Variation in migration distance does not affect arrival date in the subsequent breeding season of Dutch Barn Swallows *Hirundo rustica*

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Long distance migrants like Barn Swallows have to operate within narrow time-frames to fit post-breeding migration, wintering (including wing moult) and pre-breeding migration into their annual cycle. As a short-lived passerine, Barn Swallows have evolved towards maximising annual reproduction in order to increase fitness. To achieve this, a timely arrival at the breeding location is an important precondition to realise the necessary two breeding attempts. Ringing recoveries indicate that Dutch Barn Swallows winter across large parts of Central and Southern Africa. But ringing recovery data have limitations to analyse spatial-temporal occurrence throughout the annual cycle. We used geolocators to describe spatial and temporal aspects during migration and wintering of 20 Barn Swallows, breeding in The Netherlands (2011–2013). The results of our geolocator research and the ringing research showed broadly similar northern and southern limits of the wintering areas: from Ghana to South Africa. However, the centres of gravity of both methods differed completely. Geolocator-based wintering areas were mainly in the Congo Basin, from which no ringing recoveries are known. We evaluated correlations between timing, duration and distance travelled for the different stages of the annual cycle. The result that a longer post-breeding migration distance did not lead to a later arrival at the breeding location in the subsequent year, was contrary to our expectations. Despite methodological improvements made between research years, the results of this study came with a 'cost' for the birds involved. In both research years, the return rates of both geolocator groups were 17 percent points lower than their respective control groups.

Key words: geolocator, migration distance, wintering region, arrival date, annual cycle, repeated track, migration strategy, control group, return rate

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The well-known proverb “One swallow doesn’t make a summer” reflects the observation that the earliest individual Barn Swallows *Hirundo rustica* return to The Netherlands from their African wintering sites in spring, when adverse weather conditions still can occur. Results of Dutch migrating bird count sites for the timeframe 1993–2023 suggest that the ‘main force’ arrives mainly between 23 April and 23 May (10% and 90% percentile, respectively), with 8 May as the median date (www.trektellen.nl, accessed 12-8-2024). This large temporal variation in arrival makes one wonder about the factors that steer the timing of arrival, which is the subject of the current study.

As a generally appreciated passerine, nowadays breeding in The Netherlands predominantly in cow sheds and horse stables (van den Bremer *et al.* 2012), the Barn Swallow is familiar to a lot of people as an appealing example of a long-distance migrating bird. The species is notably well studied (e.g. Turner 2006). Concerns about the severe decline in the population by two-thirds since the mid-1950s (van Kleunen *et al.* 2017), combined with an urge to unravel population dynamics, were important motivations for the start of the Barn Swallow Project Netherlands in 1993 (B. van den Brink pers. comm.). As a result of this project, the life histories of hundreds of initiated breeding attempts are registered annually to date (B. Goffin, Sovon Vogelonderzoek Nederland pers. comm.), in general in combination with systematic ringing of nestlings and breeding adults to monitor annual recruitment and survival (van der Jeugd 2012). Between 1991 and 2023 (from May until July), about 244,000 Barn Swallows were ringed as nestling, fledgling or adult birds in The Netherlands (database of the Dutch Centre for Avian Migration and Demography). The Barn Swallow Project Netherlands was an inspiration for the EURING Swallow Project that was launched in 1997. In addition to the research goals outlined above, the EURING Swallow project promoted large scale ringing at communal Barn Swallow roosts throughout the flyway (see e.g. Spina 1998, 2001, van den Brink *et al.* 2000, Rubolini *et al.* 2002, Burman 2016).

Due to these large scale and long-lasting ringing efforts, the sub-Saharan wintering areas of Barn Swallows are relatively well known, especially for a small passerine. Western breeding birds mainly winter in Western and Central Africa, and birds breeding in eastern parts of Europe winter in central to eastern parts of Africa. Birds breeding in Northern Europe and the United Kingdom leapfrog these populations and winter in the southernmost regions of Africa (Zwarts *et al.* 2009, Ambrosini *et al.* 2011). Despite this migratory connectivity, ringing recoveries also show a notably large within-population variation in wintering sites. For example, ringing recoveries from Barn Swallows ringed in The Netherlands suggest that the majority of these birds winter in Central Africa (Nigeria), but that the wintering range spans from Western Africa all the way to South Africa (this study). This implies an up to two-fold difference in migration distances between individuals.

Migration takes time, and to cover a longer migration distance more time is required. This puts pressure on the annual cycles of long-distance migrants because they have to fit three major life-events (breeding, moult and migration) within each year. As these are physiologically demanding processes, species generally avoid temporal overlap between these events (Pérez-Tris *et al.* 2001, Jenni & Winkler 2020b). It is the reason why most long-distance migrants moult in the wintering quarters instead of during their relatively short stay at the breeding grounds. Being an aerial forager, Barn Swallows are faced with the additional challenge that their flight feather moult is rather slow compared to other similar sized passerines (Jenni & Winkler 2020a). The duration of the flight feather moult in Barn Swallows is on average 4.2 months (Burman 2016) but can take more than five months if environmental conditions are poor (van den Brink *et al.* 2000). So even though Barn Swallows spend 6–7 months outside their breeding area each year, they might have difficulty to migrate back and forth to sub-Saharan Africa and complete their flight feather moult within that period. This seems to be especially applicable to the individuals that winter farthest south and would supposedly have the longest migration durations.

The notable within-population variation in migration distance (and thus potentially migration duration), in combination with a relatively long duration of the flight feather moult, makes the Barn Swallow an excellent subject for a study on the consequences of variation in migration distance on annual cycles. A longer migration duration might carry over to a later arrival to the breeding area in the successive spring. However, as early arrival is associated with gaining a higher quality mate, enhanced reproductive success and higher recruitment rates for offspring, there is selection pressure for male Barn Swallows to arrive early at their breeding locations (see e.g. Pancerasa *et al.* 2022).

Despite all efforts and knowledge gained, ringing research has its limitations in unravelling detailed spatial (distances covered) as well as temporal parameters (date of arrival or departure) within the annual cycle of individual birds. It also requires large numbers of ringed birds, because the chance of recovery of a ringed small passerine is (very) low (Newton 2024). At the end of the first decade of the 21st century a new tool became available with the potential to fill both knowledge gaps: geolocators – tracking devices that were small and light enough to deploy on Barn Swallows. The application of any new type of device on a bird may cause unexpected effects on e.g. apparent survival, condition and breeding performance (Brlík *et al.* 2020). To detect undesirable effects, we compared the return rates of birds with and without a geolocator.

In this paper we explore the annual cycles of Barn Swallows breeding in The Netherlands by describing the 22 temporal migration patterns of 20 adult males tracked with geolocators in the years 2011–2012 and 2012–2013. Subsequently, we present their wintering regions, including within-winter relocations, and compare this pattern with the locations of historical ringing recoveries. Two repeated annual tracks provide a glimpse on interannual spatial variation within individuals.

As a final step, we evaluated correlations between timing, duration and distance travelled for the different stages of the annual cycle (for details see the method section). We hypothesize that there is a positive relation between distance covered during post-breeding migration and date of arrival in the wintering region. As all Barn Swallows, regardless of migration distance covered, must deal with a long period to complete the moult of their primaries, we expect that those individuals wintering farther from their breeding areas depart later from their wintering region. Therefore, we expect them to arrive later at their breeding location than individuals that migrated over shorter distances.

METHODS

Framework

Study system and study areas

This geolocator study was one of the activities of 'The Year of The Barn Swallow' (2011), a joint project in The Netherlands between Birdlife Netherlands and Sovon Dutch Centre for Field Ornithology (van den Bremer *et al.* 2012). The Dutch Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), selected the five study areas, containing a total of 18 breeding locations (Figure S1) including many that already participated in the Barn Swallow Project Netherlands or the national Retrapping Adults for Survival (RAS) monitoring programme (van Hoogen *et al.* 2014). As a result of this long-term annual systematic trapping effort, the (minimum) age of each bird could be determined during our study. The exception was the West-Betuwe area, where three extra RAS sites had to be added to the existing RAS site, to meet the annual threshold of 10 male geolocator birds and 10 male control birds per study area.

Geolocators

Geolocators record ambient light levels at pre-set intervals. Individuals must be caught again to remove the geolocator and retrieve the data. From the recorded timings of sunrise and sunset, locations can be calculated to indicate longitude, and the duration of daylight to indicate latitude. The accuracy of geolocator positions is rather coarse, especially around the equinox (particularly during the two weeks before and two weeks after 21 March and 21 September), when daylength is equal around the globe and latitude cannot be estimated (Lisovski *et al.* 2020).

Field procedures

This study was conducted exclusively with male Barn Swallows due to their higher annual survival rates compared to females (van der Jeugd 2012). Males also show in general a higher fidelity to their breeding sites than females (Shields 1984). As this study was conducted in the breeding season, the sex of the adults was determined by the absence (male) or presence (female) of a brood patch. Male Barn Swallows in Europe do not incubate (Turner 2006). All caught birds were weighed (accuracy 0.1 g) and their wing length and tail fork (R1–R6) were measured (in mm). Geolocator birds were semi-randomly selected by preferring birds with relative long wings and long outer rectrices (R6), as these characteristics imply good physical health (Turner 2006).

