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Article

Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant

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For migratory birds optimal timing of the onset of reproduction is vital, especially when suitable conditions for reproduction occur only for a short while during the year. With increasing latitude the suitable period becomes shorter and we expect the organization of annual cycle to be more synchronized to the local conditions across individuals of same population. This should result in low variation of arrival and departure date in breeding sites at higher latitudes. We quantify the temporal and geographical variation in pre- and post-breeding migration between individuals from four different populations of alpine swifts *Tachymarptis melba* along a latitudinal gradient. We tracked 215 individuals in three years with geolocators. The two western and two eastern populations showed separate migratory flyways and places of residence in Africa. Length of stay at the breeding sites was negatively correlated with latitude and differed by more than a month between populations. Duration of migration was similarly short in all populations (median 6.2 days in autumn and 8.7 days in spring). However, variation in timing of migration was unrelated to latitude and individuals everywhere arrived in the same asynchrony at the breeding site.

Keywords: annual schedule, long-distance migrant, migration phenology, non-breeding season, non-passerine

Introduction

Migration is an adaptive response to periodically changing resources and mortality risks. The annual cycle of migratory animals is adapted to match patterns of favourable conditions in space and time (Alerstam and Christie 2004, Newton 2008). As a consequence, even within a species, the organization of the annual cycle may vary among populations from different locations (Buehler and Piersma 2008, Briedis et al. 2016b, Gow et al. 2019). The main constraint in the evolution of the annual cycle is to match timing of reproduction with the peak availability of resources (Alerstam and Lindström 1990, van Noordwijk et al. 1995, Both 2010). The second most important constraint is attending sites with high survival probability during the remaining time of the year

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(Lack 1968, Cheng et al. 2019). However, animals might not always attend sites with the highest possible survival probability (or resource availability) as trade-offs may exist for maximizing fitness over the annual cycle, for example (Wingfield 2008, Finch et al. 2014, Zúñiga et al. 2017). Similarly, predictability in the seasonal availability of peak resources affects how much flexiblilty or rigidity there can be in the annual cycle (Wingfield et al. 1992, Dawson 2008). In many migratory species an endogenous circannual clock, which is triggered by the seasonal change in day length, serves as the main cue to adjust timing during the annual cycle (Gwinner 1986, 1990, Gwinner and Helm 2003). Additionally, environmental conditions such as temperature, precipitation and wind have the potential to fine-tune timing of individual stages (Erni et al. 2002, Liechti 2006, Tøttrup et al. 2008, 2010, Shamoun-Baranes et al. 2017).

Although the influence of the local environmental conditions on the organization of the annual cycles is well recognized, we lack understanding of how flexible the timing of the transition between stage of the phases of annual cycles can be adapted to changes in the environment (Åkesson et al. 2017). There is evidence that individuals even within a population have great flexibility in varying timing of the annual cycle (van Wijk et al. 2018, Brisson-Curadeau et al. 2019). Part of this variation might be due to the high plasticity in behavioural traits in the organization of different annual cycle stages (Vardanis et al. 2011, Briedis et al. 2017), while another part might have an underlying component of genetic variation between individuals (Battley 2006, Stanley et al. 2012, Conklin et al. 2013). Our knowledge on the flexibility of the annual cycle is still sparse, mainly because there are biases in studies analysing only parts of the annual cycle – mostly the breeding stage (Marra et al. 2015). To date only a few studies have compared the variation in the organisation of the annual cycles between individuals from geographically distinct populations (Conklin et al. 2010, Ouwehand and Both 2016, van Wijk et al. 2017). A comparison of the plasticity between populations could provide valuable information on how different local environmental conditions lead to different organization in the annual cycle, e.g. flyways might differ in season-specific wind supports (Nilsson et al. 2013, La Sorte et al. 2014, Kranstauber et al. 2015). This could affect an individual's ground speed and energy expenditure, and thus travel speed (Liechti 2006, Shamoun-Baranes et al. 2010). Therefore, the optimal timing of migration might differ between flyways (Åkesson et al. 2016, La Sorte and Fink 2017, Shamoun-Baranes et al. 2017, Anderson et al. 2020). Studies including more than just one flyway provide an opportunity to comprehensively describe a species' potential to optimize the organisation of the annual cycle.

