Highly mobile insectivorous swifts perform multiple intra-tropical migrations to exploit an asynchronous African phenology

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Abstract

With timely allocated movement phases, mobile organisms can match their space-use with the seasonality of the environment and thereby optimise their resource utilisation over time. Long-distance avian migrants are known to move with the seasonal dynamics on an annual basis, but how individuals respond to seasonality within their tropical non-breeding range has been less studied. Here we analyse the movement pattern of a highly mobile aerial insectivorous bird, the pallid swift *Apus pallidus,* and its association with the local habitat phenology during the non-breeding period, using individual-based light-level geolocation. We extracted timing and location of 21 birds´ residence periods, as well as characteristics of the intervening movements, such as distance and speed. We used time series of precipitation and vegetation data for each residence area to extract the timing of the local end of the rainy season and the onset of the dry season. The pallid swifts repeatedly upgraded their habitat by undertaking 2–5 intra-tropical migrations correlated with the withdrawal of the rains and the onset of the local dry season. The birds arrived to the sites on average 12 days after rains ended and departed about two weeks after the onset of dry season suggesting that the birds closely tracked a spatiotemporal window presumably timed with optimal foraging conditions. Our results provide insights in the ways Palaearctic-African migrants respond to the asynchronous phenology within their sub-Saharan non-breeding range. We confirmed that pallid swifts actively respond to deteriorating conditions by repeated upgrades in habitat quality, which likely have substantial consequences for an individual´s access to an essential, spatiotemporally ephemeral food resource. However, the pallid swifts did not surf an apparent resource wave per se as would be expected in a highly mobile species, indicating that also other factors, such as spatial patchiness of resources, may influence the movement decision.

Keywords: insectivorous bird, phenology, intra-tropical migration

Introduction

Mobile organisms have the capacity to respond to spatiotemporal variability in resource abundance by actively move to areas with higher resource density. In annual migrants, this is generally recognised as periods of directional movements between areas of residency incorporated within their annual cycle (Dingle 1996). Timely allocated, the movement phases can be matched with the seasonality in the local environment and relate individual space-use to temporally fluctuating food resources (Yang et al. 2008, Armstrong et al. 2016). However, migratory birds meet several challenges in matching their movement relative to local environmental conditions, while keeping track of time during their annual cycle (Åkesson et al. 2017). In the Palaearctic – Africa bird migration system, where billions of trans-Saharan migrants spend the northern winter on the African continent (Hahn et al. 2009), birds face an asynchronous and variable resource landscape also within their sub-Saharan non-breeding ranges (Moreau 1972, Morel 1973, Jones 1996). As the migrants arrive to the Sahel zone south of the Saharan desert in September/October the environment is still green and lush after the rains, but it is soon deteriorating with the commencement of the dry season. This habitat change is related to the southward movement of the Intertropical Convergence Zone (ITCZ) and the associated rains broadly characterising the primary productivity and phenology on the African continent (Waliser and Gautier 1993). Given the cyclic movement of ITCZ around the equator the rain seasons in Western Africa become progressively shorter and more unpredictable with increasing distance from equator (i.e. closer to the Saharan desert), with an earlier onset of the dry season in the northern regions. There are ample historical data providing evidence for massive movements of Palaearctic-African migrants within Africa outside the expected seasonal migration periods (Moreau 1972, Pearson and Backhurst 1976, Curry-Lindahl 1981), which on local basis has been related to environmental seasonality (e.g. Lack 1983, Salewski et al. 2002), and food dynamics (e.g. Dingle and Kamala 1972, Sinclair 1978, Lack 1986). Recent advances in animal tracking have enabled studies associating bird locations to increased food resources (Trierweiler et al. 2013, Schlaich et al. 2016) or potential proxies thereof (e.g. Tøttrup et al. 2012, Thorup et al. 2017). Our understanding is however still limited when it comes to how birds performed their intra-tropical migrations (e.g. if they are nomadic movements along a resource gradient in the landscape or directional migratory movements between specific areas of residence), and how timing of both departure and arrival to areas relate to local phenology (Stutchbury *et al.* 2016).

