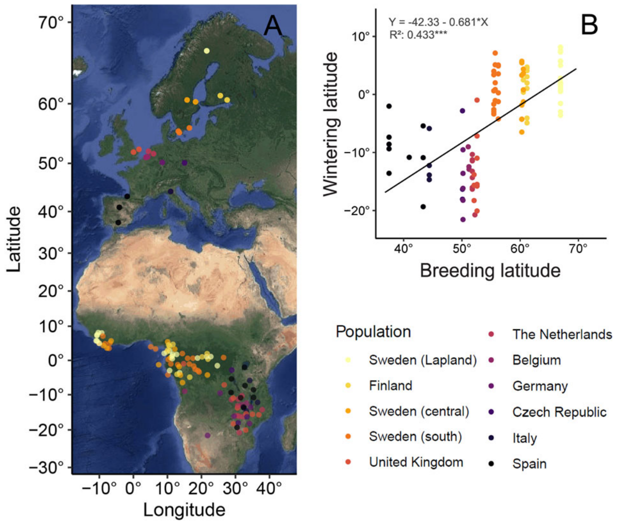

Figure 3. Geographic distribution of breeding and wintering locations for European common swifts. (A) The breeding and wintering locations of all tracked individuals. Locations for each individual are color coded for each population (see color in legend for Fig. 3), with breeding locations north of 30°N and wintering sites south of 10°N. (B) The relationship between the mean latitudes of the locations during breeding and wintering season for each individual (color coded with respect to population).

Methods

STUDY SITES AND CAPTURE OF BIRDS

We tracked a total of 102 adult breeding common swifts at 21 sites grouped into 11 populations in Sweden (three populations), Finland, United Kingdom, the Netherlands, Belgium, Germany, the Czech Republic, Italy, and Spain (Table 1; Fig. 3A). Complete annual tracking data from six birds have been used in a previous study (Åkesson et al. 2012), whereas the rest remain unpublished for the nonbreeding period. Data are stored at the publically available CAnMove tracking database (www.canmove.lu.se and at https://doi.org/10.5061/dryad.cz8w9gj1w). The locations were selected to cover as extensive parts as possible of the European breeding range (37.48° to 66.92°N) of the common swift, and were located at study sites where we were able to work for at least two seasons, as we needed both to attach and retrieve the archival data loggers from individual birds at the same location after 1 year of data recording. The swifts were captured with mist nets outside the entrance of the nest in nest boxes or inside

Table 1. Median date and ranges of departures from and arrival to breeding areas for the European common swift populations as revealed by common swifts tracked by geolocation. Average one-way migration distance (±SD) calculated as great circle route distance (in km) from the breeding site to the average winter location in November–December is given.

		Departure date breeding area		Arrival date breeding area			
Population	N	Median	Range	Median	Range	Average migration distance (km)	SD migration distance (km)
Sweden, Lapland	19	15 Aug	7 Aug–9 Sep	31 May	17 May–9 June	7304	247
Sweden, Central	11	10 Aug	29 July–22 Aug	23 May	12 May–7 June	6760	399
Sweden, South	19	12 Aug	28 July–27 Aug	26 May	11 May–6 June	6200	272
Finland	10	29 July	26 July–14 Aug	21 May	10 May–27 June	6717	355
The Netherlands	9	17 July	1 July–28 July	6 May	3 May–8 May	7776	387
United Kingdom	9	23 July	19 July–30 July	9 May	5 May–19 May	7800	802
Belgium	3	29 July	8 July–4 Aug	7 May	6 May–18 May	7331	434
Czech Republic	3	14 July	13 July–16 July	4 May	30 Apr–8 May	7118	946
Germany	5	2 Aug	31 July–4 Aug	4 May	20 Apr–7 May	7620	496
Italy	4	15 July	7 July–18 July	27 Apr	12 Apr–3 May	6656	408
Spain	9	19 July	3 July–8 Aug	29 Apr	4 Apr–18 May	6628	561

Table 2. Mean (±SD, *N*) wing length (mm) and mass (g) for adult common swifts captured at the breeding sites (Latitude and Longitude in degrees) in Europe.

Population	Site	Latitude (°)	Longitude (°)	Mean wing length (mm)	SD wing length	*N*	Mean mass (g)	SD mass (g)	*N*
Sweden (Lapland)	Hakkas	66.92	21.55	173.0	4.01	118	41.6	2.42	116
Finland	Lammi	61.17	25.55	176.0	5.00	28	43.6	2.56	28
Sweden (central)	Falun	60.55	15.78	174.6	3.54	22	40.6	2.80	20
Finland	Harju	60.55	27.55	172.4	3.23	23	41.6	2.31	24
Sweden (central)	Barkö	60.28	18.26	173.2	3.51	37	39.5	2.37	36
Sweden (south)	Ås	56.24	16.45	174.0	3.54	53	40.2	2.28	56
Sweden (south)	Lund	55.71	13.21	173.7	3.54	39	42.5	2.97	41
Sweden (south)	Skurup	55.47	13.50	174.0	4.28	11	44.5	2.87	11
United Kingdom	Great Yarmouth	52.59	1.66	175.5	3.02	41	43.8	2.14	6
United Kingdom	Fowlmere	52.08	0.06	175.0	1.73	3	–	–	–
Netherlands	Groesbeek	51.78	5.94	175,9	2.60	18	44.4	4.80	19
Belgium	Gent	51.08	3.73	173.8	3.42	5	43.1	1.47	3
Belgium	Hechtel	51.20	3.81	174.3	2.11	17	44.0	2.98	18
Belgium	Melsele	51.22	4.28	172.5	4.36	14	40.6	2.31	13
Germany	Kronberg	50.18	8.52	176.7	5.16	6	41.6	2.31	24
Czech Republic	Pečky	50.09	15.03	173.9	5.84	10	45.2	2.86	10
Italy	Modena	44.39	10.95	174.3	3.75	221	42.7	2.32	15
Spain	Guipúzcoa	43.34	-1.79	173.4	3.42	36	41.1	2.59	36
Spain	Lugo	43.01	-7.56	176.8	3.35	146	44.7	4.02	146
Spain	León	42.66	-5.61	173.5	3.87	4	40.6	2.39	4
Spain	Barcelona	41.93	2.26	176.7	3.51	66	41.1	3.47	65
Spain	Segovia	40.95	-4.11	175.1	4.19	100	40.8	3.53	100
Spain	Madrid	40.37	-3.24	173.0	4.20	44	43.5	2.80	44
Spain	Ciudad Real	38.99	-3.93	173.6	2.19	5	43.0	5.24	5

