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ORIGINAL ARTICLE

Movements throughout the full annual cycle of three migratory swift species breeding in the Levant

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Abstract

Movements throughout the annual cycle evolved as an adaptation to seasonality across different bird species with a continuum of migration strategies and behaviours at the non-breeding range. Swifts are particularly mobile, aerial insectivores with a distinctive lifestyle. However, the spatiotemporal properties of swift migration, including timing, routes, and non-breeding movements, remain poorly understood in populations from the Levant. To address these knowledge gaps, we tracked Common Swift (*Apus apus*), Pallid Swift (*A. pallidus*), and Alpine Swift (*Tachymarptis melba*) from breeding colonies in Israel, using light-level geolocation. The three swift species differ significantly in their timing and movement patterns, especially in their non-breeding range. The Common Swift had the shortest breeding period, though it was longer than northern populations, and they exhibited distinct between-individual variation in itinerancy, with some individuals performing long-distance movements over 10,000 km. The Pallid Swift showed a hitherto undescribed longitudinal itinerancy pattern, moving from the Central Sahel to the east, as well as a prolonged stopover at the eastern coast of the Red Sea during spring migration. The Alpine Swift spent a substantially longer period at the breeding range; both compared to the other two swift species studied and to other Alpine Swift populations. At their confined non-breeding range, Alpine Swift remained stationary, though for only a relatively short period, in contrast to the other two species. These new insights regarding the timing and movement patterns of Levant swift populations, emphasises the need for further comprehensive and spatially expanded studies on swifts' movement ecology.

Keywords Alpine Swift · *Tachymarptis melba* · Annual cycle movements · Common Swift · *Apus apus* · Migration · Pallid Swift · *Apus pallidus*

Zusammenfassung

Bewegungen dreier in der Levante brütender Seglerarten während des gesamten Jahreszyklus

Das Zugverhalten entwickelte sich als Anpassung an Saisonalität bei verschiedenen Vogelarten, mit einem Kontinuum an Zugstrategien und Verhaltensweisen im Überwinterungsgebiet. Segler sind besonders mobile, insektenfressende Vögel mit einem charakteristischen an den Luftraum angepassten Lebensstil. Allerdings sind die räumlich-zeitlichen Eigenschaften ihres Zugverhaltens, einschließlich Zeiteinteilung, Zugrouten und Bewegungen im Überwinterungsgebiet, bei Populationen aus der Levante noch immer unzureichend erforscht. Um diese Wissenslücken zu schließen, haben wir Mauersegler (*Apus apus*), Fahlsegler (*A. pallidus*) und Alpensegler (*Tachymarptis melba*) aus Brutkolonien in Israel mithilfe von Geolokatoren verfolgt. Die drei Seglerarten unterscheiden sich erheblich in ihrer Zeiteinteilung und ihren Bewegungsmustern, insbesondere im Überwinterungsgebiet. Der Mauersegler hatte die kürzeste Brutperiode, wenn auch länger als bei nördlichen Populationen.

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Außerdem wiesen sie ausgeprägte individuelle Unterschiede hinsichtlich ihrer Bewegungsmuster auf, wobei einige Individuen Langstreckenbewegungen von über 10.000 km durchführten. Der Fahlsegler zeigte ein bisher unbeschriebenes Bewegungsmuster im Überwinterungsgebiet, bei dem er sich von der zentralen Sahelzone nach Osten bewegte und während dem Frühjahrszug einen längeren Zwischenstopp an der Ostküste des Roten Meeres einlegte. Sowohl im Vergleich zu den beiden anderen untersuchten Seglerarten als auch zu anderen Alpenseglerpopulationen verbrachte der Alpensegler einen wesentlich längeren Zeitraum im Brutgebiet. In ihrem begrenzten Überwinterungsgebiet blieb der Alpensegler stationär, und im Gegensatz zu den beiden anderen Arten nur für einen relativ kurzen Zeitraum. Diese neuen Erkenntnisse hinsichtlich der Zeiteinteilung und der Bewegungsmuster von Seglerpopulationen aus der Levante unterstreichen die Notwendigkeit weiterer umfassender und räumlich ausgedehnter Studien zur Bewegungsökologie der Segler.