In this study we compare the timing of migration across the entire annual cycle in four different populations of alpine swifts *Tachymarptis melba*, covering the main latitudinal range of the breeding area of the nominate subspecies *T. m. melba* (Chantler et al. 2014). Our main aims are to examine the timing of all migratory events (departure and arrival) for the entire annual cycle and investigate the variation in timing between individuals and populations. Both timing and variation in timing are most likely linked with the temporal resource abundance at each site. Swifts are exclusively aerial insectivores, but we hardly know anything about specific preferences of prey items in habitats outside Switzerland (Arn 1960). Indeed, insect development is tightly linked with minimal temperature requirements (Grüebler et al. 2008). Therefore, the transition between periods with available and not-available food resources for any insectivore might be much sharper at high latitudes compared to low latitudes due stronger seasonal fluctuation in temperature (Cucco and Malacarne 1996, Kelly et al. 2013, Briedis et al. 2016b, Gow et al. 2019). As a result, we expect shorter and more synchronized residence times for individual in breeding areas at higher latitudes. Individuals at these sites might all show very similar higher synchrony in timing because a shorter stage inevitably reduces flexibility in varying arrival and departure date because environmental conditions do not allow individual flexibility in timing of the annual schedule. We also test whether such differences in synchrony between populations might exist for arrival and departure for the non-breeding sites. As a proxy whether different wind conditions exist between the flyways of different populations we also compare travel speed among populations.

Methods

Data collection

Alpine swifts spend almost all of their life aloft (Arn 1960). They breed in colonies, and only during this period do they regularly rest on the ground (Liechti et al. 2013, Meier et al. 2018). We studied the spatio-temporal organization of their annual cycle in four different countries across the western part of the breeding range (Cramp 1985). In total we equipped 552 individuals with geolocators in breeding colonies located in Pırasalı Island in southern Turkey (36.34°N, 30.53°E), in Tarragona, Spain (41.12°N, 1.25°E), in Sofia, Bulgaria (42.66°N, 23.36°E), and at six colonies in Switzerland (Baden 47.14°N, 8.31°E, Biel, 47.14°N, 7.25°E, Lausanne, 46.52°N, 6.63°E, Lenzburg, 47.39°N, 8.18°E, Luzern, 47.06°N, 8.31°E, Solothurn, 47.21°N, 7.53°E) over three years (2014–2016, Supplementary information). For simplicity we treated all birds from Swiss colonies in our analysis as the Swiss population. All colonies except in Turkey are located under the roof of buildings. In Turkey birds are breeding in crevices of a natural rocky island near the coastline. Breeders usually roosted on their nests every night for as long as they attended the breeding site (Meier et al. 2018). We attached the geolocators towards the end of the breeding season when most chicks had fledged (for details on the sampling and recapture rate see Supplementary information). We aimed at detaching geolocators before egg-laying started the next year, but kept collecting devices while monitoring breeding in the colonies. At all colonies except Spain, we ringed untagged birds as a control to test for logger effects (n = 1094).

For this study we used three different types of geolocators GDL1, GDL2v2 and GDL3pam, all made by the Swiss Ornithological Institute (Bächler et al. 2010, Liechti et al. 2013, Briedis et al. 2016a). Additionally, 30 loggers (GDL2v1 and prototypes) have also been used during the course of this study, but because they were not suited for this analysis, they were only used to calculate recapture rate of tagged birds. GDL1 and GDL2v2 record light only and weighed 1.5 g and 1.0 g with harness, respectively. They were used during the first two years of the study. GLD3pam, weighing 1.6 g, records light, pressure and acceleration, and was used across all years (for details see Meier et al. 2018 and Supplementary information). The additional load in relation to body weight (mean body mass 96 g, SD: 87–105 g, n = 10 623) corresponded to 1.52–1.84% (n = 552). Tags were placed on the bird's back just behind the wing near the body's centre of mass (Bowlin et al. 2010, Morganti et al. 2018). We attached them around the wings with a body harness made from nylon cord (diameter 1 mm, Lavorazione reti Bonardi, Italy) partly coated with PVC tubing to prevent constriction of the wings and adjusted the harness size to the individual's body size.

Data analysis

We recaptured a total of 266 birds (48%) with tags and could successfully extract the migration phenology from 215 tags (81%), of which nine (4%) recorded only parts of the journey. These tags belonged to 110 Swiss birds, 27 Bulgarian birds, 17 Spanish birds and 61 Turkish birds. Analysing geolocator data of a cavity breeder, like alpine swift, can be challenging because entering and leaving the cavity creates shading which might almost look like a sun event on the tag but will not yield a reasonable coordinate in the geolocation analysis (Lisovski and Hahn 2012, Meier et al. 2018). To separate periods with shading we screened all data using the methods in the SGAT package (as described in Lisovski et al. 2019). Implausible short days were observed only at the beginning and the end of the year-round logging period, when birds stayed at their breeding colonies and shading concealed the true twilight. Consequently, we could analyse the entire phase of annual movements with geolocation and for the birds equipped with pressure sensors we could confirm that they were stationary during the entire breeding season (Supplementary information).