In 2011 and 2012, geolocators were deployed during the second brood period. In 2011, Barn Swallows (n = 47) were equipped with geolocator type Mk20ASLT (Migrate Technology Ltd., UK), which had an extended light stalk of c. 10 mm. During this first deployment, between 1 July and 23 July, the geolocators were attached by trained volunteer ringers. The leg-loop harness was adjusted for each individual to ensure an optimal fit (Rappole & Tipton 1991). The total weight of logger and harness was 0.8 g (4.5% of the swallows' body mass, 17.8 ± 1.3 g (±SD), n = 47). This was in accordance with the – in those years – commonly accepted rule of thumb in bird research of adding a maximum of 5% extra weight to an animal (Kenward 2001). Each research year, a number of male Barn Swallows, similar to the number that received a

Male Barn Swallow on the wing, with the geolocator(stalk) clearly visible (photo JA, Culemborg, 4 July 2011).

RK attaching a geolocator with full-body harness to a male Barn Swallow (photo Hans Peeters, Culemborg, 7 July 2012).

geolocator, was caught in the same stables and sheds, ringed if necessary and assigned as a control group to monitor any potential differences in return rates (46 in 2011–2012, 49 in 2012–2013).

The return rates in the first research year (2011–2012) were low and differed between geolocator group and control group (see results). The animal welfare protocol for this project (Figure S2) therefore prescribed aborting the pilot study, unless another approach could solve this problem. On the basis of the studies by Bowlin *et al.* (2010) and Fraser & Stutchbury (2011) we chose to use a stalkless, 'flat' geolocator type to reduce the extra drag from the tracking device in the second research year. Furthermore, we chose to use a full-body harness, meaning that the device was placed between the wings, instead of on the rump, i.e. closer to the centre of gravity of the bird. During the 2012 breeding season (27 July to 8 August) geolocator type MkW65 (Migrate Technology Ltd., UK) was deployed on 50 male swallows. The total mass of logger and harness was 0.7 g (3.9% of the body weight, 17.8 ± 0.9 g (±SD), n = 50).

From the start of each consecutive breeding season the ringers visited the selected breeding locations (Figure S1) at least every ten days. Whenever a geolocator bird was identified visually, a targeted catch using mist nets was undertaken. An early morning mist net session – with the aim to catch every bird that spent the night at a breeding location – was performed during the first as well as the second brood period in 2012 and 2013. These general catching sessions guaranteed an equal chance for birds from the geolocator group as well as the control group to be recaptured and generated annual return rates.

Geolocators were removed by the ringers following a protocol. Birds were photographed before and after the devices were removed. Relevant body parts and legs of geolocator birds were checked for feather anomalies, skin abrasions or any other indications of nuisance or injury. Harnesses were checked after removal: fat deposition on or wear of the harness string were used as indicators for a (slightly) too tight fit.

Definitions and abbreviations

Behavioural stage characteristics were assigned and based on timing and site. Main temporal value was (Julian) Day of Year (DOY). For each Barn Swallow the location and time (days elapsed) spent at the breeding location was assigned as 'BL'. Elapsed time and locations between BL and arrival day at the Wintering Region (WR) was qualified as 'Post-breeding Migration' (PostM). Due to the autumn equinox period, we were not able to discern post-breeding local dispersal to communal roost sites from the 'real' PostM as advised by López-Calderón *et al.* (2021). Consequently, the duration values of PostM should be assessed with caution. Elapsed time and locations between the departure day of WR and day of arrival at the BL were qualified as 'pre-breeding migration' (PreM). Note that although the terms 'wintering' and 'wintering region' are commonly used in studies on migration ecology of birds (see e.g. Newton 2008), this is meteorologically not correct for a trans-equatorial migrant. Nevertheless, we do use the terms for convenience.

Data collection

Sample size

A total of 97 (47 + 50) male birds were tagged with a geolocator. In both 2012 and 2013, two individuals that lost their tracking devices were recaptured. As the exact moment that their geolocator was lost was unknown, and following López-Calderón *et al.* (2021), these four birds were excluded from return rate analysis. In the first research year, eight out of 45 geolocators were retrieved; the result in the second research year was 14 out of 48 geolocators. In total, the data contained 21 year-round tracks and one partial track from breeding season until the first part of PreM in the successive year. These 22 tracks were collected by 20 individuals, because two (out of four) birds that were tagged in successive years returned successfully. The control group consisted of 95 (46 + 49) male Barn Swallows. For details see Table 1.

Analysis

Age and return rates

As second calendar year (cy) birds experience lower survival rates than birds of 3 cy and older (van der Jeugd 2012), we evaluated the age structure of the geolocator group versus the control group for each research year. For every bird in the dataset, the minimum age in years was estimated for life-stage at ringing date (nestling, fledgling, adult). The variation in age of the combined geolocator groups (45 + 48 males) versus the control groups (46 + 49 males) was not significant (unpaired t-test: $t_{167} = -0.203$, $P = 0.84$) This test was also performed with the exclusion of the birds from the three newly added RAS-sites in

Table 1. Number of birds deployed and recaptured each research year, presented per age class for geolocator group vs. control group.

	2011–2012				2012–2013			
	Geolocator group		Control group		Geolocator group		Control group	
	deployed	recaptured	deployed	recaptured	deployed	recaptured	deployed	recaptured
Min. 2nd calendar year/ adult age unknown (Euring: 2, 4, 5)	14	2	20	7	21	6	30	13
Min. 3rd calendar year (Euring: 6, 7)	19	3	10	5	17	6	9	4
Min. 4th calendar year (Euring: 8 and higher)	12	3	16	4	10	2	10	6
Subtotal	47	8	46	16	50	14	49	23
Number of devices lost	2	0	0	0	2	0	0	0
Available for analysis	45	8	46	16	48	14	49	23

West-Betuwe (n = 87 geolocator males versus 89 control males) with the same non-significant result (unpaired t-test: $t_{155} = -0.324$, $P = 0.75$). In conclusion, there were no indications that the geolocator group and the control group differed in age structure.

Analysing raw light level data

We followed the general guidelines for geolocation analysis in Lisovski *et al.* (2020). We analysed data with the threshold method (Figure 2 in Lisovski *et al.* 2012) and used movement analysis R-package 'GeoLight' group model (Lisovski & Hahn 2012). Movement analysis distinguishes periods of residency and movement based on a set of user defined thresholds such as minimum stopover days and maximum flight speed. The analysis consisted of four steps: (1) determination of sun events (based on estimated sun angles), (2) discrimination of stationary or movement periods, (3) calibration, and (4) calculation of positions (Lisovski & Hahn 2012).

Light levels were recorded in the two research years (2011–2012 and 2012–2013) with two different types of geolocation tags. The tag type used in the 2011–2012 season recorded maximum light levels per two minutes; for the season 2012–2013, maximum light levels were recorded per five minutes. Light level data was corrected for clock drift (Fox 2010). Twilight transitions were visually inspected with package 'TWgeos' (Lisovski *et al.* 2016) and manually edited. Raw light level plots (Figure S3) were created and inspected. Since Barn Swallows breed inside stables and barns, nest site attendance is clearly recognizable in the raw light level plots. The actual departure dates from and arrival dates at the breeding locations were derived from these plots (for details see Figure S4).

Sun angles were calibrated per tag on the longest stationary period, usually in 'midwinter' (for result see Table S1). Probable 'stationary' locations were estimated with the 'group model' described in Lisovski & Hahn (2012) and Lisovski *et al.* (2020). We used a probability of change (quantile) of 0.8 and a minimum duration of four days within the changeLight function and pooled sites with a conservative threshold of 300 km (both threshold values based on Briedis *et al.* 2018). For the movement model we assumed a theoretical distribution of flight speeds (gamma distribution, shape = 2.5 and scale = 0.2) implying a rapid movement between stopover sites (values based on Briedis *et al.* 2018).

All time spent at each stopover location on land south of the Sahara with a minimum duration of 14 days (value adapted from Briedis *et al.* 2018), was assigned as WR. The average location of a WR was determined as the median latitude/longitude; spatial variation was described with 2.5–97.5 percentiles of latitude/longitude per location.

Estimation of migration start, length and duration

Since temporal and spatial resolution of light level data is rather coarse, we calculated migration speed as the total distance travelled in kilometres between BL and WR divided by the duration of PostM or PreM in days. As the onset and duration of PostM in both research years (almost) fully coincided with the equinox period (7 September – 5 October), we were not able to discern intermediate stopovers during PostM. Distance was calculated as the great circle distance between the BL and WR.

Statistics

To explore correlations between departure or duration from stages and distance travelled, we fitted linear mixed models (estimated using Restricted Maximum Likelihood) with 'research year' as random effect. We explored correlations between: (1) duration of PostM with distance travelled to WR (Figure 4A), (2) day of arrival at the WR with duration of stay in WR (Figure 4B), (3) departure day from WR with duration of PreM (Figure 4C) and (4) arrival day at BL with distance travelled in PreM (Figure 4D). For all models, standardised parameters were obtained by fitting the model on a standardised version of the dataset. 95% Confidence Intervals (CIs) and P-values were computed using a Wald t-distribution approximation.

RESULTS

Time-budgets per stage and migration speed

Temporal aspects of migration

An overview of the time budgets per stage per individual is presented in Figure 1. Summarized statistics are presented in Table 2. The mean duration of PostM differed on average 6.4 days between both research years, but the difference was not statistically significant ($t_{20} = -1.9$, $P = 0.07$). The mean duration of stay in the WR was highly comparable between both research years ($t_{18} = -0.09$, $P = 0.93$). Mean duration of PreM differed 10.4 days between years, but this difference was not statistically significant ($t_{16} = 0.004$, $P = 1.0$).