The pallid swift *Apus pallidus* is a highly mobile aerial insectivorous Palaearctic-African migrant with a non-breeding range covering vast areas of the seasonal Sahel and Guinea Savannah zones in northern sub-Saharan Africa (Chantler and Driessen 2000). Similar to the closely related common swift *A. apus*

(Pellegrino et al. 2017), the pallid swift show general morphological modifications to an aerial life-style, such as high aspect ratio wings, a streamlined body and an energy efficient flight style (Hedenström et al. 2016, Sachs 2017). It was recently also empirically shown that pallid swifts mainly spend the non-breeding season on the wings (Hedenström et al. 2018), something earlier described in alpine swifts *Tachymarptis melba* (Liechti et al. 2013) and common swifts (Hedenström et al. 2016). Despite their energy-saving modifications, swifts are still likely facing higher daily energetic costs relative to other species with a more terrestrial life-style due to the elevated expenditure related to flapping flight (Norberg 1990). As swifts do not regularly land during the non-breeding season (Liechti et al. 2013, Hedenström et al. 2016, 2018), finding areas abundant with energy rich food resources is likely a critical factor to enable maintenance, (i.e. feather moult, Boano et al. 2015) and preparations for future energy expenditures (such as migratory phases when time is mainly spent on directed flight) while on their wings. We, thus, expect pallid swifts to have developed means to effectively exploit spatiotemporal variations in food resources as they spend their annual cycle in their vast and seasonally fluctuating non-breeding range.

The aims of this study were to analyse the large-scale non-breeding movement pattern of a highly mobile avian migrant and explore the potential associations with local environmental factors related to the seasonal phenology within the northern sub-Saharan Africa. We hypothesise that the pallid swifts regularly would improve their habitat by moving as the conditions deteriorate and that the timing of these movements should be related to important changes of the habitat quality in both the departure and arrival sites. We also aimed to describe the spatiotemporal characteristics of the movements within the non-breeding range, and put them into perspective by comparing them with the seasonal migrations to and from the breeding area.

Materials and Methods

Trapping and deployment

Pallid swifts were captured at three study sites in Italy (Carmagnola 44.86°N, 7.72°E; Cannobio 46.06°N, 8.70°E), and Switzerland (Locarno 46.17°N, 8.79°E) during the breeding period. The colonies were located in buildings where the birds were captured inside the nests at night or by using nets outside the nest entrance (Carmagnola) or only by using nets (Cannobio and Locarno). Overall 84 geolocators (models: Intigeo-W55B1 and Intigeo-W65A9 by Migrate Technology, SOI-GDL 1.0 Swiss Ornithological Institute) were deployed in breeding seasons 2011-2014. In total we retrieved 31 tags (37 %), which was significantly lower than the recapture rate of only ringed birds during the same period (63/111, 57 %; p = 0.009, Fisher´s exact test). Investigating the recapture rate separately for Carmagnola,

where some birds were trapped in the nest boxes, we found significant difference between the recapture rate of tagged (14/39, 36 %) and untagged birds (39/66, 59 %; p = 0.027). In Cannobio and Locarno, where the birds exclusively were trapped with nets, the combined recapture rate of tagged birds was 17/45, (38 %), which did not differ significantly from the return rate of only ringed birds (24/45, 53 %; p = 0.20). We note that the recapture rate of tagged pallid swifts varied extensively between years (0-82 % for specific sites and years) and that some individuals were recaptured first after four years. The above analyses indicate that there is a site-specific negative effect on the recapture rate of the tagged birds. This may be due to differences in trapping method and breeding site configuration or another unknown factor. It is currently not established in what ways a reduced recapture rate may be associated with the movement pattern of the recaptured birds, but we have not found any apparent differences in the tracks between the sites included here cf. (Morganti et al. 2017). All but one pallid swift returned to their nests after tag deployment as reflected by the repeated shadings during day-light hours in the light-data, indicating that the birds did not abandon the nests as an effect of handling. We did not find any apparent differences in the tracking data of the single bird that did not return to the nest relative to the rest of the individuals.