buildings, or by catching the breeding birds inside the nest (Table 2). The attachment of geolocators was timed to the late stages of the breeding period when the young were near to leaving the nest for migration departure or the adults were still active feeding the young (second half of the feeding period). Return rates for logged common swifts are high in the Scandinavian study populations (Åkesson et al. 2016), but the loggers may still have some impact on the survival of swifts (Morganti et al.

Table 3. Mean maximum number of young in nest (±SD), number of nests (*N*), and range of years for common swifts at 14 breeding colonies (Latitude and Longitude in degrees) in Europe.

Population	Site	Latitude (°)	Longitude (°)	*N*	Mean max young	SD	Year
Sweden (Lapland)	Hakkas	66.92	21.55	29	1.81	0.47	2015
Finland	Lammi	61.17	25.55	59	1.90	0.48	2013–2014
Sweden (central)	Falun	60.55	15.78	25	1.92	0.49	2011–2014
Finland	Harju	60.55	27.55	12	2.16	0.58	1999–2009
Sweden (central)	Barkö	60.28	18.26	44	1.75	0.53	1984–2003
Sweden (south)	Lund	55.71	13.21	32	1.84	0.57	1998–2014
Sweden (south)	Skurup	55.47	13.50	66	2.15	0.52	1992–2014
United Kingdom	Great Yarmouth	52.59	1.66	33	2.09	0.63	2004–2014
United Kingdom	Fowlmere	52.08	0.06	12	2.25	0.62	2010–2013
Belgium	Zelzate	51.20	3.81	8	1.75	0.71	2010–2014
Germany	Kronberg	50.18	8.52	928	2.28	0.62	1990–2014
Italy	Modena	44.39	10.95	812	2.40[1]	–	1991–2015
Spain	Barcelona	41.93	2.26	41	2.02	0.65	2009–2018
Spain	Ciudad Real	38.99	-3.93	75	2.35	0.80	2006–2018

[1] Mean maximum young in nest calculated based on maximum total number of nests and young in a given year, and calculated as an average for all years.

2017). The adult birds were later recaptured upon arrival or at the same stage of breeding the second year. Permissions to trap birds were obtained from the land owners and national bird ringing organizations, and permissions to attach geolocators to common swifts at breeding colonies were given from the local authorities in the respective countries.

Wing length (maximum chord; Svensson 1992) was measured to the nearest mm using a ruler and body mass (to the nearest 0.1 g, excluding logger) was recorded by an electronic balance or a Pesola spring balance for adult swifts with and without loggers being attached and captured at the breeding sites (Table 2). Wing length and body mass were measured by experienced ringers. Common swifts lay one clutch of eggs per season (Lack 1956), and therefore maximum young in nest can be used to measure annual breeding investment. Maximum number of young in nest during mid to end of the breeding period were recorded for 1389 clutches in 14 breeding colonies from where adult swifts were tracked, or ringed and measured at time of feeding young (Table 3).

GEOLOCATION

For the first year (South Sweden; 2009–2010), we retrieved six archival Mk10 geolocators from the British Antarctic Survey (BAS), whereas for the remaining period we retrieved 96 archival light loggers (Model Intigeo-W55B1 and W65B1) from Migrate Technology Ltd. All geolocators used were without a stalk (Morganti et al. 2017). The geolocators were attached to the common swifts with a full body harness made of a soft nylon string, with three loops around neck and each wing, respectively (Åkesson et al. 2012). Depending on model, the mass of the geolocators, including harness, was 0.7–1.3 g, which never reached above 3% of the birds' body mass (Åkesson et al. 2012). We had carefully evaluated the attachment method and monitored the effect of attachment on breeding birds in an initial study year (summer 2009) before the loggers were mounted to birds in the same colony over winter (2009–2010). During this time, we did not observe any negative effects of attachment on the breeding performance, returns, and timing of migration (Åkesson et al. 2012). In later years (2010–2016), we attached geolocators in the remaining colonies with the same attachment method. We did not find any negative effects on plumage or skin caused by the attachment of the geolocators on recaptured common swifts the year after attachment.