Migration speed

Calculations of the average distance covered per day for PostM were similar in both research years being on

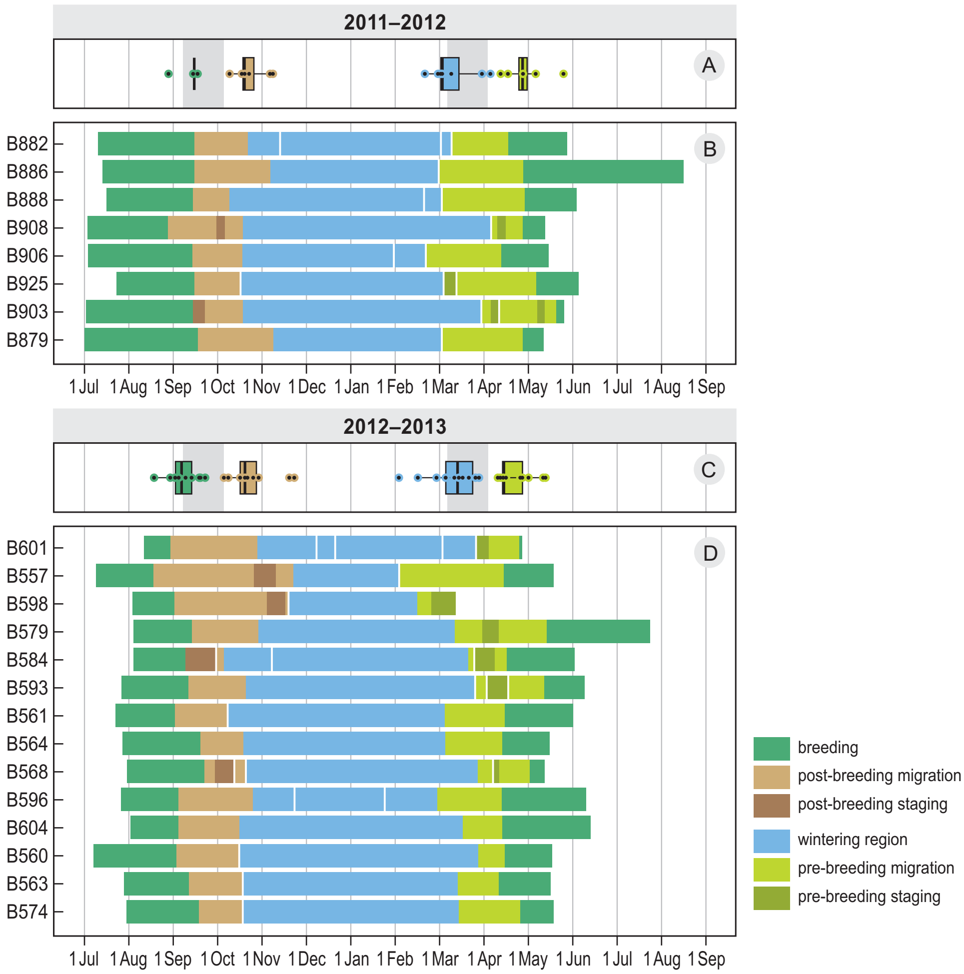

Figure 1. (A, C) Boxplots showing average departure date from breeding location, average date of arrival in and average departure date from wintering region and average date of arrival at breeding location in 2011–2012 and 2012–2013. Boxes represent 25–75% percentiles, whiskers show 10–90% percentiles, dots represent outliers. Equinox periods are shown by a grey background. (B, D) Horizontal bar plots show individual schedules of 22 Barn Swallow tracks, sorted by decreasing maximum distance between wintering and breeding areas during post-breeding migration in 2011–2012 and 2012–2013. Relocated birds during wintering can be recognised by the small white bars.

Table 2. Temporal details of the three discerned non-breeding stages of the annual cycle: Post-breeding Migration (PostM), Wintering Region (WR) and Pre-breeding Migration (PreM). For easy comparison between research years the table is structured pair-wise by stage. None of the differences of the Mean ± SD between research years was statically significant.

	Stage	Start of stage			End of stage			Duration
		Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD
2011–2012	PostM	12 Sept ± 6.4 d (*n* = 8)	28 Aug	17 Sept	22 Oct ± 10.5 d (*n* = 8)	9 Oct	8 Nov	39.5 ± 10.7 d
2012–2013	PostM	7 Sept ± 9.4 d (*n* = 14)	18 Aug	22 Sept	23 Oct ± 13.6 d (*n* = 14)	5 Oct	22 Nov	45.9 ± 20.0 d
2011–2012	WR	22 Oct ± 10.5 d (*n* = 8)	9 Oct	8 Nov.	11 Mar ± 15.6 d (*n* = 8)	21 Feb	7 Apr	138.8 ± 20.4 d
2012–2013	WR	23 Oct ± 13.6 d (*n* = 14)	5 Oct	22 Nov	11 Mar ± 16.1 d (*n* = 14)	3 Feb	29 Mar	139.2 ± 27.7 d
2011–2012	PreM	11 Mar ± 15.6 d (*n* = 8)	21 Feb	7 Apr	29 Apr ± 12.9 d (*n* = 8)	13 Apr	26 May	49.5 ± 13.6 d
2012–2013	PreM	11 Mar ± 16.1 d (*n* = 14)	3 Feb	29 Mar	21 Apr ± 11.4 d (*n* = 13)	11 Apr	14 May	39.1 ± 14.7 d

average 177.2 ± 48.6 km/day in 2011 (n = 8) and 162.8 ± 55.1 km/day in 2012 (n = 14). Calculations of the average distance covered per day during PreM were 152.9 ± 64.2 km/day (n = 8, 2012) and 184.1 ± 63.3 km/day (n = 3, 2013). For the graph see Figure S5. The difference in migration speed between years was statistically significant for PreM (t_{15} = –2.18, P = 0.05), but not for PostM (t_{16} = 0.002, P = 1.0).

Spatial distribution of wintering region (WR)

Figure 2A shows the cumulative map of the WRs for 2011–2012 and 2012–2013 with indications of accuracy for latitude and longitude. Changes in WR within a wintering period were detected for three out of eight tracks in 2011–2012 (one Barn Swallow changed twice). In the second research year, two out of 14 birds changed WR within the wintering period (one Barn Swallow changed three times). The extent of wintering locations can be compared with the locations of ringing recoveries of Dutch Barn Swallows during 1990–2020 (Figure 2B). Both maps show near identical min-max boundaries for the WRs: south of 10°N and north of 30°S. Spatial-temporal maps of each individual are presented in Figure S6.

Repeated use of Wintering Regions

A total of two Barn Swallows were followed over two consecutive years. Their WR choice and spatial migration pattern are illustrated in Figure 3. Both birds were fairly consistent in their choice of their WR between years; both wintered in the Congo basin. The comparison of PostM and PreM within research years and between years is hampered by the large to almost full overlap with equinox during PostM and partial overlap during PreM.

Phenology of non-breeding stages

First, we analysed the correlation between distance travelled during PostM and the duration of PostM (Figure 4A): it was significant and positive (β = 9.47, 95% CI: 2.73–16.21, t_{18} = 2.95, P = 0.009; β_{std} = 0.55, 95% CI: 0.16–0.94). Thus, the farther a bird travelled the more days its journey took. Second, we analysed the arrival date at the WR and the duration of this stage (Figure 4B). The model's explanatory power related to the fixed effects alone (marginal R^2) is 0.73. Within this model the effect of arrival at WR (DOY) was statistically significant and negative (β = –1.73, 95% CI: –2.22– –1.24, t_{18} = –7.45, P < 0.001; β_{std} = –0.86, 95% CI: –1.10– –0.62). In other words: the later the birds arrived in their WR, the shorter the duration of their stay.

As a third step we analysed the correlation between the departure date from WR versus the duration of PreM (Figure 4C). The model's explanatory power related to the fixed effects alone (marginal R^2) was 0.50. Within this model the effect of departure from

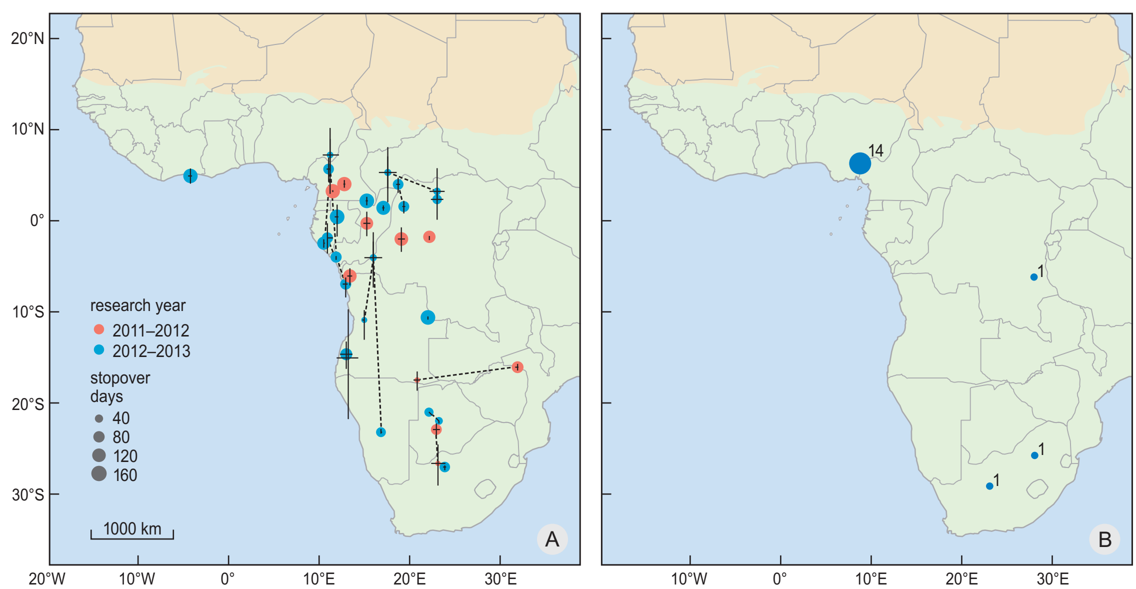

Figure 2. (A) Cumulative map of wintering regions of Barn Swallows with geolocators for 2011–2012 (n = 8) and 2012–2013 (n = 14). The size of the winter location dots was scaled for duration of stay in days. Crossed bars show 10–90% variation intervals for latitude and longitude. Wintering regions of relocated Barn Swallows are connected by dashed lines. (B) Locations of Dutch Barn Swallows, ringed as nestlings or as breeding adults, from which the ring was recovered south of the Sahara between 23 October (median end PostM) and 3 March (median start Prem; 1990-2020, n = 17). Dots scaled to the number of recoveries. The extent of the Sahara is indicated in beige.