We processed light data with the FLightR ver. 0.4.7 (Rakhimberdiev et al. 2016, Rakhimberdiev et al. 2017). We applied Hill–Ekström calibration on stationary phases between November and February and then defined constant calibration parameter values for all tags of the same type to make the result of different tags comparable (see supplement). Timing of stationary periods during the annual cycle was calculated using the function *stationary.migration.summary*. FlightR estimates probability of movement for each twilight event and we defined stationary behaviour if the cut-off probability was less than 0.1. Because birds were migrating around the equinox, when light level data are less informative for geolocation, we applied a rigid threshold of 14 days before we considered stationary behaviour. To discriminate between the migratory and the non-migratory season we defined any stationary site below the latitude of the Tropic of Cancer (=23.4°, Supplementary information) as non-breeding sites, and stationary periods less then 50 km from the breeding colony as part of the breeding site. Arrival and departure at either breeding or the non-breeding site were defined by the date of the first and last position, respectively, within these sites. FlightR is able to estimate timing and positions near the equinox, but the uncertainty becomes very large, especially if a bird moves predominately along the same latitude. We acknowledged this uncertainty in all spatial interferences of all following models. Since we had no evidence for stopovers during the migration we defined travel speed as distance between the breeding site and the non-breeding site divided by the time between departure and arrival.

We conducted two statistical analyses to test the following two hypotheses. Firstly, we predict that populations breeding at higher latitudes, where the summer season is shorter, should adjust their annual schedule to spend less time at the breeding site. To test this, we analysed the timing of all individuals at each of the four major stages (departure from and arrival times at the breeding and non-breeding sites) during the annual cycle. We fitted linear mixed models (Table 1, M1a–M4a) for the Julian date of each stage as dependent variable, latitude of the breeding range as a fixed factor, and included year and breeding population as random factors. We did not include latitude of the non-breeding range because all populations spend the winter at the same latitude. Since previous stages might affect the timing at the current stage (carry-over effect), we additionally included, where available, individual date of the previous stage as second fixed factor in the models; this factor was unavailable for departure from the breeding site because geolocators had been attached only shortly before. Secondly, we predict that populations breeding at higher latitudes should be more time constrained by the short season and this might afford less variation in migratory timing (Alerstam et al. 2006, Conklin et al. 2013, Verhoeven et al. 2019). To test for differences in the synchrony of timing, we calculated the correlation between the latitude of the breeding site and variation in timing at any stage during annual cycle. Variation in timing was defined for each stage and each year as inter-individual standard deviation at the population level. Again, we used the same model as above but without the factor for carry over effects. All variables were z-transformed for comparing effect sizes between them. Models were run in R (ver. 3.6.3) with the package lme4 (Bates et al. 2015) and we report effect size and credible interval (CrI). These intervals were calculated using the R package 'arm' with the function 'sim' (Korner-Nievergelt 2015).

Results

Spatial patterns

For all four populations the places of residence in Africa were between latitudes 5 and 10°N (Fig. 1). The two western

Table 1. Output of the models testing the relationship between (a) date of migration, year of attachment of the geolocator and latitude (Lat.), and (b) variation in timing and latitude. Both models (a + b) were run for each stage of the annual cycle: At departure from the breeding site (B-Dep), at arrival at the non-breeding site (NB-Arr), at departure from the non-breeding site (NB-Dep) and at arrival at the breeding site (B_Arr). To address carry over effects we included date of previous stage as additional variable where possible (Ma2, Ma3, Ma4). Bold estimates show effects for which the range of the 95% CrI does not included zero.

Variable: →	Intercept			Lat.			Timing at the previous stage		
Model: ↓	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
Timing									
M1a: at B-Dep	0.24	−0.53	1.07	−0.51	−1.44	0.37			
M2a: at NB-Arr	0.06	−0.25	0.34	−0.18	−0.52	0.15	**0.78**	**0.70**	**0.85**
M3a: at NB-Dep	0.13	−0.28	0.56	0.38	−0.10	0.85	−0.17	−0.32	0.00
M4a: at B-Arr	0.02	−0.07	0.10	0.08	−0.02	0.18	**0.84**	**0.77**	**0.92**
Variation in timing									
M1b: at B-Dep	8.71	−15.88	33.79	0.06	−0.54	0.63			
M2b: at NB-Arr	18.90	−5.00	40.80	−0.20	−0.75	0.34			
M3b: at NB-Dep	6.49	−16.08	31.30	0.11	−0.49	0.62			
M4b: at B-Arr	8.41	−20.01	36.48	0.06	−0.61	0.74			