We attached the geolocator to the back of the bird, using a full body harness made out of a soft string following the protocol given in Åkesson et al. (2012). Depending on model the mass of the geolocator varied between 0.47 g and 0.77 g and a harness mass of ca 0.3 g resulting in a total weight <3% relative to body mass of the bird in all cases (Boano et al. 2015).

Light-data analysis

The retrieved light-level data were linearly corrected for clock drift by using the software BASTrack (Fox 2010). The data were then translated into two daily geographic positions in the software IntiProc ver. 1.03 (Migrate Technology 2015), using a threshold level of 10 on the full-range data. The data from the SOI-GDL geolocators were analysed using the R-package GeoLight ver 2.0 with a threshold level of 2 (Lisovski and Hahn 2012). The light-data were visually inspected for erroneous transitions, such as those caused by repeated shading events throughout the day. Pallid swifts are like common swifts predominantly aerial during the non-breeding season (Hedenström et al. 2018), and thus the continuous light exposure has resulted in very clean light data (Åkesson et al. 2016). The exception was the breeding season when the birds repeatedly visited the nest-cavities. We therefore used the 'Hill-Ekstrom' procedure (Ekstrom 2004) to derive logger-specific sun-angles corresponding to the threshold values for each geolocator following the procedure described in Åkesson et al. (2012).

Annotating movement data

Geolocator-derived positions are associated with relatively large errors, with especially error in the latitudinal component increasing near the equinoxes (Fudickar et al. 2012, Lisovski et al. 2012). We therefore smoothed the data twice (supplementary file 1). We then excluded the latitudinal component of the positions in three weeks prior and after autumn and spring equinoxes, respectively. Periods of residency was recognised in the time-series of longitudes and latitudes, or only longitudes when close to the equinoxes, as periods where the components showed variation around a mean. We evaluated the validity of each stationary period as well as the timing of each movement by using the two-dimensional, non-parametric, kernel density estimation (KDE) based approach described in Norevik et al. (2017). This approach allowed us to objectively delineate regions of relative high use during different periods of the non-breeding season and to extract the location of highest use based on the distribution of geolocation estimates (see supplementary file 1). The smoothing parameter for each KDE, representing each stationary period, was calculated separately for latitude and longitude, respectively, with the function "kde2" in MatLab (release 2010b The Mathworks, Natick, MA, USA). This function uses a non-parametric approach to calculate the KDE´s smoothing factor that minimizes the risk of under- or over-smoothing when applied to non-normal distributed data such as geolocator-derived positions (Botev et al. 2010). We merged subsequent stationary periods and derived a new KDE if the areas within the arbitrarily chosen isocline of 60 % KDE overlapped. We distinguished the timing of each movement phase as the series of smoothed geolocator estimates, linking subsequent residence areas, that fell outside the two areas´ isocline of 60 % KDE (i.e. the date of the final position estimate within 60 % KDE of the site of departure represented the day of departure and the date of the first position estimate within the 60 % KDE of the site of arrival represented the date of arrival). We used the centroid location for each density surface representing each residence period. We calculated travel time as the number of days spent in transition between successive residence areas. We calculated the great circle distance between consecutive areas of residence, along series of locations representing three-day average positions, as a conservative measure on distance travelled, and excluded distance estimates including areas where the latitudinal component was missing (i.e. areas visited during the period close to the equinoxes). Travel speeds were calculated by dividing cumulative distance with travel time.