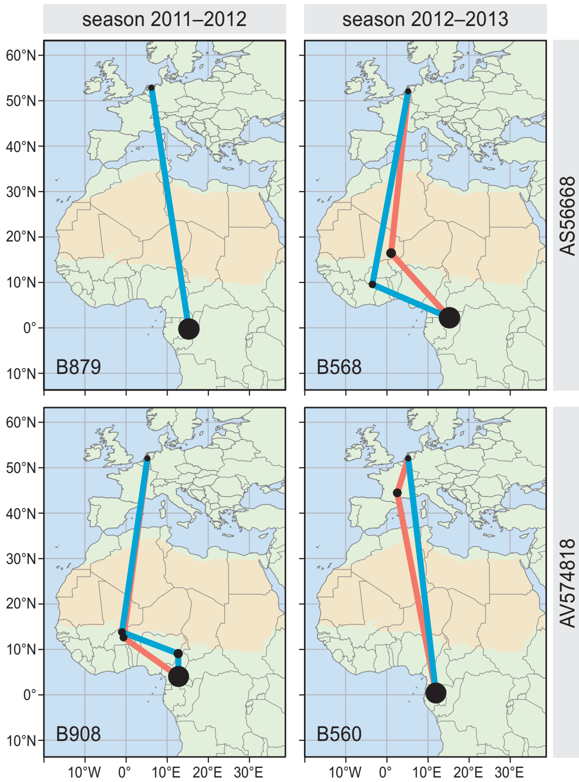

Figure 3. Wintering regions and spatial migration strategies of two individuals (top AS56668: geolocators B879 and B568, and bottom AV57481: geolocators B908 and B560), which carried geolocators in both research years. Red lines indicate post-breeding migration, blue lines indicate pre-breeding migration. Scaled black dots indicate duration of stay in winter regions and on staging sites en route. Lines connect the wintering, stop-over and breeding sites per individual and do not reflect actual routes travelled.

WR (DOY) was statistically significant and negative (β = –0.64, 95% CI: –0.99– –0.29, t_{17} = –3.89, P = 0.001; β_{std} = –0.64, 95% CI: –0.99– –0.29). This result implies that the later a bird departed from its WR, the shorter the duration of its PreM lasted.

As a final step we analysed whether migration distance correlated with date of arrival at the BL and research year (Figure 4D). The model's explanatory power was very weak (R^2= 0.02). Within this model the effect of distance to WR (km) was statistically non-significant and positive (β = 2.76, 95% CI: –2.74–8.25, t_{18} = 0.98, P = 0.325; β_{std} = 0.22, 95% CI: –0.22–0.65]) and the effect of research year was statistically non-significant and negative (β = –6.99, 95% CI: –17.69– 3.72], t_{18} = –1.28, P = 0.201; β_{std} = –0.57, 95% CI: –1.43–0.30). In summary, independent of research year, birds migrating farther did not arrive later at their BL than birds wintering at closer range.

Return rates

In 2012, eight out of 45 leg-loop-attached light stalk geolocator birds (17.8%) and 16 out of 46 control birds (34.8%) were recaptured (χ^2_1 = 5.74, P = 0.017). Based on this result, we changed the geolocator and harness type in an attempt to improve the return rate. In 2013, 14 out of 48 geolocator birds (29.2%) were recaptured and 23 out of 49 control birds (46.9%). Despite these changes to the design, the return rates in this second year remained significantly lower than that of the corresponding control group (χ^2_1 = 6.09, P = 0.014).

DISCUSSION

This discussion is structured following the consecutive non-breeding stages of the Barn Swallows' annual cycle, starting with post-breeding migration (PostM).

Temporal aspects of PostM

As a preliminary comment, it is good to keep in mind that PostM of adult Barn Swallows might be more or less synchronised by their post-nuptial dispersion and pre-migratory fattening at communal roosts (Turner 2006, van den Brink & Klaassen 2019, López-Calderón *et al.* 2021). Both research years showed the same temporal pattern for the start and duration of PostM. Rubolini *et al.* (2002) established that PostM of Barn Swallows from Western Europe was interrupted by a fattening stage in southern parts of Europe or Northern Africa to build up enough fat reserves to be able to cross the Sahara. Due to the huge temporal overlap between PostM and the equinox period (Figures 1A, C), we could not detect this element of the Barn Swallows' migration strategy.

Duration of PostM and location of WR

As mentioned above, the real start date of PostM could not be precisely defined in our study. As a consequence, our established positive correlation between duration of PostM and distance travelled to the WR must be assessed with some caution. Nevertheless, the later arrival in more southern WRs versus more northern WRs was in line with our expectation. The results of our study showed large variation in the distances travelled between the BLs and WRs of Barn Swallows breeding in The Netherlands (Figure 2A). Even though these distances can only be estimated rather coarsely, due to the limitations of geolocators as a tracking tool, a factor of c. 1.7 could be applied for the minimum and maximum distance between BL and WR: 5617–8994 km

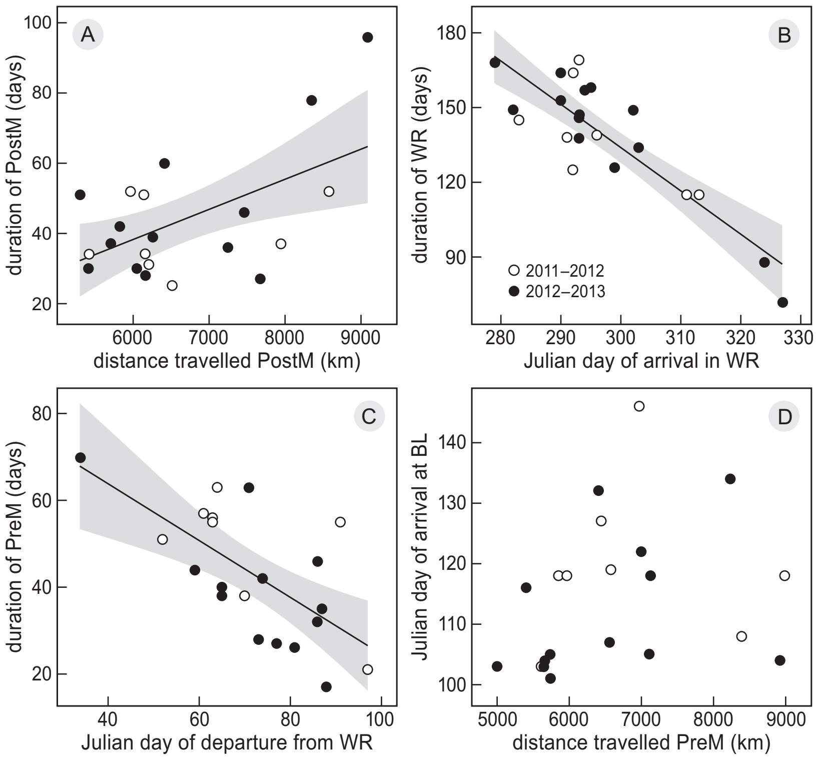

Figure 4. Analysis results of four spatio-temporal aspects. Data from both research years were combined to maximise the robustness of the results presented. Solid lines show significant correlations, grey shading showing 95% confidence intervals. (A) Duration of post-breeding migration (PostM) correlated positively with distance travelled during PostM. (B) The Julian day of arrival in Wintering Region (WR) negatively correlated with the duration of stay in the WR. (C) The Julian day of departure from the WR negatively correlated with the duration of Pre-breeding Migration (PreM). (D) The Julian day of arrival at the Breeding Location (BL) had no correlation with PreM distance.

(2011–2012) and 5004–8936 km (2012–2013). Such a large within-population variation in migration distance of 30 latitudinal degrees or more has been demonstrated for some other passerines, such as e.g. the Eurasian Siskin *Spinus spinus* (Newton 2024). But in general, the use of a less extensive area seems to be a more common strategy for sub-Saharan wintering passerines breeding in Western Europe (see e.g. Zwarts *et al.* 2009).