We used a linear correction function for our light data to correct for clock drift using the program BASTrack, and extracted times for sunrise and sunset using a single light threshold of 2 by the program Trans Edit (BAS 2010). Thereafter, we used the Bird-Tracker software to calculate latitude and longitude positions (BAS 2010), by inferring latitude from the length of the solar day/night and longitude from the time of local noon/midnight. The critical sun angle corresponding to a light-level value of 2 on the arbitrary geolocator light scale (BAS loggers) and based on light values in lux (Migrate Technology Ltd) was used. The critical sun angle used minimized the difference in latitude between pre- and postequinoxes, and at the same time minimized the uncertainty in latitude close to equinox for periods when the birds were stationary as defined by the estimations of longitude. We used the "Hill-Ekstrom" procedure (Ekstrom 2004) to evaluate which sun angle to use for each respective track and model of geolocator as outlined in Åkesson et al. (2012). The sun angles used varied between –3.0 to –5.0 (BAS) and –6.0 to –7.0 (Integeo) degrees. We excluded data on latitude and longitude corresponding to approximately 14 days before and after autumn and vernal equinoxes, respectively, and 21 days after and before autumn and vernal equinoxes, respectively. In addition, single erroneous light measurements outside the equinox periods were deleted from the tracking data (0–3 instances per individual). The errors generated by archival light-level geolocators are influenced by geographic location, time of year, habitat, and weather and correspond to values of 143 ± 62 km (mean ± 95% confidence interval) in terrestrial environments (Fudickar et al. 2012) and 186 ± 114 km (mean ± SD) in marine areas (Phillips et al. 2004) for latitude. Errors of longitude estimates are lower at 50 ± 34 km (mean ± 95% confidence interval) (Fudickar et al. 2012) and 85 ± 47 km (mean ± SD) (Phillips et al. 2004), for the two habitat types, respectively. For terrestrial birds, weather, topography, and vegetation have the strongest impact on accuracy in geolocator tracking data leading to shading and variations in light intensity (Lisovski et al. 2012). However, for common swifts spending the nonbreeding period on the wing (Hedenström et al. 2016), mainly weather will influence the precision, resulting in typically very clean light measurements without shading effects (Åkesson et al. 2016). More in-depth discussions on effects of location errors on evaluations of common swift geolocation data and examples of typical light level curves are presented in Åkesson et al. (2012, 2016).

In this study, our aim was to characterize timing of migration and seasonal range use. Based on light measurements resulting in two positions per day, we calculated a mean location per day. The daily latitude and longitude positions were used to calculate average latitude and longitude positions used for different periods and migration displacement. We calculated the average latitude and longitude positions per month for the period of late autumn and winter residency (October–December), for individual swifts belonging to the northern and southern part of the range. We also correlated the breeding latitude with the average winter latitude (November–December) for each tracked individual, for all birds combined as well as separately within each breeding region (North: Fennoscandia; South: central and southern Europe). Migration displacement was calculated as the great circle distance (Imboden and Imboden 1972) from the breeding locations to the average winter positions in November–December.

NORMALIZED DIFFERENCE VEGETATION INDEX

Many terrestrial animal species are known to synchronize their migratory movements to the changes in availability of food, often measured by an index of changing greenness such as the Normalized Difference Vegetation Index (NDVI; varies between 0 and 1) (Singh et al. 2010; Thorup et al. 2017; Norevik et al. 2019). We acquired NDVI data from MODIS – Product MYD13A2 (http://modis-land.gsfc.nasa.gov/vi.html) (NASA Land Processes Distribution Active Archive Center 2001), and filtered and interpolated it to daily scale for the entire swift range, using a Whittaker smoother function (Atzberger and Eilers 2011). To demonstrate changes in habitat suitability across latitudes over the winter months, we created delta (change) NDVI (rasters), as a difference between the ActualNDVI at a pixel, on a particular time point, and AnnualMeanNDVI at the same pixel, for the entire wintering period. We did this for the entire latitudinal gradient and for the entire time period of the study to then obtain a mean temporal trend (Forkel et al. 2013) at each swift location and plotted the variation against latitude (Fig. S1).

STATISTICAL ANALYSES

We expected to find a linear relationship between breeding and wintering latitude for the common swifts, either with the northern breeding populations wintering furthest to the north corresponding to a chain migration pattern or the northern populations wintering furthest to the south as for leapfrog migration. Clutch size of birds has been shown to be affected by resource availability (e.g., Lack 1954) and may vary with latitude (Ashmole 1963). We used maximum number of young in nests as a measure of breeding investment, and a proxy for resource availability (suitability) for the breeding season. We expected to find the largest clutch size in the northern part of the range, as predicted by Ashmole (1963). In addition, we used an index of changing greenness, NDVI (e.g., Singh et al. 2010), extracted from the nonbreeding range of the tracked common swifts to evaluate latitudinal gradients of food resources within the African nonbreeding range (i.e., insects associated with growing vegetation; Sinclair 1978; Thorup et al. 2017) by using R (R Development Core Team 2013). We expected the highest resource availability measured as NDVI trend to be available in the southern part of the nonbreeding range in midwinter.