breeding populations, from Spain and Switzerland, shared most of their non-breeding range in western Africa. Eight birds from Switzerland (8% of the population) also visited more eastern sites in Togo and the Lake Chad area for at least part of their non-breeding season. The latter site was also visited by birds from Bulgaria and one individual from the Turkish population. The majority of Bulgarian and Turkish birds shared their non-breeding range in eastern Africa. While both, Spanish and Swiss birds mainly migrated via the Iberian Peninsula in autumn, Swiss birds frequently short cut their journey in spring across the western Mediterranean Sea (Fig. 1b). Bulgarian and Turkish birds generally crossed the eastern Mediterranean Sea directly in autumn (Fig. 1a), but in spring many individuals took a detour of several hundred kilometres crossing the Arabian Peninsula and flying back via Israel and Jordan (Fig. 1b).

Timing of migration

Birds from colonies at higher latitudes arrived earlier at the non-breeding site and departed later from that site compared with birds from colonies at lower latitudes (Fig. 2, 3, Supplementary information). Consequently, the breeding season at northern colonies (Switzerland) was up to 48 days shorter compared to southern colonies (Spain). Migration lasted only about a week in all four populations. In all populations median duration of migration was shorter in autumn with 6 (3.8–6.9 IQR), 7.5 (5.3–12.2), 5 (4.3–7.3) and 3.4 (2.4–7.1) days than in spring with 8.3 (4.4–14.5), 9.6 (6.1–12.8), 8.6 (6.6–13.3) and 8.2 (5–10.7) days (Fig. 2). The Turkish birds showed the fastest overall travel speed during migration of 840 (408–1200, IQR) km day^{-1} for the 2900 km distance between south Turkey and south Sudan.

The model results supported a negative correlation between latitude of the breeding site and departure at the breeding site (M1a, Table 1) and a positive correlation between latitude of the breeding site and departure from the non-breeding site (M4a). Although the effect sizes of latitude were large in both models, the credible intervals included zero, likely due to the low number of populations. Arrival date and the departure date at the non-breeding site were also negatively correlated among populations with the resulting pattern of a longer non-breeding season for populations from higher latitudes (M2a and M3a). The arrival dates, both at the non-breeding site and at the breeding site in the following year, were strongly positively related to the corresponding former departure dates (M2a and M4a), providing evidence for a strong carry-over effect due to quite constant durations of migration between individuals. Although departure date from the non-breeding site explains most of the variation in arrival dates in spring, there was an additional component (with a credible interval including zero though) depending on the latitude of the breeding site which led to an additional delay upon arrival in populations further north in Bulgaria and Switzerland.

Variation in timing

Variation in timing was not related to latitude in any departure or arrival events (M1b–M4b, Table 1, Fig. 4). In contrast to our expectation, the Turkish population situated at the lowest breeding latitude in our study showed the lowest variation in timing. Instead, the northern population (Switzerland and Bulgaria) showed intermediate variation across all years and across all stages of migration.

Discussion

As expected, the length of stay at the breeding site was strongly related to latitude and, thus, affected all annual cycle events. On average, the potential breeding season became 3.4 days shorter with every degree of latitude. This effect is about 25% stronger than what Wyndham (1986) reported for a wide range of species across the globe. This is a pattern we typically would expect in species with facultative second broods