Duration of stay in WR

The moult of their primary feathers is a time-consuming process for Barn Swallows. It takes 120–130 days under good feeding conditions but can last 155–190 days under adverse circumstances (van den Brink *et al.* 2000). Duration of stay in the WR was significantly negatively correlated to day of arrival. Wing moult can potentially affect the ability to migrate over longer distances. Nevertheless, in our study three out of eight and two out of 14 tracks, in 2011–2012 and 2012–2013, respectively, showed relocations to other WRs (see Figure 2A) despite it being highly unlikely that the primary moult of these birds was at that moment complete. Change of WR was also established by Pancerasa *et al.* (2022) for eight out of 73 tracks. Speculating, relocation during the boreal winter to areas with better feeding conditions, which can occur in Africa when rains start after drought periods, might be a beneficial strategy. This speculation of rain induced relocation is supported by field observations. In November 2009, 2010 and December 2009, large numbers of migrating Barn Swallows were observed in Zambia, heading in southerly directions after heavy rains had ended long periods of drought (B. van den Brink pers. comm.). Ambrosini *et al.* (2011) hypothesised that high rainfall enhances winter survival and phenotypic quality, possibly via linked food availability. Saino *et al.* (2013) concluded that high quality individuals with advanced moult also had relatively large pectoral muscles. Speculating, individual condition and or foraging qualities might compensate for the handicap of an incomplete set of flight feathers and enable relocation to another WR.

Geolocator versus ringing-based Wintering Regions

This geolocator study shows the same northern and southern limits for the WRs as the 17 recovered Dutch-ringed Barn Swallows between 1990 and 2020. A comparison of the two respective distribution maps in Figure 2 reveals a different and more differentiated density pattern for the geolocator birds. Most of the geolocator birds wintered in the Congo Basin. None of the ringing recaptures occurred in this vast area comprising Gabon, Cameroon and both Congo states. This difference between ringing- and geolocator-based locations can likely be attributed to the 'catching-effort' and/or 'chances of recovery' factor, which are inevitably associated with ringing research (e.g. López-Calderón *et al.* 2021). The chances of Dutch-ringed Barn Swallows being recovered at roost sites with focused research, e.g. Boje in eastern Nigeria (see e.g. Saino *et al.* 2013), are much higher than at random sites elsewhere in Africa. It is worth mentioning that in each research year several Barn Swallows extended the location of their WR as far south as Namibia, Botswana or South Africa. Despite its small sample size and being limited to two research years, we expect our geolocator study to provide a more reliable pattern of the WRs of the Dutch breeding population across Africa than the combined ringing recoveries between 1990 and 2020.

Start and duration of Pre-breeding Migration

From an evolutionary point of view, there is pressure for male Barn Swallows to arrive early at the breeding locations (e.g. Pancerasa *et al.* 2022). Putting aside the caveat about primary moult as a limiting factor for the onset of Barn Swallow migration (Saino *et al.* 2013), it is tempting to assume that the Barn Swallows with WRs farthest from the BL are likely to set off earlier to compensate for the longer travel time needed. Accordingly, we analysed if variation in duration of PreM influenced the day of arrival at the BL. Contrary to Liechti *et al.* (2015) and to our expectation that individuals migrating farther would arrive later at their BL, we did not detect this correlation (Figure 4D).

The optimal strategy for a Barn Swallow would be to choose a WR that allowed an early arrival to the breeding area in order to achieve higher breeding success (Ambrosini *et al.* 2011). As optimal feeding conditions favour a quick wing moult (e.g. van den Brink *et al.* 2000) and good physical condition (Saino *et al.* 2013), migrating farther to a WR in southern parts of Africa might be advantageous, when these conditions are met. The apparent differences in total distance covered between Barn Swallows that choose a relatively stationary wintering strategy with daily 'commuting' between foraging areas and a good quality roost site versus a more opportunistic 'following rains' wintering strategy covering greater distances might be limited when environmental conditions for the 'stationary' strategists become poor. In such circumstances the 'stationary' strategists may have to increase their daily flight effort significantly (van den Brink *et al.* 2000). That also raises the question: with which strategy do birds cover the greatest total distance during the non-breeding season?

Speculating, and analogous to the stepwise migration strategy of Barn Swallows during PostM (Rubolini *et al.* 2002), weather circumstances and foraging possibilities during PreM may also have a levelling effect on the duration of PreM (e.g. Sicurella *et al.* 2016). Pancerasa *et al.* (2022) stated that late arrival of an individual at the breeding grounds depended on the departure date from the WR, which was strongly correlated to the arrival date at the WR in their study. The findings of Pancerasa *et al.* (2022) that individuals departing late from their WR did not take a western detour to cross the Sahara zone, had shorter migration routes and migrated at a faster pace, are also relevant arguments for the apparent contradictory result of our study. A strong potential explanation for the outcome of our study was provided by Schmaljohann (2019). Based on a multi-species meta-analysis, he concluded that the generality with which the timing of the start of migration was correlated with arrival at the BL, rather than migration distance, suggested that the start of migration acted broadly as a mechanism for regulating arrival time.

Return rates

In both research years, the return rates of the geolocator group were significantly lower than the control group. In the second research year – with a 'flat' geolocator and optimised harness – the return rate improved from 17.8% to 29.2%. Nevertheless, the difference between both groups remained approximately 17 percentage points. An experimental setup is required to disentangle the methodological change and the year-component. Speculating, the improved annual return rate in 2012–2013 could well have been due to more favourable environmental conditions compared to 2011–2012. Both annual return rates of geolocator birds in our study (17.8% and 29.2%) are within the range of variation of return rates of other Barn Swallow geolocator studies elsewhere in Western Europe. These range between 13.3% and 29.1% (Liechti *et al.* 2015, Klvaňa *et al.* 2018, Briedis *et al.* 2018, López-Calderón *et al.* 2021). Corrected for sample sizes, but disregarding the effect of sex-specific differences in annual return rates, which were not provided by every study, the overall average return rate of geolocator tagged birds in these studies amounted to 22.5%. This was lower than the return rates of the untagged control groups. For details see Table S2. Our study and the publications mentioned are in line with a main result of the meta-analysis by Brlík *et al.* (2020): geolocator tagging may impact apparent survival of birds negatively, especially when birds are small and the relative load of the device is high. Nevertheless, we are convinced that our study has contributed to a better understanding of Barn Swallows' life cycle.

Final remark

Since 2010, geolocator studies in at least five European countries have been conducted to study the migratory and wintering behaviour of many hundreds of Barn Swallows. We suggest a reanalysis of the collective data with state-of-the-art methods. A reanalysis might explain actual contradictory results, establish new insights or even reveal causal relationships. Such additional knowledge is highly valuable, also with regards to understanding the potential effects of the ongoing climate change.

ACKNOWLEDGEMENTS

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SAMENVATTING

In het kader van het Jaar van de Boerenzwaluw (2011) werd in de jaren 2011/12 en 2012/13 een onderzoek uitgevoerd naar het trek- en overwinteringsgedrag van Nederlandse Boerenzwaluwen *Hirundo rustica*. In elk van de vijf onderzoeksgebieden werden maximaal twee keer tien volwassen Boerenzwaluwen voorzien van een geolocator. Geolocators meten de lichtsterkte over de tijd en slaan het maximum per minuut of enkele minuten op. Het tijdstip 'zon op' respectievelijk 'zon onder' en de daglengte vormen de sleutelgegevens waarmee de breedtegraadpositie van een vogel dagelijks kan worden vastgesteld. De lengtegraad kan worden afgeleid uit de hoogte van de zon om 12 uur. Omdat de najaarstrek voor een groot deel samenviel met de periode waarin de daglengte op de hele wereld vrijwel gelijk was (equinox), waren daar geen betrouwbare locatiegegevens voor af te leiden.

Vanwege hun grotere jaarlijkse kans op terugvangst dan vrouwtjes kregen alleen mannetjes een geolocator. Om het eventuele effect van het onderzoek op hun terugkeerkans te kunnen monitoren, werden geringde volwassen mannetjes die in dezelfde schuren en stallen broedden, aangemerkt als 'controlegroep'. De mannetjes zijn zeer plaatstrouw aan hun broedlocatie. Exemplaren die het daaropvolgende jaar niet waren teruggekeerd waren hoogstwaarschijnlijk niet meer in leven. Relevant voor dit onderzoek is het verloop van de slagpenrui van de Boerenzwaluw: behoud van een goed vliegvermogen is cruciaal voor de dagelijkse vangst van vliegende insecten en voor het succesvol overbruggen van grote afstanden. De slagpenrui van Nederlandse Boerenzwaluwen vindt (pen voor pen) in het overwinteringsgebied plaats. Onder goede omstandigheden neemt deze 120–130 dagen in beslag. Onder slechte omstandigheden kan de duur oplopen tot wel 190 dagen. Het starten van de trek voordat de vleugelrui voltooid is, is voor Boerenzwaluwen een risicovolle strategie. Evolutionair gezien staat er voor mannetjes een grote druk op vroeg aankomen in het broedgebied.

Ons onderzoek leverde plaatsbepalingen van 21 volledige reizen en één gedeeltelijke reis op (acht in 2011/12 en 14 in 2012/13). De overwinteringsgebieden lagen wijd verspreid: van Ghana tot aan Zuid-Afrika, al overwinterden de meeste vogels in het Congobekken. We analyseerden de correlatie tussen aankomstdatum in overwinteringsgebied en de duur van het verblijf daar evenals de correlatie tussen de vertrekdatum uit het overwinteringsgebied versus de duur van de voorjaarstrek. De afstand tussen broedlocatie en overwinteringsgebied varieerde met een factor 1,7 tussen de meest noordelijk en meest zuidelijk overwinterende vogels. Deze bevinding leidde tot de sleutelvraag of de afstand tussen broedlocatie en overwinteringsgebied effect heeft op de aankomstdatum in het broedgebied.