Geographic variation in wing length (mm) and body mass (g) in relation to breeding latitude was analyzed with linear mixed models. To control for yearly variations in mass and wing length, we used year of capture as a random factor and latitude as a fixed factor. The relationship between body mass and wing length for individual birds was evaluated with a linear model. To analyze how maximum number of young in nest vary with breeding latitude, we used latitude as fixed factor and year and site as random factors in the linear mixed model. Timing of migration and migration displacement (great circle route distance) in relation to breeding latitude and population were analyzed with a linear mixed model, with year as a random factor and breeding latitude as fixed factor. We used JMP Pro 14.3.0 (SAS Institute Inc. 2018)

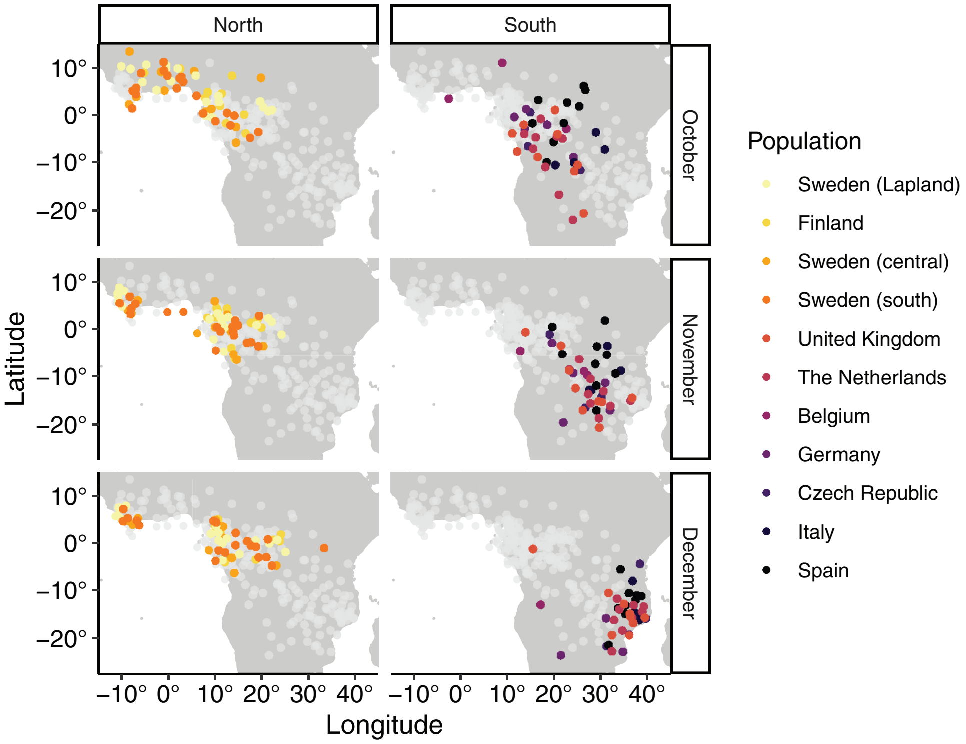

Figure 4. Average locations per month for all common swifts in sub-Saharan Africa in winter with respect to breeding region (North, South) in Europe. Each location refers to the average latitude and longitude position for one individual during one month (October, November, and December) and are color coded with respect to population. North includes populations (>55°N Latitude; N = 60 individuals) in Sweden and Finland, whereas South refers to populations (<55°N Latitude; $N = 42$ individuals) in Belgium, the Czech Republic, Germany, Italy, the Netherlands, Spain, and the United Kingdom.

for all statistical tests and R (R Development Core Team 2013) for producing maps.

Results

MOVEMENT PATTERNS

Across all populations, we found that the breeding and average wintering latitudes of European common swifts ($F_{1,101} = 76.24$, $P < 0.0001$; Fig. 3A) were positively correlated (Fig. 3B). The more northern, that is, Fennoscandian (Finland and Sweden), populations wintered in western and central Africa, whereas the central and southern European populations wintered in central to southeast and southern Africa (Figs. 3A and 4), to where they arrived later in winter (December; Fig. 4). The locations of individual birds in December show three major wintering regions in Africa (west, central, and southeast), where northern populations of common swifts spend the winter in west and central sub-Saharan Africa, and southern European swifts aggregate in central and southeast Africa (Fig. 4). There was overlap between nearby populations in area used (Fig. 4). The migration displacement (i.e., great circle route distance between breeding site and center of nonbreeding area in December) was on average 6739 km (±SD: 539 km; $N = 60$) for northern populations (November–December), whereas the average distance for the southern populations was 7331 km (±SD: 752 km; $N = 42$). There was no difference in migration displacement (calculated as great circle route distance between breeding site and average wintering area in November–December) in relation to breeding latitude ($F_{1,27} = 0.15$, $P > 0.05$).

ANNUAL TIMING

The common swifts departed from their breeding grounds later in the season with increasing breeding latitude ($F_{1,56} = 82.41$, $P < 0.0001$; Fig. 5). The most northern population in Swedish Lapland migrated approximately 1 month later from the breeding area than the birds breeding furthest to the south in Italy and Spain (Table 1; Fig. 5). The median departure dates for all populations leaving the breeding areas ranged from 14 July to 15 August (Table 1). In spring, arrival to the breeding areas first occurred in the southernmost breeding populations, with the most northern populations arriving approximate 5 weeks later (range of median arrival dates for all populations: 27 April to 31 May; Table 1) ($F_{1,21} = 96.17$, $P < 0.0001$). Autumn departure from the breeding areas and spring arrival date to the same locations thus show an annual cycle shift in timing, where the most northern