Environmental data preparation

We downloaded the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra 16-day 0.05 degree surface reflectance product MOD13C1 corresponding to the time period of the tracking data (2011-2014) from https://reverb.echo.nasa.gov/reverb/. The 16-day composite map was produced by assembling the most cloud-free pixels within each period into one single image. Satellite derived vegetation indices

correlate with vegetation productivity, and are thus useful measures of phenology on a regional scale (Reed et al. 1994, Pettorelli et al. 2005). The MODIS product Enhanced Vegetation Index (EVI) that uses a feedback adjustment to minimize canopy background variations and to reduce atmospheric influences was used for the analyses (Huete et al. 2002). We filtered the EVI time-series (with a window size of 5 and a polynomial degree of 2) using the function *sgolayfilt* in the signal R-package (Ligges et al. 2015). The Savitzky-Golay smoothing filter is a robust method to filter out and replace erroneous data points (due to e.g. cloud obstruction) from relatively smooth time-series (Chen et al. 2004). We then standardised the filtered data-set to the interval [0, 1] to take into account between pixels variation due to difference in EVI-values due to e.g. vegetation cover, to be used in the phenology analysis. Finally, water was masked in the standardised images.

The 3-hourly Tropical Rainfall Measurement Mission (TRMM) 0.25 degree satellite derived product 3B42 corresponding to the time period of the tracking data (2011-2014), were downloaded from ftp://disc3.nascom.nasa.gov/data/s4pa/TRMM_L3/ and transformed to daily sums. 3B42 consists of infrared (IR) estimates from a series of remote sensors adjusted to monthly IR calibration parameters derived using high quality retrievals by the TRMM instruments (MacRitchie 2015). TRMM was specifically developed for the study of precipitation within the tropical region, and by being an all-satellite system it avoids interpolation issues related to ground-based systems involving sparsely located metrological stations, as is often the case in the tropics.

Extraction of local environmental data

After locating the centroid of each KDE, representing the different residence sites used by the pallid swifts, we extracted time-series of standardised EVI and precipitation data within a radius of 100 km. We selected periods corresponding to the annual cycles of each individual bird from the time-series (e.g. July 2012 – June 2013 for birds tracked between 2012 and 2013). From these periods, we extracted standardised EVI values corresponding to the date of movement between areas in order to evaluate relative difference in habitat quality. We also extracted timing and value of annual local minima in EVI as a proxy for the most deteriorated conditions, as well as the timing of the highest rate of change in the autumn as a proxy for the local drop in habitat quality (Zhang et al. 2003). A generalised additive model (GAM) was fitted for each extracted time-period from which the standardised mean EVI values and derivatives were extracted (Wood 2011, Supplementary file 2).

We used the extracted time-series of daily precipitation to calculate the cumulative sum of local annual precipitation on which we fitted a GAM (Supplementary file 2). This enabled us to extract the date

corresponding to the end of the previous rain season. We defined the end of the rain season as the date when the average daily precipitation did not exceed 4 mm following Zhan et al. (2016).

To explore the relationship between the birds´ relocations and measures of local phenology a Linear Mixed Model (LMM) was fitted with date of movement as response factor, date of environmental factor as independent variable and individual as random factor using the *lmer* function in the R package lme4 (Bates et al. 2015). We performed *post-hoc* Tukey´s pair-wise comparisons of means for the travel speed model using linear hypothesis testing using the function *glht*, in the R package *multcomp* (Hothorn et al. 2008). We conducted all analysis using statistical software program R version 3.4.1 (R Core Team 2017). The data will be available from the Dryad Digital Repository upon publication.

Results

The annual cycle

The average departure date from the breeding areas was 27 September (SD = 13.4 days, range = 28 August – 24 October, n = 21), and the mean arrival date to the first sub-Saharan non-breeding area was 7 October (SD = 12.9 days, range = 9 September – 8 November, n = 21). One individual stopped for seven days in Libya prior the crossing of the Sahara desert, while the rest made a more or less direct migration from the breeding area to the non-breeding range (Fig 1, Supplementary file 3). The birds used 2-5 different areas of residence within the sub-Saharan non-breeding range (median duration of stay = 39 days, range = 8-155 days). The average departure date from the final area was 9 April (SD = 13.9 days, range = 18 March – 4 May, n = 20), and the mean arrival date to the breeding area was 20 April, (SD = 13.1 days, range = 30 March – 13 May, n = 20). Seven birds stopped for on average eight days (SD = 4.9 days, range 4-17 days), after crossing the Sahara desert, at locations in northern Africa in Morocco (2 individuals), Libya (3) and in Tunisia (2).