De verst trekkende Boerenzwaluwen kwamen later aan in hun overwinteringsgebied. Ze bleven er ook significant korter. Deze vogels wisten zich – ondanks de mogelijke handicap van de nog niet voltooide slagpenrui – tussentijds te verplaatsen naar een ander overwinteringsgebied. De verst trekkende vogels begonnen ook significant eerder aan de terugtrek naar de broedlocatie. In tegenstelling tot onze verwachting leidde een grotere afstand tussen het overwinteringsgebied en de broedlocatie niet per definitie tot een latere aankomst op de broedlocatie.

Een bijzonder resultaat van ons onderzoek betreft het overwinterings- en trekgedrag van twee Boerenzwaluwen die elk in

beide onderzoeksjaren een geolocator terug wisten te brengen. Herhaalde trekgegevens kunnen voor kleine zangvogels maar zelden worden gepresenteerd. De twee vogels kozen in beide jaren het Congobekken als overwinteringsgebied. Binnen een onderzoeksjaar hanteerde elk van de vogels een vergelijkbare trekstrategie voor hun najaars- en voorjaarstrek. Voor beide migratiefases van deze vogels zijn verschillen en overeenkomsten tussen jaren helaas niet te duiden, omdat deze qua timing grotendeels samenvielen met de equinox.

Ondanks de zorgvuldige uitvoering van het onderzoek en tussentijdse aanpassingen (lichter, meer gestroomlijnd geolocatortype en andere bevestiging) lag de terugkeerkans van vogels met een geolocator in beide onderzoeksjaren significant lager dan die van de vogels uit de referentiegroep. Dit verschil is vergelijkbaar met andere internationale boerenzwaluwstudies waarin geolocators werden toegepast.

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Supplementary Material is available online
www.ardeajournal.nl/supplement/s113-###-###.pdf

SUPPLEMENTARY MATERIAL

Table S1. Table with estimated sun angles (zenith0) per geolocator. Departure and arrival dates are based on raw light level patterns (Figure S3 and S4)

Tag	Season	Deploy on	Departure	Arrival	Deploy off	Zenith0	Remark
B908	2011–2012	2-7-2011	28-8-2011	28-4-2012	17-5-2012	94.8	
B888	2011–2012	20-7-2011	14-9-2011	29-4-2012	1-6-2012	91.3	
B903	2011–2012	9-7-2011	14-9-2011	26-5-2012	30-5-2012	93.5	
B906	2011–2012	2-7-2011	14-9-2011	13-4-2012	17-5-2012	93.4	
B882	2011–2012	8-7-2011	15-9-2011	18-4-2012	30-5-2012	96.2	
B886	2011–2012	8-7-2011	15-9-2011	28-4-2012	20-8-2012	95.2	
B925	2011–2012	22-7-2011	15-9-2011	7-5-2012	30-5-2012	93.5	
B879	2011–2012	1-7-2011	17-9-2011	28-4-2012	14-5-2012	96.7	
B557	2012–2013	7-7-2012	18-8-2012	14-4-2013	19-5-2013	91.5	
B601	2012–2013	10-8-2012	29-8-2012	28-4-2013	28-4-2013	95.8	
B561	2012–2013	22-7-2012	1-9-2012	17-4-2013	5-6-2013	95.8	
B598	2012–2013	2-8-2012	1-9-2012		16-6-2013	96.0	11-3-2013
B560	2012–2013	7-7-2012	3-9-2012	15-4-2013	19-5-2013	95.0	
B596	2012–2013	25-7-2012	4-9-2012	13-4-2013	13-6-2013	95.7	
B604	2012–2013	2-8-2012	4-9-2012	14-4-2013	16-6-2013	93.9	
B584	2012–2013	3-8-2012	8-9-2012	17-4-2013	5-6-2013	95.8	
B563	2012–2013	27-7-2012	11-9-2012	11-4-2013	19-5-2013	96.5	
B593	2012–2013	25-7-2012	11-9-2012	12-5-2013	11-6-2013	96.5	
B579	2012–2013	3-8-2012	13-9-2012	14-5-2013	27-7-2013	92.7	
B574	2012–2013	30-7-2012	18-9-2012	26-4-2013	22-5-2013	96.8	
B564	2012–2013	27-7-2012	19-9-2012	13-4-2013	19-5-2013	94.2	
B568	2012–2013	27-7-2012	22-9-2012	2-5-2013	16-5-2013	97.7	
Mean	2011–2012		12-9-2011	29-4-2012			
Mean	2012–2013		7-9-2012	22-4-2013			
Mean						94.93	
SD						1.69	

Table S2. Annual Return Rates derived from geolocator tracking studies on Barn Swallows in Europe.

Year	Return Rates Geoloc. group	Return Rates Control group	Country	Study	Sex[1]
2011–2012	17.8%	34.8%	The Netherlands	This study	males
2012–2013	16.7%	NA	Lithuania	Briedis *et al.* (2018)	males
2012–2013	29.2%	46.9%	The Netherlands	This study	males
2013–2014	18.9%	NA	Czech Republic	Klvaňa *et al.* (2018)	males
2014–2015	21.7%	NA	Czech Republic	Klvaňa *et al.* (2018)	males
2015–2016	13.3%	NA	Lithuania	Briedis *et al.* (2018)	males
2010–2013	20.6%	NA	Italy/Switzerland	Liechti *et al.* (2015)	males and females
2016–2017	32.8%	56.3%	Spain	López-Calderón *et al.* (2021)	males and females
2017–2018	13.6%	20.0%	Spain	López-Calderón *et al.* (2021)	males and females
2018–2019	29.1%	47.6%	Spain	López-Calderón *et al.* (2021)	males and females

[1]Barn Swallow return rates can be sex-dependent; females can experience lower annual return rates

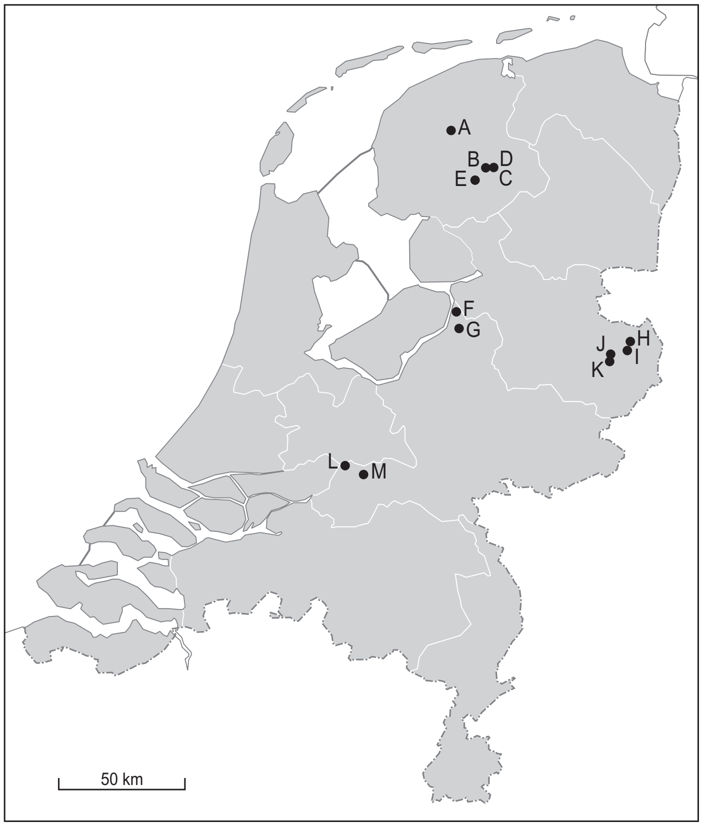


Figure S1. Locations of the five participating study areas in The Netherlands: Midden Friesland (c. 53°09'N – 5°51'E: A), Zuid-Oost Friesland (c. 53°00'N – 6°05'E: B, C, D, E), Veluwe (c. 52°26'N – 5°53'E: F, G), Twente (c. 52°21'N – 6°51'E: H, I, J, K) and Noord- and West-Betuwe (c. 51°56'N – 5°13'E: L, M). Name of village/settlement and number of constant effort ringing sites (Retrapping Adults for Survival project) or breeding locations: A = Warga (1), B = Terwispel (3), C = Hemrik (1), D = Lippenhuizen (1), E = Langezwaag (2), F = Noordeinde (1), G = Oldebroek (1), H = Agelo (1), I = Weerselo (1), J = Albergen (1), K = Hertme (1), L = Culemborg (3), M = Asch (1).