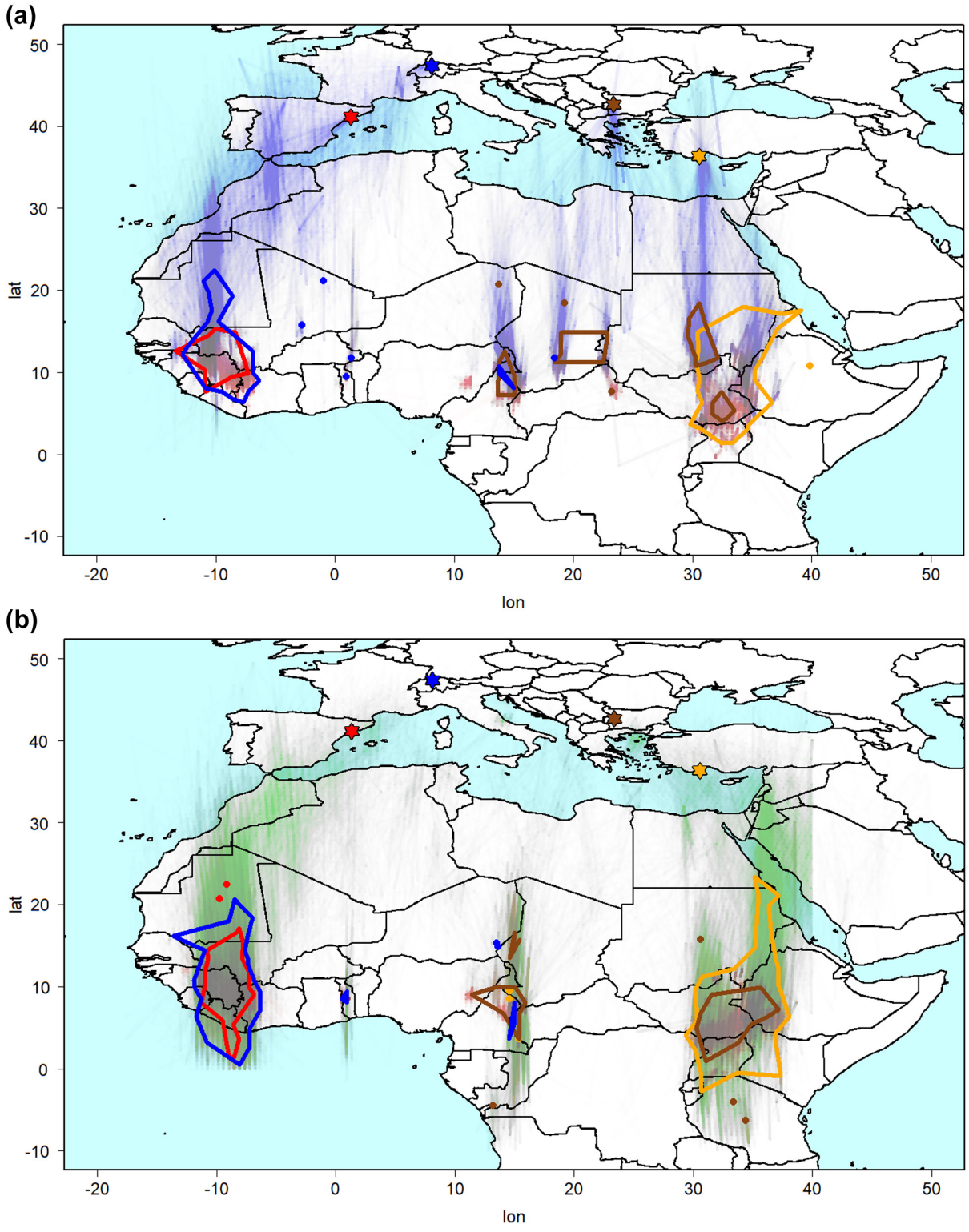

Figure 1. Map showing the major flyways and places of residence of all four populations from (a) post-breeding to the end of the calendar year (incl. post-breeding migration) and (b) the beginning of the calendar year until the onset of breeding (incl. pre-breeding migration). Stars indicate the breeding sites of the four populations. Shaded areas show the flyways and were generated by superimposing resamples of 100 individual tracks of each population from the posterior distribution of the FLightR output. Colours of the tracks vary with date ranging in (a) from blue to dark red and in (b) from dark red to green and intensities indicate the relevance of each flyway. Alpha-concave hull polygons with $\alpha = 330$ km indicate the core non-breeding sites used in each season (Asaeedi et al. 2014). Dots represent isolated places of residence visited by a single bird – colour refers to the breeding population.