The tracked birds spent on average 44 % and 50 % of the annual cycle in the breeding area and on the sub-Saharan non-breeding grounds, respectively. Both autumn and spring migration lasted on average 10 days, meaning that 6 % of the annual cycle was allocated to the migration between the breeding area and the sub-Saharan non-breeding grounds. Most individuals performed their migration without any apparent stopover, suggesting that the main preparations including fuel accumulation for the migrations likely were conducted while still in the breeding area and the non-breeding grounds, respectively. The average distance covered by the birds within sub-Sahara was 2800 km (SD = 1039, range = 1160-4356, n = 17) corresponding to about 60 % of the autumn route (mean 4340 km, SD = 493, range = 3784-5479, n = 20). In spring the birds migrated on average 4706 km (SD = 446, range = 4358-6390, n = 17), which was

significantly longer than in autumn (t_{paired} = 6.12, df = 15, p < 0.001). The n-values represent the number of tracks not affected by the equinox.

Non-breeding movement and local habitat phenology

All birds performed at least one intra-tropical migration within the sub-Saharan non-breeding range. We used each residence site´s standardised vegetation index (see method) to take into account the site specific variation in raw greenness due to e.g. difference in vegetation type or cover. The birds generally moved to areas with higher standardised vegetation index (arrival area versus departure area, t_{paired} = 4.84, df = 35, p < 0.001), suggesting a movement towards areas with relatively later seasonal phenology (i.e. where the habitat deteriorated later).

Across all pallid swifts we found a positive relationship between the local end of the rainy season and the arrival of the birds (slope = 1.02, t = 8.83, p < 0.001; Fig 2). On average the swifts arrived 12 days after the end of the rains. There was also a positive relationship between timing of departure and local maximum drop in greenness (slope = 0.84, t = 6.04, p < 0.001; Fig 3). The temporal relationship however differed within the season, and the birds on average departed about two weeks after the maximum drop in early November while they departed in tandem with the local drop in greenness in late January.

The timing of the driest point of the annual cycle as reflected in the raw vegetation index of all the sampled areas was on average 1 February. At that time the pallid swifts were located at the 'greenest' of the residence areas visited during the non-breeding season (current area versus the greenest optional area, t_{paired} = 5.14, df = 20, p < 0.001; Fig 4).

The median travel speed in the sub-Saharan non-breeding range, calculated as the distance divided by the time spent on travel only, was 369 km day^{-1}. This was slower than during migration in both autumn (518 km day^{-1}) and spring (625 km day^{-1}; Table 1).

Discussion

Our results show that the pallid swifts were highly mobile within their sub-Saharan non-breeding range, and that the birds successively improved their local habitat quality as reflected by the greenness measurements. These movements were temporally associated with the habitat deterioration on the departure areas, as well as with the withdrawal of the rains at the arrival areas indicating that the birds tracked a spatiotemporal niche following the end of the rainy season, presumably exploiting local ephemeral pulses of air-borne insects that become profitable for the pallid swifts after the rains (Dingle and Kamala 1972, Sinclair 1978, Lack 1986). Interestingly, concentrations of aerial insects can occur already with the first rains, but they become more abundant during the rainy season (Sinclair 1978).

Hence, the relatively late arrival of the pallid swifts in relation to the local rains indicates that they primarily focus on prey that concentrates in the variable weather following the main rains. This temporal strategy may make them vulnerable to unusually dry years when late rains and insect concentrations do not occur (Boano and Bonardi 2005). Pallid swifts are mainly aerial outside the breeding season and given the large movements within the sub-Saharan non-breeding range documented here, they seem predisposed to opportunistically respond to variation in prey availability between and within years (Hedenström et al. 2018). However, another common non-breeding visitor south of the Sahara from the temperate zone, the common swift, winters further south in Africa in areas where the general timing of the birds in relation to the rainy season may differ from that in the Sahel (Åkesson et al 2012, 2016). It is currently not clear if the two species compete for the same general foraging niche or if they after their genetic divergence have specialised into different spatiotemporal niches in relation to the dynamics of the African rainy seasons (Pellegrino et al. 2017).