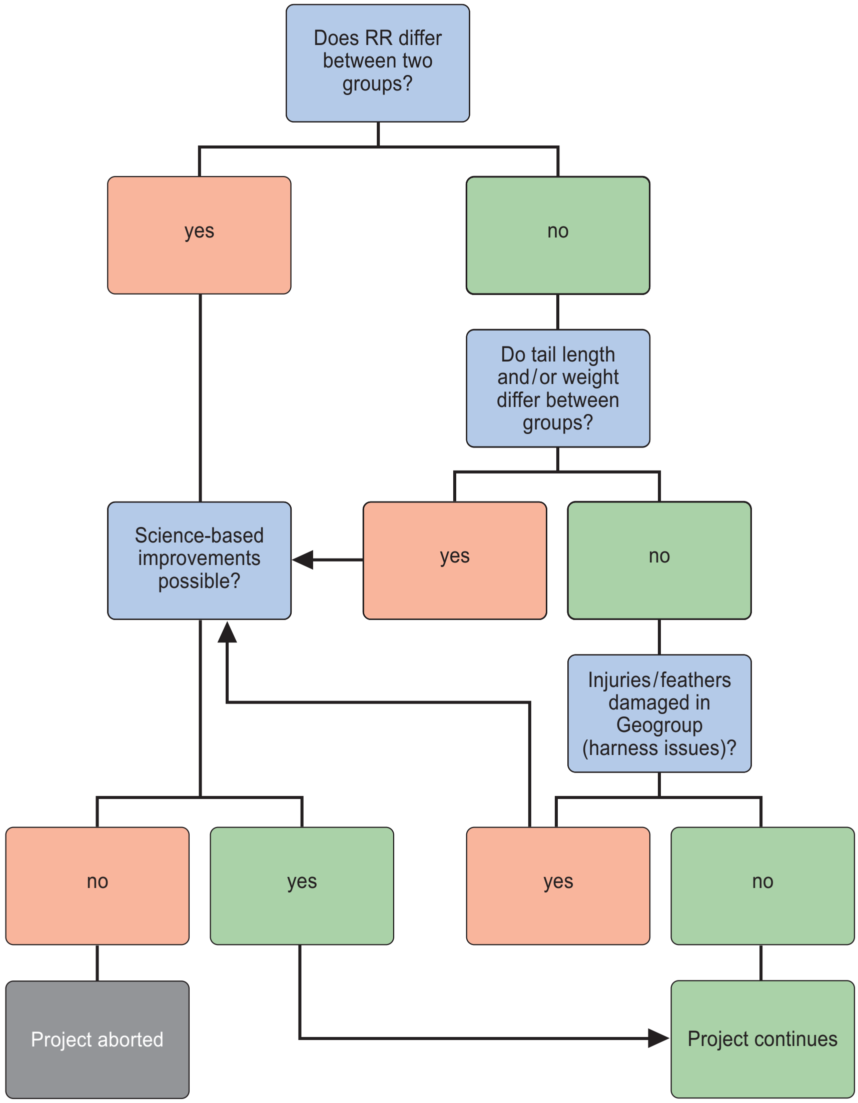
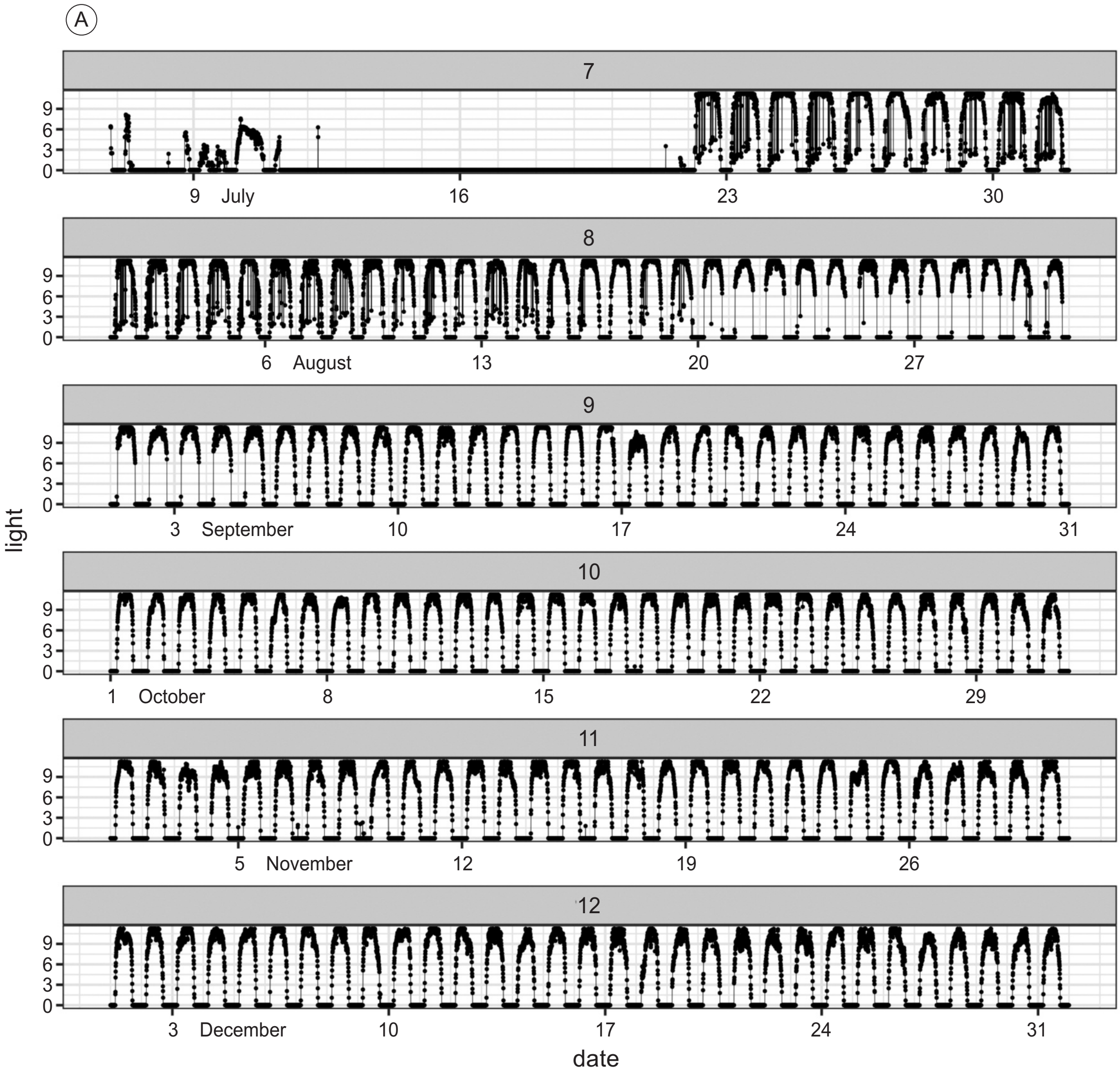


Figure S2. Diagram illustrating the steps of the inter annual evaluation protocol. RR= Return rate.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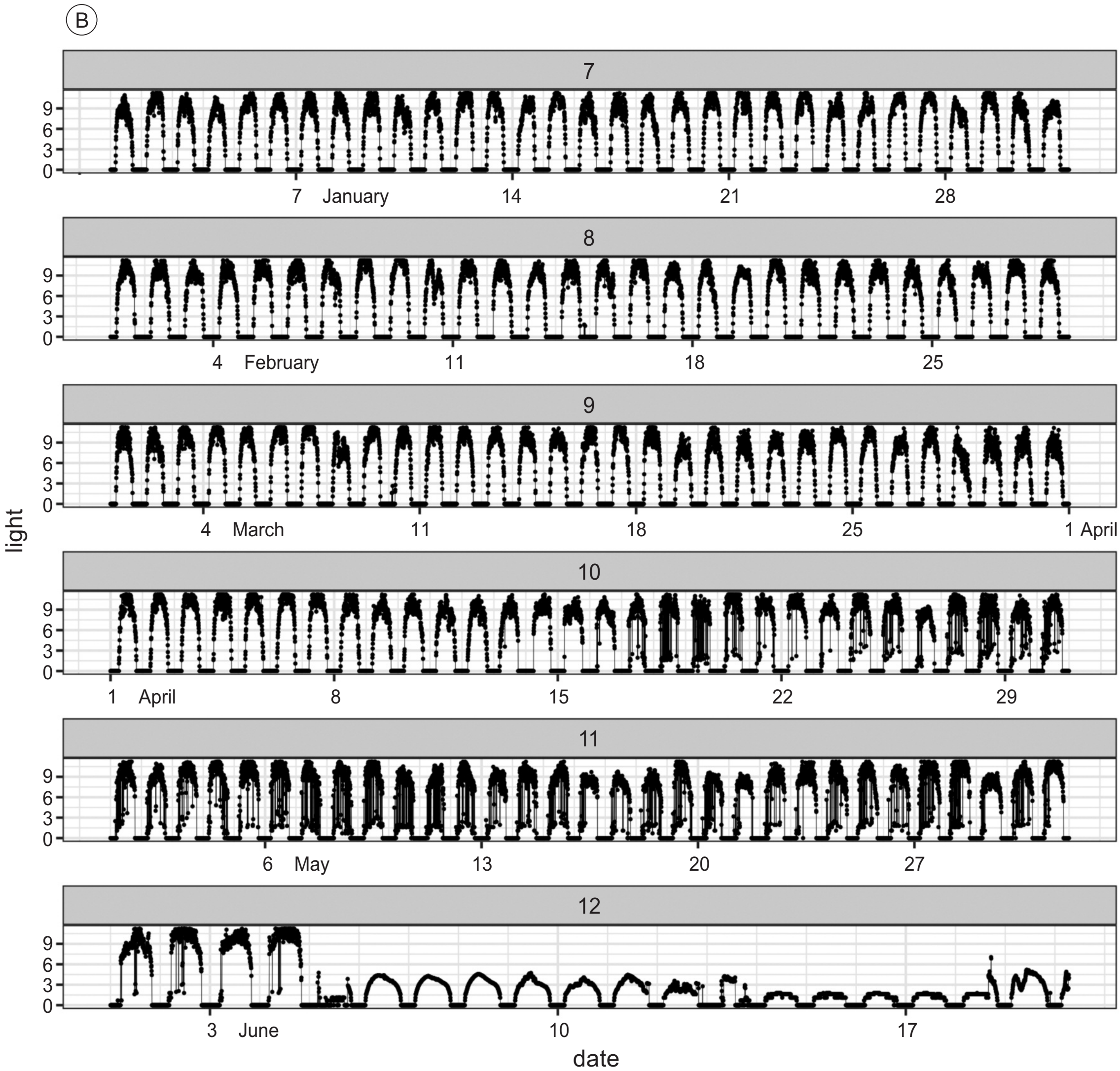

Figure S3. Raw light level plot of Barn Swallow ID B561. This illustrates a full year of the raw light level data as collected by a geolocator. The irregular patterns of light levels between 23 July and 20 August and between 17 April and 4 June are the result of the Barn Swallow's (nest) visits to the barn.