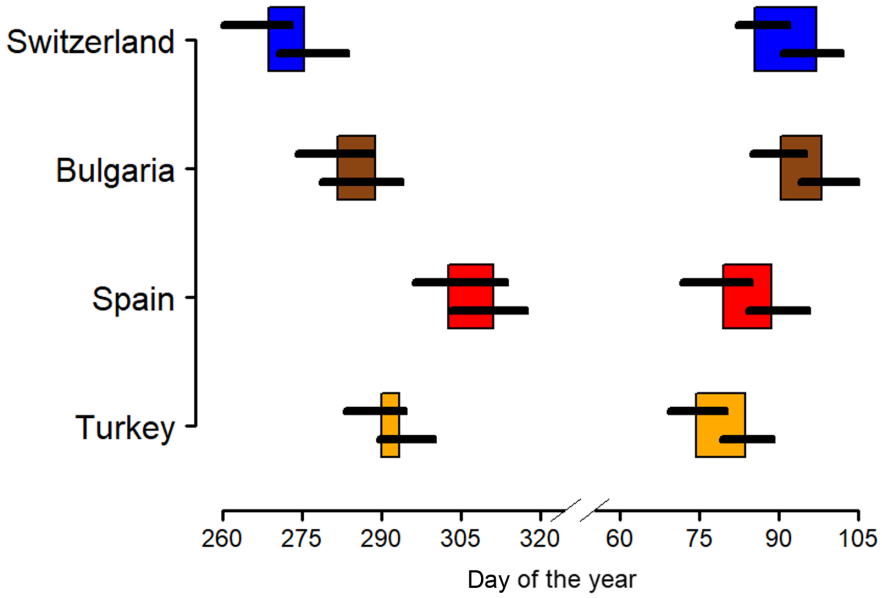

Figure 2. Time of migration in autumn (left boxes) and spring (right boxes) between the breeding colonies and places of residence in Africa for the four populations. Box margins show median departure date (left edge) and median arrival time (right edge). Bars show the variation IQR in timing between individuals of the same population for departure (in the upper half of the box) and arrival (in the lower half of the box). For colours, see Fig. 1 and for details, see Supplementary information.

or multiple broods to maximize fecundity as breeding season becomes longer (Jenni and Kéry 2003, Hedenström et al. 2019, Jahn et al. 2019). However, alpine swifts mainly have single broods (Arn 1960, Cramp 1985 but see Antonov and Atanasova 2001). None of the birds in our study gave evidence for a second brood. The minimal time for a successful brood is almost 100 days preceded by an additional month for pair formation and renewing of the nest, which makes it hardly possible even for the southern populations to add a second brood (Arn 1960). This poses the question, why even birds from the northern-most population (Switzerland) still spend more than five months at the breeding site? We can only speculate that colonial alpine swifts need additional time for nest site defence, courtship behaviour and other social interactions among colony members. Also until the autumnal equinox, daytime is longer further north providing more time for hunting flying insects. Alternatively, food supply might still be better than elsewhere, and the opportunity

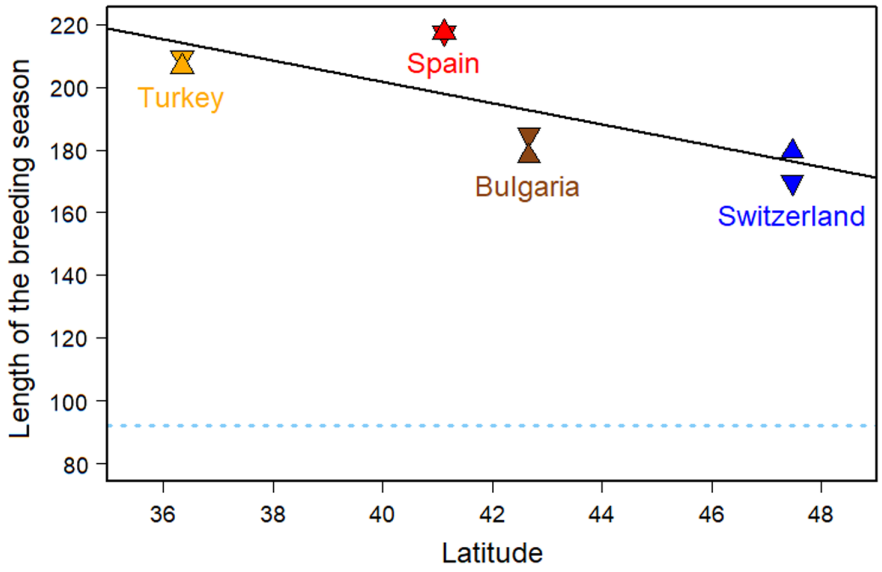

Figure 3. Relationship between the latitude and the length of the period that birds attended the breeding colony indicated with a solid linear regression line. The broken line marks the minimal duration required to successfully complete a brood according to the literature (Arn 1960). The symbols indicate the length of breeding period in 2015 (downwards arrow) and 2016 (upwards arrow) for each population.