Intra-tropical migrations in an asynchronous and variable resource landscape

The pallid swifts mainly spent the non-breeding within the species´ currently known non-breeding range, largely covering the Sahel and Guinea Savannah zones in northern sub-Saharan Africa (Chantler and Driessen 2000). This African region is associated with highly dynamic seasonality with a profound dry season during the northern winter as well as an unpredictable between-year variation in the severity of the annual drought (Waliser and Gautier 1993, Nicholson 2012). How Palaearctic migrants manage to survive the dry season and prepare for an energy-demanding spring migration has been an apparent puzzle ('Moreau's paradox') since described by Moreau (1972). Later studies have proposed various (probably not mutually exclusive) ways in how birds have solved the paradox; for example by opportunistically exploiting relatively productive areas (Morel 1973), switching diet (Fry 1992) or by adjusting foraging efforts (Schlaich et al. 2016). Additionally, many intra-African and Palaearctic-African migrants leave for wetter areas to track resources and to escape the competition for food in the Sahel (Moreau 1972, Hedenström et al. 1993, Ottosson et al. 2005). Flycatchers, swallows and swifts, which are specialized in catching air-borne insects, are underrepresented among the birds spending their non-breeding season in the Sahel and the occurrence of one of the more common non-breeding aerial insectivores, the bank swallow *Riparia riparia*, is mainly associated to areas with permanent waters (Morel 1973, Curry-Lindahl 1981, Zwarts et al. 2009). Here we show that also pallid swifts escape the deteriorating ecological conditions during the dry season in the Sahel by successively moving to wetter areas.

Hopping along rather than surfing on a wave of resources

Given their mobility and aerial life-style (Hedenström et al. 2018) the pallid swifts have the prerequisites to prey upon air-borne insects while flying and would thus have the potential to continually 'surf' the resource wave as it moves through the landscape. Apparently, the pallid swifts of this study did not exhibit such a movement strategy, but instead alternated long periods of residency with relatively rapid and directed movements similar to what have been described in other Palaearctic-African migrants (e.g. Thorup et al. 2017). The strategy of using long periods of residency is likely superior to a more nomadic life-style if food resources are unevenly distributed in the landscape (see below), or if familiarity of the local area is beneficial (Wolf et al. 2009) and the costs associated with gathering of accurate information regarding the spatiotemporal arrangement of recourses outweigh the benefits with surfing (Bishof et al. 2012). A radar study on presumed non-breeding common swifts in Sweden showed that birds spending the nights in aerial roosts adjusted their orientation and airspeed resulting in a reduction in potential displacement (Bäckman and Alerstam 2001), indicating that they strived to remain in familiar areas. The pallid swifts still undertook the within-season movements at lower travel speed compared to the travel speeds recorded during the migrations to and from the breeding area. This may be an effect of the two ecological barriers, i.e. the Saharan desert and the Mediterranean Sea, dominating the migration routes and promoting the birds to extend the daily travel time during the seasonal migrations (Åkesson et al. 2012). But given that a pallid swift flies at about 10.5 m s^{-1}, which is the recorded flight speed of radar-tracked pallid swifts (Bruderer and Bolt 2001), the corresponding potential daily travel speed would be 916 km day^{-1} (assuming a 24 h flight in neutral winds). Provided that the true paths of the birds were not considerably longer than those estimated by the geolocators the median travel speed in the non-breeding season was about 40 % of the potential flight speed, suggesting that the pallid swifts allocated potential daily flight time on other activities such as foraging.