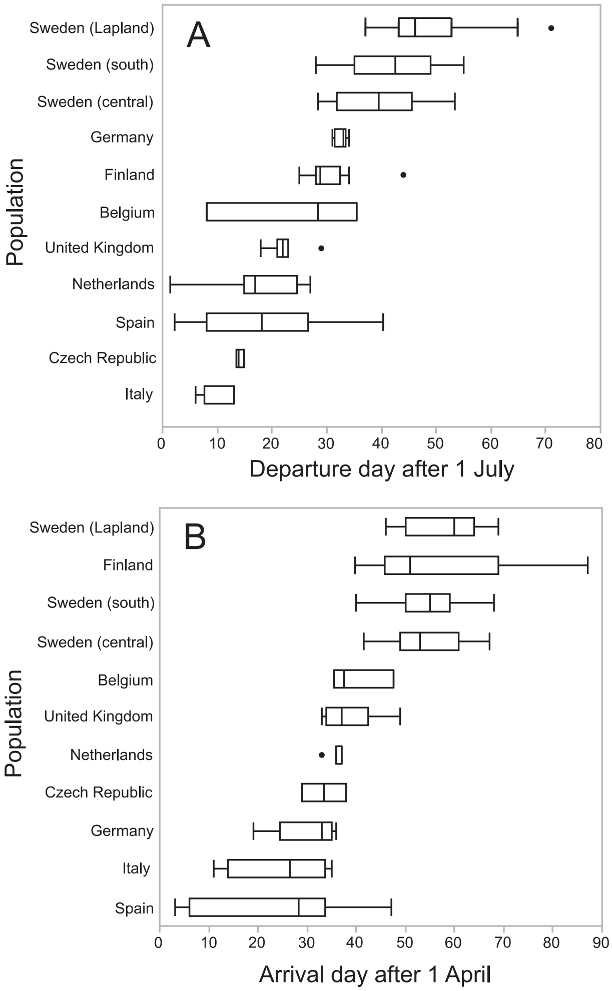

Figure 5. **Time of departure from and arrival to the breeding sites from the different populations of European common swifts. Box plot of mean day of departure from breeding areas relative to 1 July (A) and mean arrival day to breeding sites relative to 1 April (B) is given for 11 study populations.**

(Fennoscandia) and southern (Central and South Europe) populations differ in timing by approximately 1 month (Fig. 5).

Movements to nonbreeding areas in sub-Saharan Africa coincided with the local green-up after rainfall and inferred availability of newly hatched insects in southeast Africa as the Inter-Tropical Convergence Zone (ITCZ) moved south in winter, resulting in a positive NDVI trend for this region at this time of year (Fig. S1). Despite the partial overlap between the two groups (i.e., Northern: Fennoscandia; Southern: central and southern European) in the central African wintering range (Figs. 3 and 4), the temporal separation leads to an overall chain migration pattern for European common swifts.

BODY SIZE AND REPRODUCTIVE OUTPUT

We were able to collect wing lengths from 1108 adult common swifts at 24 study sites and body mass from 862 individuals captured at 23 sites across the European breeding range. We found a significant positive correlation between wing length and body mass ($F_{1,853} = 37.53$, $r^2 = 0.042$, $P < 0.001$; Fig. 6A) for swifts with both measurements recorded. There were further significant negative relationships between wing length and breeding latitude ($F_{1,165} = 14.68$, $P < 0.001$; Fig. 6B and Table 2), and between body mass and breeding latitude ($F_{1,268} = 12.46$, $P < 0.001$; Fig. 6C and Table 2), resulting in a pattern where the smallest birds breed in the most northern part of the range and the largest birds breed in the south.

We used young in nest as a proxy for suitability during breeding, and found a significant decrease in reproductive output measured as maximum number of young per clutch with increasing breeding latitude ($F_{1,11} = 13.44$, $P = 0.0037$; Fig. 7 and Table 3).

Discussion

MOVEMENT PATTERNS AND ANNUAL TIMING

Our tracking data revealed a positive relationship between breeding latitude and average wintering latitudes of European common swifts, corresponding to a chain migration pattern (Fig. 1; Salomonsen 1955; Newton 2008). This pattern, we argue, likely emerges from differential phenology due to competitive exclusion at the breeding sites, with 4–6 weeks earlier start of breeding in the southern part of the range and earlier postbreeding departure from the same sites as compared to the populations in the north. The shifted phenological pattern across latitudes in turn translates to other parts of the annual cycle, and leads to differential arrival times to the nonbreeding areas in sub-Saharan Africa for the different populations. Differential timing of breeding related to latitude may cause cascading effects on later life history events throughout the annual cycle, as shown for American tree swallows (Gow et al. 2019). The differential timing of migration, with the most southern swift populations leaving their breeding areas first (Fig. 5), therefore likely leads to a migration pattern where the early arriving swifts occupy the most suitable wintering areas in sub-Saharan Africa (Fig. 2G). Rainfall associated with the movement of the Inter-Tropical Convergence Zone (ITCZ) in Africa, and regrowth of vegetation has been shown to affect insect prey numbers (Sinclair 1978), and associated winter movements in wintering migrants (Thorup et al. 2017), including swifts (Norevik et al. 2019). The most southern European populations of common swifts exploring the most southern nonbreeding range in Africa therefore perform substantial movements across the season following the rains and regrowth of vegetation. This in turn leads to substantial range shifts and population mixing for this group of swifts in southeastern Africa, whereas the later arriving northern swifts will remain in the northern part of the nonbreeding range with more restricted winter movements (see