Introduction

Seasonal movements evolved independently across different taxa (Alerstam et al. 2003), with a continuum of migration strategies, including partial, short-, medium- and long-distance migration (Newton 2024). Birds, in particular, show astonishing migratory movements, including journeys over thousands of kilometres (Egevang et al. 2010) that can include enduring non-stop flights (Gill et al. 2005). Advances in tracking technologies, e.g. light-level geolocation, have greatly improved our understanding of bird movements throughout the full annual cycle (McKinnon and Love 2018). Yet, migrants' behaviours and movements at the non-breeding range, which can be as diverse as the migration journey itself (Knight et al. 2019), are largely understudied (Stutchbury et al. 2016; Teitelbaum et al. 2023; Pokrovsky et al. 2024). On-going environmental changes, e.g. climate change (Both et al. 2006), land-use change (Adams et al. 2014), and new anthropogenic structures (Loss et al. 2015), challenge migratory birds and cause large scale population declines, particularly of long-distance migrants (Bairlein 2016). Consequently, it is timely to study movement patterns of migrants throughout the full annual cycle, including their timing, ranges, and connectivity. This knowledge is critical for enhancing our understanding of factors affecting individuals' fitness, and hence for developing effective conservation practices.

Species-specific movements throughout the annual cycle evolved in respect to birds' time and energy constraints, leading to optimised migration routes and speeds, as well as timing of migratory and stationary stages in the annual cycle (Alerstam and Lindström 1990). In addition to the migratory journey, many long-distance migrants show additional migratory movements across a dynamic non-breeding range. These can be slow and rather constant movements, i.e. 'foxtrot migration', or fast migratory movements between two or more prolonged stationary sites, i.e. 'itinerancy' (Pokrovsky et al. 2024). Movement patterns in the dynamic non-breeding range show pronounced inter- and intraspecific variation (Newton and Dale 1997). Within species and populations, these movements can be obligate (Heckscher et al. 2011; Stach et al. 2012; Renfrew et al. 2013) or partial (Delmore et al. 2012; Liechti et al. 2015; Stutchbury et al. 2016). The latter often evolved to avoid interspecific competition (Stutchbury et al. 2016) and can lead to age- or sex-specific movement patterns (Liechti et al. 2015; Gow et al. 2019). Furthermore, spatiotemporal movements frequently evolved in response to temporally available, species-specific environmental niches throughout the dynamic non-breeding range (Trierweiler et al. 2013; Stutchbury et al. 2016; Kearsley et al. 2022) or as part of a resource tracking strategy throughout the entire annual cycle (Thorup et al. 2017; Rime et al. 2025).

Some extensive movements during the non-breeding season can be found in swifts, a particularly mobile species group (Bäckman and Alerstam 2001) with a distinctive aerial lifestyle. Specifically, several Palearctic swift species spend nearly the entire non-breeding season airborne (Liechti et al. 2013; Hedenström et al. 2016, 2019). Their highly aerial lifestyle is supported by morphological, biomechanical, physiological, and behavioural adaptations that minimise the costs of their flight. These include a streamlined body, high aspect ratio wings (Henningsson et al. 2010; Henningsson and Hedenström 2011), wing surface roughness (Van Bokhorst et al. 2015), a flap-glide flight style (Bäckman and Alerstam 2001; Sachs 2017), and a fly-and-forage migration strategy (Hedenström and Alerstam 1998). While the Western, Central, and Northern European populations of migratory swifts are well studied (Åkesson et al. 2012; Wellbrock et al. 2017; Norevik et al. 2019; Meier et al. 2020), we lack knowledge on the migratory routes and the non-breeding range movement of swift populations further east, in particular from the Levant. To fill part of this knowledge gap, we studied the movements of Common Swifts (*Apus apus*), Pallid Swifts (*A. pallidus*), and Alpine Swifts (*Tachymarptis melba*) from breeding colonies in Israel. Using light-level geolocation, we tracked the timing of departures and arrivals at the stationary ranges, as well as their movements during the migratory journey and while at the non-breeding range. All three swift species spend the non-breeding season in sub-Saharan Africa. However, they differ in their diet (Cramp et al. 1985; Collins et al. 2009), moult strategy (Boano et al. 2015; Demongin 2016), and breeding biology, such as

clutch size, number of broods, and breeding phenology (Cramp et al. 1985; Billerman et al. 2022).