Conclusions

By investigating how individual pallid swifts undertook their large-scale intra-tropical migrations, we gained insights in the ways Palaearctic-African avian migrants move in relation to the asynchronous phenology within their sub-Saharan non-breeding range. We demonstrate that the repeated movements of the pallid swifts were related to local habitat phenology, suggesting that the birds spatiotemporally matched their space-use with the seasonality in sub-Saharan Africa. Interestingly, given the pallid swifts´ aerial and highly mobile life-style, the birds did not surf the resource wave *per se*, but instead undertook multiple rapid movements between successive sites of residence over the course of the non-breeding season. This suggests that other factors, such as spatial variation in resources and prior knowledge, are

more important than the individual´s movement potential in shaping the spatiotemporal patterns of migratory animals. Avian long-distance migration is a complex phenomenon that involves both endogenous and external components, which depending on each situation may trigger a migratory movement (Terrill 1987, Gwinner et al. 1988), and for which timing movement events across the annual cycle is crucial (Åkesson et al. 2017). How migrants alternate between an obligate and a facultative migratory mode can now be studied as both individual animal tracks and environmental data are becoming increasingly available. Using repeated high resolution tracking of individuals of multiple annual cycles where the spatiotemporal pattern can be related to local resources (or a relevant proxy thereof) may, furthermore, prove very useful to disentangle environmental effects from endogenous mechanisms of animal movements.

Authors´ contributions

GN, AH and SÅ conceived the ideas; GB, RL and FL were involved in data collection; GN analysed the data and led the writing of the manuscript with input from AH and SÅ. All authors contributed critically to the draft and gave final approval for publication.