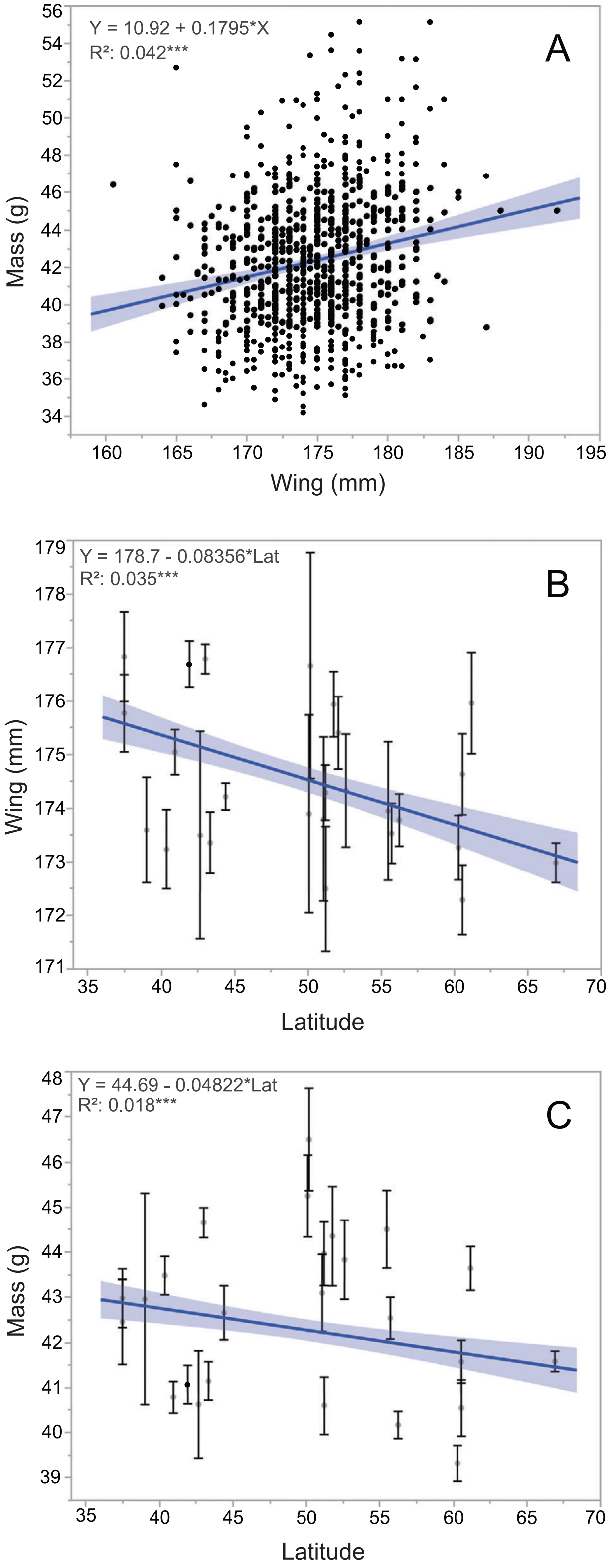

Figure 6. Latitude variations of body mass measured as wing length and mass. Relationships between mass (g) and wing length (mm) (A), wing length (mm) and breeding latitude (deg N) (B), and mass (g) and breeding latitude (deg N) (C).

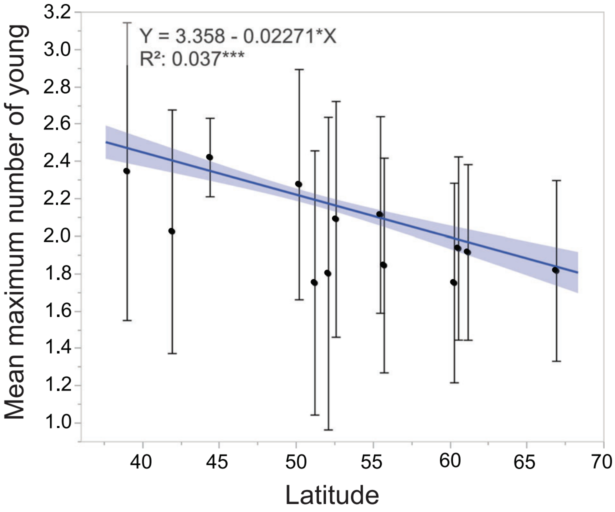

Figure 7. Mean maximum number of young (±SD) in relation to breeding latitude for common swifts in Europe. The maximum number of young per nest was recorded after hatching in the middle of the breeding period for 13 populations.

seasonal movement trend in panels for north and south populations; Fig. 4), as also shown in previous tracking studies (Åkesson et al. 2012).