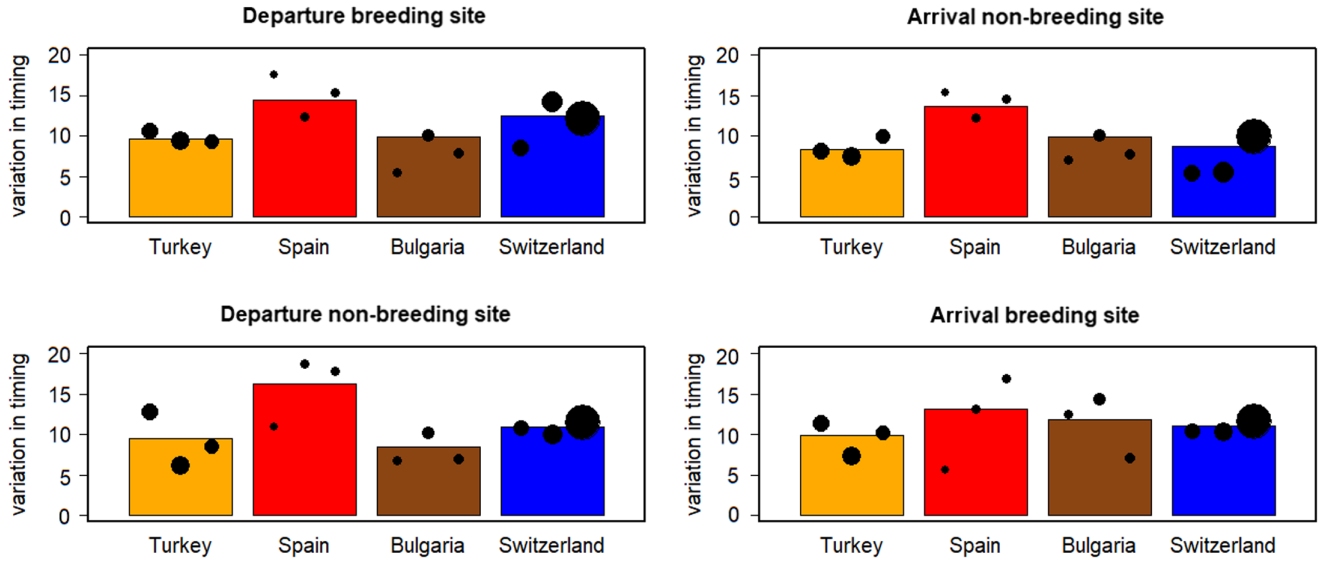

Figure 4. The four panels show the variation in departure or arrival, respectively, for each of the four study sites. The four bars show the amount of variation observed in each population over the entire study period. Units of the y-axes denote standard deviation in days. Dots show the variation observed per year and per population and the size of the dot corresponds to the number of sampled individuals.

to roost in the colony at the night reduces energy costs and predation risk.

This is the most comprehensive study of the total annual schedule for this species so far. Most striking is the very short migration period of only one week per season. The short duration for the entire migration provides strong evidence that alpine swifts migrated nearly non-stop. To our knowledge this is shortest migration time of any long-distance migrant and thus, migration covers only a small fraction of their entire annual cycle. Pallid swifts *Apus pallidus* are very similar in their ecological requirements and also migrate for only ten days in autumn and spring (Norevik et al. 2018) whereas common swifts *Apus apus* regularly include a stopover for their much longer migration route (Åkesson et al. 2016). Anyway, the short journey of alpine swift leaves little scope for late individuals to catch up with the migration schedule of earlier ones. Therefore, birds which are in a competition for limited breeding territories and need to arrive early at the breeding site might begin the race already at the non-breeding site with an early departure (Kokko 1999, Ouwehand and Both 2017). Possibly birds refuel en route while migrating as they are aerial feeders all year round (Liechti et al. 2013, Meier et al. 2018). Fly-and-forage migration is considered a possible strategy mainly for species hunting or locating their prey in flight (Strandberg and Alerstam 2007). This could be an alternative strategy to accumulation of energy reserves before long flight bouts which reduces total migration time and allows for a spontaneous departure in the most favourable conditions. Migratory insects travelling along the routes of alpine swifts might further support the fly-and-forage strategy (Stefanescu et al. 2013).