Here, we characterise the timing and movement patterns throughout the full annual cycle of Common, Pallid, and Alpine Swifts, breeding in the Levant. We expect that clear inter- and intraspecific differences have evolved between the three migratory swift species studied and between individuals from the Levant compared to populations studied in Western, Central, and Northern Europe (e.g. Åkesson et al. 2012; Wellbrock et al. 2017; Norevik et al. 2019; Meier et al. 2020). We specifically ask: (1) What is the timing of the swifts' annual cycle stages, i.e. breeding, migration, and the period at the non-breeding range? Since swifts from the Levant breed further southeast than the populations described in most previous studies, we can expect some differences in their annual cycle timing (Åkesson et al. 2016). Furthermore, their different breeding biology (Cramp et al. 1985; Billerman et al. 2022) and moult patterns (Boano et al. 2015; Demongin 2016), likely resulted in shifts in the timing of different annual cycle stages and movements throughout the annual cycle (Winger et al. 2024). (2) Which migratory routes are selected by the swifts, and are there differences in migration speed between autumn and spring migration? Migrants are believed to be under stronger time pressure during spring migration, as they must arrive promptly at the breeding range. Therefore, we expect higher travel speeds, fewer stopover days, and a faster total migration speed compared to the autumn migration (Pearson and Lack 1992; Hedenström and Alerstam 1998; Nilsson et al. 2013). This difference may be particularly pronounced in males because of the frequently occurring pattern of protandry (Morbey and Ydenberg 2001). Due to their larger size, Alpine Swifts showed the fastest flight speeds when recorded by radar (Bruderer and Boldt 2001) and we consequently expect higher migration speeds. (3) Do the swifts exhibit static or dynamic non-breeding range behaviour with potential foxtrot migration or itinerancy? We predict that the different swift species breeding in Israel will use similar non-breeding ranges with similar movement patterns as their conspecific Central and Eastern European populations (e.g. Åkesson et al. 2012; Wellbrock et al. 2017; Norevik et al. 2019; Meier et al. 2020).

Answering these questions will shed light on the movements of three, highly mobile, migratory swift species from understudied populations in the Levant, throughout the full annual cycle. By advancing the understanding of their natural history, including migration timing and routes, as well as movements at their non-breeding range, we lay the foundation for further research to unravel their complex movement ecology.

Methods

We captured Common, Pallid, and Alpine Swifts from breeding colonies at three different locations in Israel (Ramat-Gan: 32.07, 34.84; Mount Sodom: 31.07, 35.39; and Haifa: 32.80, 35.01) during the breeding season in the years 2017 to 2020. Using a full-body harness, we attached multisensory light-level geolocation (ms-GLS) loggers, each weighing 1.3 g, on 29 Common Swifts, 20 ms-GLS loggers on Pallid Swifts and ten ms-GLS loggers on Alpine Swifts. Additionally, we equipped another ten Pallid Swifts with light-level geolocation loggers that had the ability to remotely download data by radio link (rd-GLS). Of these, we recaptured and recovered data of the ms-GLS loggers from 35% (10/29) of the Common Swifts, 25% (5/20) of the Pallid Swifts, and 80% (8/10) of the Alpine Swifts. For the rd-GLS loggers, we successfully downloaded data from 70% (7/10) of the tagged Pallid Swifts. These relatively high return rates suggest low negative effects of the GLS loggers, consistent with findings for Common Swifts by Wellbrock and Witte (2022). As our loggers were of low relative load and attached with individually fitted harnesses, we did not expect negative effects on the swifts' flight performance or survival (Casper 2009; Brlík et al. 2020). We were able to use data over the full annual cycle from ten loggers for Common Swifts, ten for Pallid Swifts and five for Alpine Swifts. Additionally, for one Alpine Swift and two Pallid Swifts, we obtained data until their arrival at the non-breeding range. One of the Pallid Swifts (20MX) provided data over two annual cycles, of which we only used the first year in the analysis. In addition to attaching the GLS to the swifts, we measured the wing length and body mass for all individuals, and collected feather samples from ten Common Swifts, three Pallid Swifts, and five Alpine Swifts for molecular sexing (Griffiths et al. 1998) that was done by the Karnieli Vet Ltd. laboratory.

To determine the spatiotemporal location (latitude and longitude) each day, we used twilight data from the light-level sensor of the geolocation loggers. For the calibration of the seven rd-GLS loggers from Pallid Swifts, we used the package *SGAT* (Sumner et al. 2009; Lisovski and Hahn 2012), while we used the package *FLightR* (Rakhimberdiev et al. 2017) for the calibration of the other ms-GLS loggers (Lisovski et al. 2020). To identify stationary periods of relative geographic stasis over at least three days, e.g. stopover and stationary behaviour at non-breeding sites, and to differentiate these periods from directional migratory flights, we analysed the twilight data with the *ChangeLight* function from the package *SGAT* (Sumner et al. 2009; Lisovski and Hahn 2012). Here, we used a quantile of 0.85 and merged sites within the distance of the

maximal error. To calibrate this maximal error, we identified the precision of the locations for the period during which birds were in the breeding range (i.e. after capture and before departure for autumn migration). For the ms-GLS loggers, the maximal error was 102 km. For the rd-GLS loggers the maximal error was larger, 264 km. Due to the low precision of spatial location, particularly from the rd-GLS loggers, we used three-day mean locations for analyses (Åkesson et al. 2012; Thorup et al. 2017). Furthermore, we excluded the spatiotemporal locations ten days on either side of the equinox times (Lisovski et al. 2020).