BODY SIZE SELECTION AND SUITABILITY GRADIENTS

The size-related pattern with smaller swifts breeding in the northern part of the range is contrary to the pattern postulated by Bergmann's rule (i.e., that the largest individuals occur in the most northern parts of the range; Ashton 2002). We propose that there may be at least three scenarios under which natural selection could favor such body size cline in our swifts related to breeding and wintering latitudes. We found that the later arriving northern (smaller) swifts explore the most northern part of the range closest to the equatorial region following a chain migration pattern. First, selection may operate in the wintering range, where warmer wintering sites and higher solar radiation close to the equator as experienced by northern breeding populations may select for smaller body size. Support for body size reduction in response to higher temperatures comes from metabolic theory, where metabolic rate, that is, the rate at which the organism expends, energy and materials vary with body size and temperature (Brown et al. 2004). Exposure to higher temperatures may, according to this hypothesis, lead to smaller body size. Second, northern breeding swifts may have evolved smaller body size because of periods of reduced food resources at their northern breeding sites. Because smaller birds have lower absolute resource requirements and lower cost of transport (Pennycuick 1989), they may more successfully get through such periods, as compared to larger conspecifics. This scenario may apply to the northern part of both the breeding and the wintering ranges, where cold spells (breeding) and droughts (nonbreeding) may be frequent due to extreme weather events (Boano et al. 2020), but needs to be confirmed by future studies. A third scenario may be, if there is strong competition for breeding sites in the south of the breeding range, larger individuals may have a competitive advantage to occupy and defend nest sites (Lack 1956), promoting early start of breeding as compared to small individuals. These three scenarios may contribute to differential body size evolution of common swifts, leading to similar patterns of body size variation across latitudes, with smaller individuals exploring the northernmost ranges. However, based on available data we cannot distinguish between these three hypotheses, or if they all contribute to the observed pattern.

For chain migration to evolve in a north hemisphere perspective, suitability gradients (i.e., food as resource) are expected to increase poleward, as proposed by Holmgren and Lundberg (1993) (Fig. 2B). This situation may lead to higher reproductive output and increased survival in birds breeding at higher latitudes (Holmgren and Lundberg 1993). As a proxy for suitability related to foraging efficiency, we used maximum number of young in nest. We found a significant decrease in reproductive output with increasing latitude, which is contrary to the theoretical predictions for chain migration to evolve (Holmgren and Lundberg 1993; Fig. 2B). The reduction in breeding success with increasing latitude as observed for the swifts in this study is in contrast to previous findings for most passerines where clutch size increases with increasing latitude (Ashmole 1963). Clutch size variation is, however, a complex trait, and may be affected by several ecological factors apart from latitude. Other ecological factors that vary with latitude that may contribute to reproductive output in avian migrants include food resources showing increasing seasonal amplitude with increasing latitudes and reduced competition for food during breeding with increasing latitude. Reduced competition could be due to population limitation of residents at northerly latitudes because of high winter mortality due to harsh winter conditions with increasing latitude (Ricklefs 1980; cf. Ashmole 1963). On a global scale, the highest clutch sizes in birds typically occur in highly seasonal environments (Jetz et al. 2008). However, there may still be several abiotic and biotic factors acting on clutch size evolution, related to, for example, life history traits, life span, and social mating behavior, which may vary independently of latitude in different species of birds (e.g., Lack 1954; Cody 1966; Godfray et al. 1991).

MOVEMENTS IN RELATION TO NDVI AND AERIAL PREY

Insect abundance in tropical Africa is largely affected by local rainfall and the associated green-up (increase in NDVI), and shows substantial variation between seasons (Sinclair 1978). Insect peak numbers occur approximately 1 month to 6 weeks after the start of rainfall (Sinclair 1978). Thus, the movement of the ITCZ south across the African continent in October to January is expected to be associated with high abundance and large concentrations of aerial insect prey (Drake and Reynolds 2012). In this geographical range particularly, swarming termites may be exploited by aerial foraging swifts (Voipio 1970).

We used vegetation green-up as a proxy for habitat suitability (i.e., measured as positive gain in NDVI, which is thought to correlate with insect abundance; Thorup et al. 2017; Norevik et al. 2019). During the wintering period in sub-Sahara Africa (November to February), NDVI increased from the equator toward the south because of increased seasonality (Fig. S1C). The southern and central European swifts seem to explore the latitude ranges with the relative highest NDVI (Figs. S1A and S1B). Reproductive output in South African birds correlates with the same suitability gradient of NDVI, with the highest output in peak NDVI areas (Hořák et al. 2015). The wintering locations for the southernmost breeding swifts overlapped with the areas with highest NDVI (Latitudes 10 to 20°S; Figs. 3 and S1). At the same time, the northernmost breeding swifts, mainly wintering in west and central Africa covered by rain forest, where NDVI is difficult to use to reveal local green-up due to low seasonal variation, still remained at latitudes with the highest values for these areas (Fig. S1). The arrival of the southernmost populations to wintering areas in eastern and southern Africa occurred when the ITCZ moves south, resulting in increased overall NDVI for the areas used (Funk and Brown 2006; Jamali et al. 2011; Fig. S1). The high abundance of aerial insect prey (i.e., NDVI) leads to the predicted high suitability in the south of the wintering range for aerial insectivores such as swifts and swallows at this time of year, which is also shown by bird preference around a positive NDVI trend (Fig. S1).

EVOLUTION OF MIGRATION PATTERNS

The evolution of migration patterns can be understood in terms of latitudinal suitability gradients and competitive exclusion (Lundberg and Alerstam 1986), either as trait- or prior occupancy-related dominance (Holmgren and Lundberg 1993). Theory has shown how both typical leapfrog and chain migration patterns may arise under different combinations of suitability gradients and competitive exclusion mechanisms (Lundberg and Alerstam 1986; Holmgren and Lundberg 1993). For the common swifts in this study, breeding season suitability decreases from south to north measured as number of young, whereas winter period suitability in sub-Saharan Africa increases from the equator toward the south (NDVI, see above). This combination of suitability gradients has not been considered previously (Holmgren and Lundberg 1993).