The short travel time especially of the Turkish birds, but also of some individuals in any population, is remarkable and suggests that these birds indeed fly in many cases non-stop. Radar studies have observed migrating alpine swifts at airspeeds of 12.6 m s^{-1}, SD ± 2.6 m s^{-1} with ground speeds up to 18 m s^{-1} (Bruderer and Boldt 2001). At this airspeed a Turkish bird would take 63 h non-stop flight without wind assistance to migrating on great circle distance between Turkey and south Sudan. In fact, the fastest quartile of Turkish birds needed less than 58 h for the journey even though many took an extended route via the Arabian Peninsula. This is a detour known for many soaring birds, as well as barn swallows *Hirundo rustica* in spring allowing them to profit from wind support (Meyburg et al. 2003, Shamoun-Baranes et al. 2003, Briedis et al. 2018). Similarly, favourable prevailing winds might also exist for the westerly populations and could explain their detour via southern Spain in autumn (Erni et al. 2005, Kranstauber et al. 2015). Surprisingly, birds travelled at greater speed in autumn than in spring suggesting that they did not travel at the highest possible speed in spring. This pattern contrasts with many other species where individuals of the same population are in a race for the best breeding territories in spring (Nilsson et al. 2013). It is likely that alpine swift are lacking good cues to predict spring conditions beyond the Mediterranean region when departing south of the Sahara and therefore, after crossing the Sahara, they might spend a few days in Mediterranean region to wait for favourable conditions (e.g. a warm front) to complete their journey (Liechti et al. 2013). The same strategy is known from common swifts which often have to stopover in this region until wind conditions become favourable (Åkesson et al. 2012, 2016). We have no indication that individuals, after arrival at the breeding site, return south if there are harsh conditions at the breeding site. Swifts sometimes may have to interrupt their migration to avoid flying into

adverse weather in spring similar as was observed in nightingales *Luscinia megarhynchos* (Emmenegger et al. 2016). A similar behaviour is known of Icelandic whimbrels *Numenius phaeopus* which delay their crossing of the Atlantic in spring to avoid headwinds (Carneiro et al. 2019).

Several studies suggest that variation in timing of migratory events decreases between individuals the closer an event gets in time with the laying date (Alerstam et al. 2006, Conklin et al. 2013, Senner et al. 2014, Lindström et al. 2016). In contrast to these studies, variation in timing between individual alpine swifts remained at a similar magnitude over the entire year and at different latitudes. In other words, the fraction of early and late birds as well as the individual's deviation from the median timing in the population was about the same at all locations and across the annual cycle. Other species show very well variation in timing between populations of different locations: Briedis et al. (2016b) compared variation in timing across the annual cycle of two flycatcher populations separated by a north–south gradient. He observed that individuals from the northern population tended to have a wider variation in timing than individuals in the southern population. Gow et al. (2019), on the other hand, found a wider variation in timing in southern populations when comparing the annual schedule of five populations of American tree swallows *Tachycineta bicolor* at different latitudes for most of the annual cycle. A comparison of three populations of common swifts across 11° in latitude showed that pattern in variation may also change with season (Åkesson et al. 2016). Variation in timing in these swifts was higher in northern populations compared to southern populations for departure from the breeding site and vice versa for arrival at the breeding site. However, the pattern in alpine swifts suggests that factors affecting the variation in timing are independent of latitude. We might expect constant variation in timing between population when competition among individuals in different populations is of the same intensity, because in a race for the best breeding territories only the relative order between individuals matters and not the absolute timing of migration (Kokko et al. 2004, Low et al. 2015, Heckscher et al. 2017).

In summary, the breeding season of birds in Switzerland was up to 25% shorter compared to birds in Spain. However, Swiss birds were not time constrained by the shorter breeding season since they stayed more than a month longer at the breeding site than was required for reproduction. It is a paradox why alpine swifts are not breeding further north, although the length of the season certainly meets the minimum requirement for survival and thus might probably also allow for reproduction. Currently, only very few breeding colonies exist further north in southern Germany (Gedeon et al. 2014). Astonishingly the ecologically very similar species, the common swift, which requires one month less for reproduction and leaves almost immediately after juveniles fledge, manages to reproduce successfully even above the Arctic circle (Cramp 1985, Chantler et al. 2014).

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Author's contributions – CMM and FL designed the experiment and wrote the manuscript. CMM, HK, RA and SGP performed fieldwork.
Conflict of interest – All authors state no conflict of interest to declare.

Transparent Peer Review

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Data deposition

Data will be available from Movebank: <http:dx.doi.org/10.5441/001/1.7kd62k00> (Meier et al. 2020a), <http:dx.doi.org/10.5441/001/1.34k562m5> (Meier et al. 2020b), <http:dx.doi.org/10.5441/001/1.96t76sg0> (Meier et al 2020c), <http:dx.doi.org/10.5441/001/1.d6n476k0> (Meier and Liechti 2020a), <http:dx.doi.org/10.5441/001/1.31v444sc> (Meier and Liechti 2020b), <http:dx.doi.org/10.5441/001/1.21nq5932> (Meier and Liechti 2020c), <http:dx.doi.org/10.5441/001/1.k4g9f2n2> (Meier and Liechti 2020d), <http:dx.doi.org/10.5441/001/1.nn518dc4> (Meier and Liechti 2020e), <http:dx.doi.org/10.5441/001/1.ff3138d1> (Meier and Liechti 2020f).

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