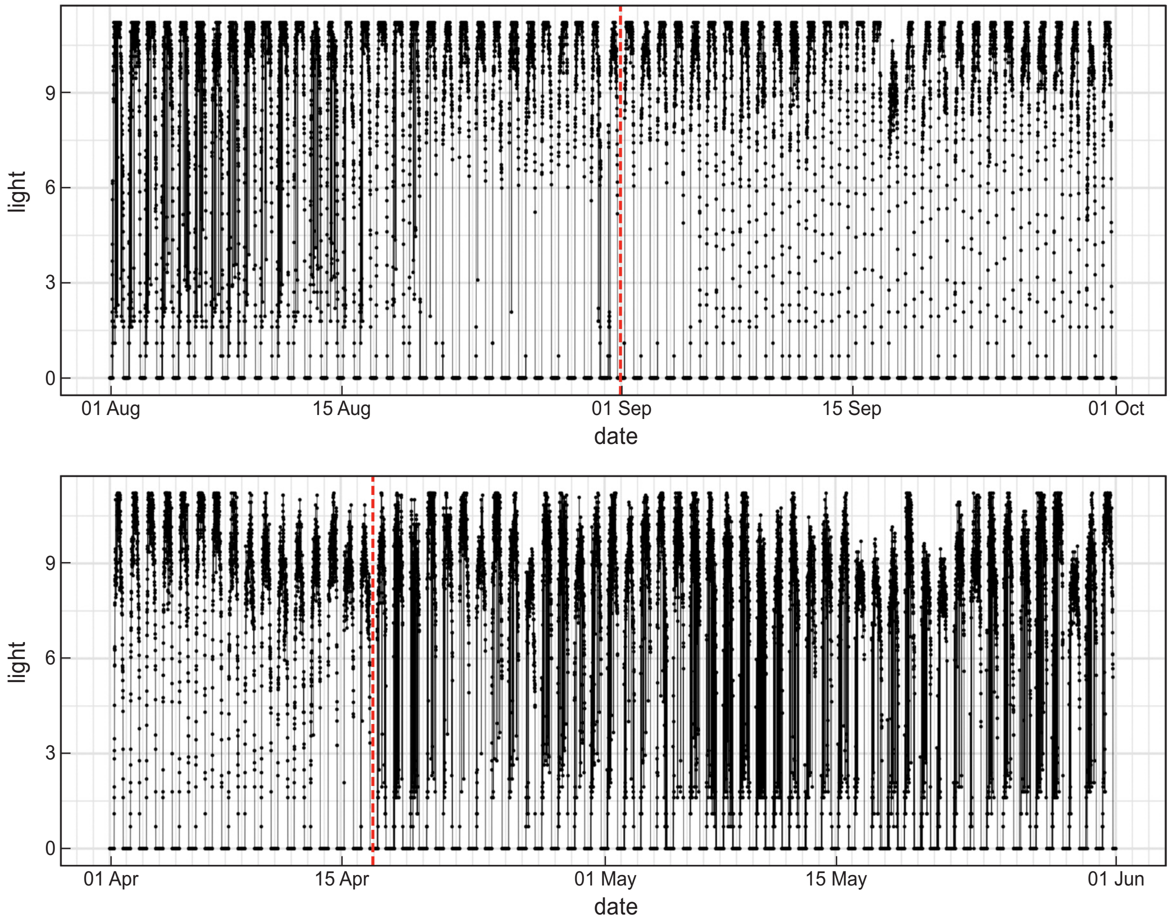

Figure S4. Illustration of the reconstruction of the day of departure from the breeding site and day of arrival in the consecutive year from raw light level data (ID 561). Departure and arrival day are indicated with a dashed red line. Visits to artificial breeding sites (barns, sheds) are noticeable in the raw light level plots when daytime light levels suddenly drop when the birds enter a darker environment. The change of natural light level patterns during breeding site visits are used as an indicator of arrival or departure of the breeding site.

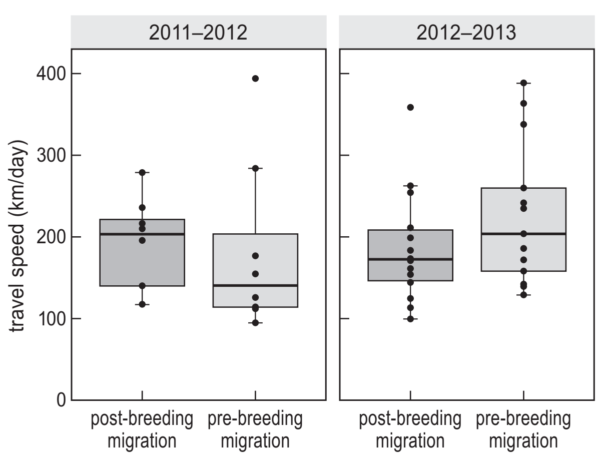

Figure S5. Travel speed presented as average distance per day for post-breeding and pre-breeding migration stage for (A) 2011–2012 and (B) 2012–2013, respectively, corrected for departure and arrival at breeding location. Box plots present 25–75% intervals, whiskers 10–90% intervals. Circles show individual average distance travelled per migration day.

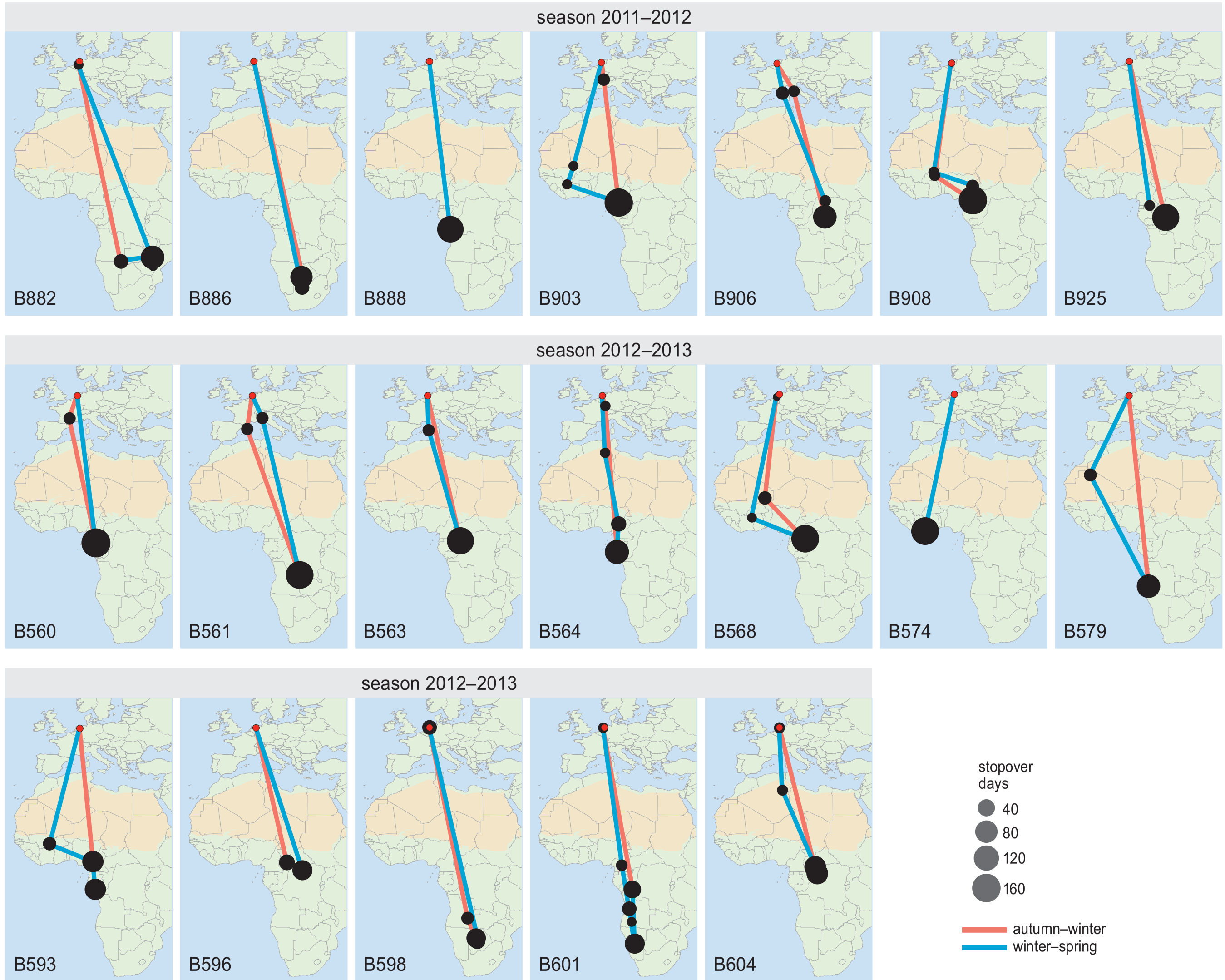

Figure S6. Wintering regions and spatial migration strategies of all individuals that returned with a geolocator. Red circles indicate breeding location. Red lines indicate post-breeding migration, blue lines indicate pre-breeding migration. Scaled black dots indicate duration of stay in wintering regions and on staging sites en route. Lines connect the wintering regions, stop-over sites and breeding locations per individual and do not reflect actual travelled routes.