Permits

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Figure Legends

Figure 1. Overview of the locations of the 21 pallid swifts showing the birds´ location up to (left) and, after (right) 1 February. Squares illustrate residence areas and dots represent three days average position estimate during movement phases. Dashed lines symbolise movements during the periods of the equinoxes where stationary areas have not been possible to discern. Maps are in a Mercator projection.
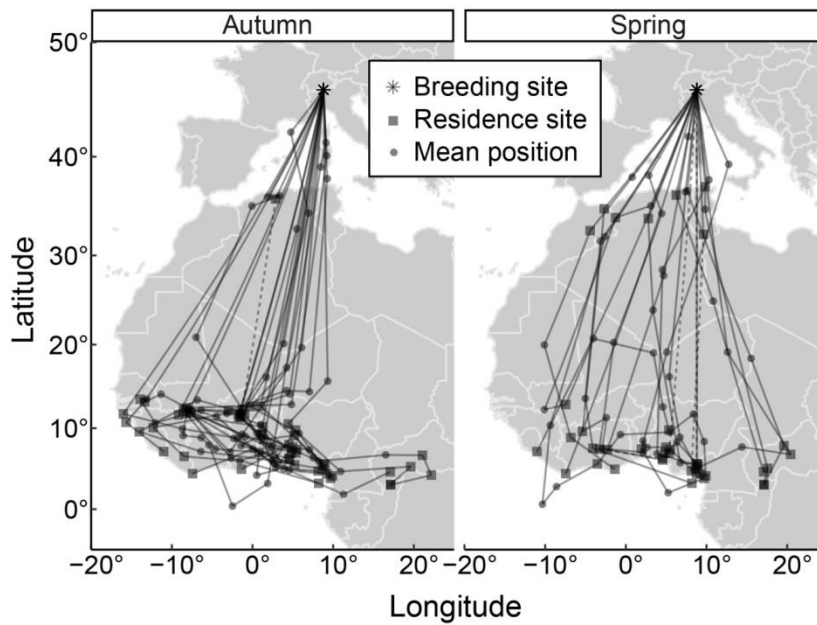
Figure 2. Arrival timing to non-breeding residence areas of pallid swifts in relation to the end of the rain season at respective location. The line represent the linear relationship (slope = 1.01) between the end of the rain season and the arrival of the birds.
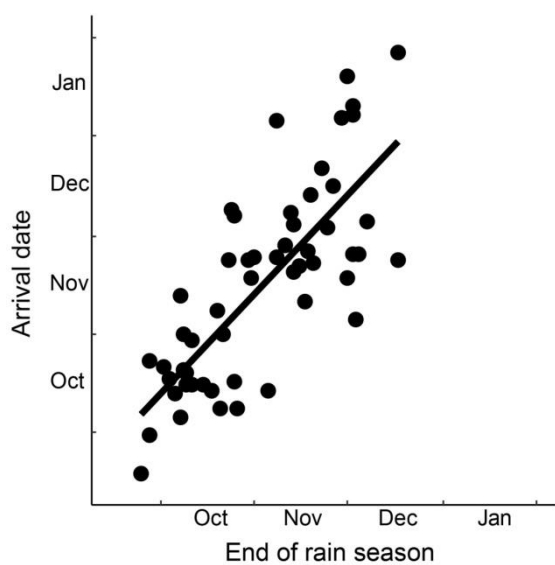
Figure 3. Departure timing from residence areas in relation to the date of the local maximum rate of deterioration. The line represents the linear relationship (slope = 0.85) between the date of local maximum deterioration rate and the departure timing of the pallid swifts.
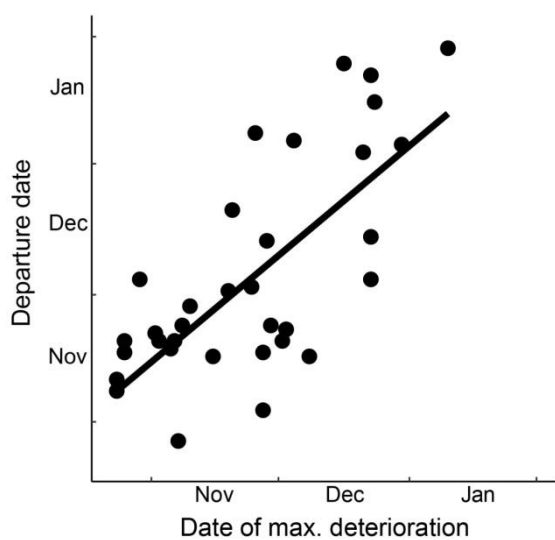
Figure 4. Graphical representation of the relative minimum greenness (based on minimum raw EVI values, see method) showing the geographic distribution of highly vegetative and relatively lush areas, overlaid with the residence areas of the pallid swifts colour coded by the relative timing of the birds´ visits. As the season progresses the pallid swifts move to successively lusher areas and spend the driest part of the non-breeding period in the greenest areas. Due to their location, these areas have the shortest annual dry season and thus provide relatively high abundance of food when conditions deteriorate further to the north.
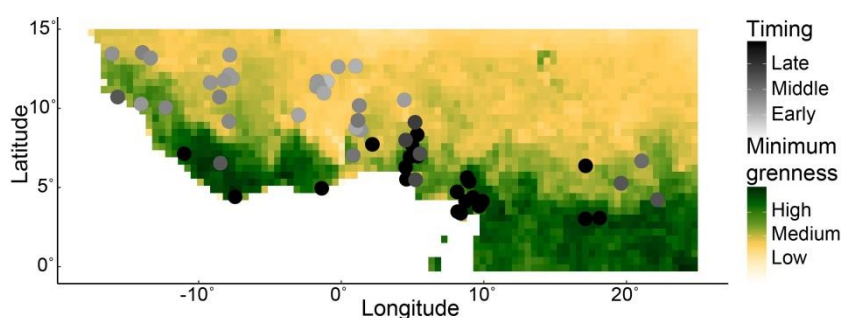
Table Legend

Table 1. Significance of comparisons of linear fit of the log-transformed travel speed (excluding recorded preceding stationary time) between three seasons: autumn, non-breeding, and spring. A Bonferroni-Holm correction of all-pair multiple comparison was used.

Linear hypothesis:	Estimate	SE	z value	P
Spr. - Aut. = 0	0.228	0.147	1.548	0.122
Win. - Aut. = 0	-0.424	0.129	-3.280	< 0.01
Win. - Spr. = 0	-0.652	0.124	-5.276	<0.0001