We proposed an alternative scenario, illustrated by a schematic model of suitability gradients during summer and winter as shown in Figure 2G, where competitive advantage due to trait-related dominance on the breeding grounds leads to chain migration. In this scenario, dominant (large) birds will exclude subdominant (small) birds from the best breeding sites in the south (c; Fig. 2G), and after breeding they will migrate to the most favorable sites (e) for wintering (Fig. 2G, upper arrow). Subdominants will be forced to adopt the b–d route leading to wintering sites further to the north (Fig. 2G, lower arrow), hence giving rise to chain migration. The shifted annual phenology of approximately 4 weeks across the common swift latitudinal breeding range will further promote the arrival time advantage of the dominant (larger) individuals breeding in the south of the range.

Competition for nest sites can be fierce in the common swift, sometimes even leading to death as a result of fighting (Lack 1956). Prior occupancy leading to diffuse competition for food in winter, by the earlier arriving swifts from southern and central Europe, may further exclude later arriving swifts from using the foraging niche of aerial insects in southern Africa. Whether competition for food is primarily expressed as diffuse competition or direct interactions between individuals of common swifts, however, needs to be further investigated. A swarm of large bodied swifts already in the south may diffusely exclude smaller, latecoming swifts from going there if competing for food (Pianka 1974). The European population of common swifts constitutes about 40% of the world population, and have been estimated at 38–65 million individuals (BirdLife International 2018). As the foraging niche in the southern part of Africa is filling up with millions of early arriving swifts from Europe as well as from Asia, the benefit for late-arriving northern (i.e., Fennoscandian) populations from remaining in the more northern wintering range may outweigh the cost of traveling further south. At this time of year (September to November), the NDVI trend is strongly positive in southern Africa because of recent rainfall due to the ITCZ moving south, whereas areas near the Sahel zone in the northern part of the wintering range are drying up (e.g., Thorup et al. 2017; Norevik et al. 2019). The highest abundance of flying insects is therefore expected in the southern part of the nonbreeding range in late autumn. We therefore think the reason for northern late arriving swifts to remain in the north could be primarily related to diffuse competition (Pianka 1974). Body size-related dominance and competition for breeding sites in combination with an unusual arrangement of breeding and wintering suitability gradients and differential annual timing of migration as we propose here are likely drivers leading to the evolution of a chain migration pattern in the common swift.

Even though the typical chain migration pattern may be rare (Salomonsen 1955; Newton 2008; cf. Smith et al. 2003; Fort et al. 2012), it seems to make perfect sense for an aerial feeder that depends on airborne insects emerging during only a short period at high latitudes, and spending most of its life on the wing (Hedenström et al. 2016). Even if our analysis is specific to a rare migration pattern in one species, our approach of identifying how large scale resource gradients vary across space and time combined with likely competitive traits such as body size could be applied more generally to understand the evolution of animal migration patterns. The annual timing of movements relative to environmental conditions is challenging for long-distance migrating birds (Åkesson et al. 2017), but seems to be essential for the evolution of chain migration in common swifts. Swifts are highly responsive to dynamic foraging conditions due to their highly mobile lifestyle (Hedenström et al. 2016), and are therefore the most likely birds not to show the kinds of historical legacies that are likely to shape the evolution of leapfrog patterns so common in other birds (Newton 2008). Swifts are thereby different from the vast majority of obligate and mostly nocturnal migrants that need to rely on evolved less temporally flexible decision-making systems (Åkesson and Helm 2020). Although competition for breeding sites may be a key driver in the evolution of chain migration and body size evolution in swifts as suggested here, we believe that the pattern likely is enforced by the differential circannual timing and habitat choice-related decisions to a dynamic resource gradient during nonbreeding that differ between northern and southern populations of swifts. It remains to be shown, however, if chain migration has evolved also in other migratory birds, and if so, if those are exposed to similar resource gradients and energetic demands as the swifts in this study.

AUTHOR CONTRIBUTIONS

SÅ designed the study, financed data collection, collected data and processed light logger information, evaluated tracking, morphological, and breeding data from different populations, and wrote the first draft of this article. NJS prepared and analyzed the NDVI and contributed to the writing of the manuscript. AH collected and prepared light logger data and contributed to the concept and writing of the manuscript. CMH, LK, and RHGK were leading data collection and prepared light logger data from The United Kingdom, Belgium, and The Netherlands, respectively, discussed concept of manuscript, and gave important input on the manuscript. PWA, AB, JP, MF, JH, EK, HK, GM, FM, GN, HP, FS, and LV contributed to data collection within their respective country and gave important input to the manuscript. Wing lengths were measured by experienced ringers (SÅ: all sites in Sweden, Harju in Finland; SÅ and EK: Germany; CMH: United Kingdom; RHGK: The Netherlands; LK: Belgium; HK: Lammi in Finland; LV: Czech Republic, MF: Italy, JP: Spain).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

The doi for our data is https://doi.org/10.5061/dryad.cz8w9gj1w.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Distributions of wintering latitudes for common swifts tracked by geolocation from breeding locations in northern (North) and southern (South) Europe in relation to NDVI trend.