To describe non-breeding season movements, we calculated various parameters from the three-day mean spatiotemporal locations provided by the geolocation loggers. Besides calculating the total distance of movements throughout the annual cycle, we calculated key migration parameters for the movement and timing of autumn and spring migration: departure and arrival date from and to the breeding range and non-breeding range; direct and actual migration route distances (in km), as well as the detour percentage of the actual migration route from a direct route; duration of the migration (in days) and the number of stopover days during the migration journey. We also divided the distance of the migration route by the total duration of the migration, as well as by the duration of only the moving periods (i.e. excluding stopovers), to infer migration and travel speeds (km per day). For movements at the non-breeding range, we calculated additional parameters: total duration spend at the non-breeding range, number of days moving, and total distance moved between the non-breeding sites. We compared interspecific migratory movements and timing between the three swift species (Table S1) using ANOVAs with Tukey post-hoc tests or Kruskal–Wallis tests with Dunn post-hoc tests if assumptions of normality of the residuals were not met. If the assumption of equality of variances was not met, we performed Games-Howell tests. To explore differences in migration properties between autumn and spring migration (Table S2), we performed paired *t*-tests or non-parametric Wilcoxon signed-rank tests. To test for intraspecific differences in the travel speed between spring and autumn migration, respectively, and movements at the non-breeding range (Table S3–5), we performed repeated-measures ANOVAs with pairwise post-hoc comparisons using Tukey's adjustment or Friedman non-parametric tests. Additionally, we tested intraspecific differences in migratory movements and timing between males and females of both Common and Alpine Swifts (Table S6) using Mann–Whitney U tests. We did not have enough data to make this comparison with Pallid Swifts. To test potential intraspecific effects of the birds' body size on migratory movements and their timing (Table S7–9), we calculate the PC1 for body size using the measured wing length and body mass. We then performed linear regressions or generalised linear models (GLMs) when the normality assumption was not met, using a Gamma distribution for skewed data and a Quasi-Poisson distribution for zero-inflated data.

To illustrate the annual movements, we smoothed mean migration routes by fitting a loess model of latitude and longitude against the reversed step number along each migration trajectory and predicted fitted values to generate continuous routes. Furthermore, we estimated species-specific 95% minimum convex polygon (MCP) home ranges for stationary sites from the three-day mean locations using the package *amt* (Signer et al. 2018).

All statistical analyses were performed in *RStudio* using *R* version 2023.12.1.402 (R Core Team 2023) and all tests were two-tailed with α of 0.05.

Results

We found that Common, Pallid and Alpine Swifts, differed significantly in their annual phenology (Fig. 1) and movements (Fig. 2). All swifts arrived at their breeding range in Israel during early spring (before March); Pallid Swifts arrived earliest, at the end of January, significantly earlier than Common Swifts ($p < 0.001$). Common and Pallid Swifts left the breeding range at the beginning of June, whereas Alpine Swifts departed significantly later, in November ($p < 0.001$ for both comparisons). During the annual cycle, Common Swifts spent 26.7% (SD = 2.77) of their time at the breeding range, 12.7% (SD = 4.75) on migration, and 60.6% (SD = 5.13) at the non-breeding range. Pallid Swifts allocated 35.8% (SD = 5.07) of the year to the breeding range, 13.3% (SD = 5.65) to migration, and 50.9% (SD = 8.18) to the non-breeding range. In contrast, Alpine Swifts spent 73.4% (SD = 3.24) of the year at the breeding grounds, 3.1% (SD = 0.98) on migration, and 23.5% (SD = 2.86) at their non-breeding range (see Fig. 1). The total length of movements throughout their annual cycle differed significantly ($p = 0.001$) between the three species. Common Swifts performed long-distance movements of about 15,000 km (SD = 3229), while Pallid Swifts performed medium-distance movements of about 10,000 km (SD = 1762), and Alpine Swifts made short-distance movements of roughly 5,700 km (SD = 699). While the length of autumn and spring migration did not differ between the species, the length of movements in their non-breeding range differed significantly between all three species ($p < 0.001$). See Table S1 for all the results comparing migration timing and movements between the swift species.

During autumn, Common Swifts migrated significantly slower than the other two species ($p < 0.001$ for both), and during spring, Pallid Swifts were significantly slower than Alpine Swifts ($p = 0.001$). Moreover, Common and Pallid

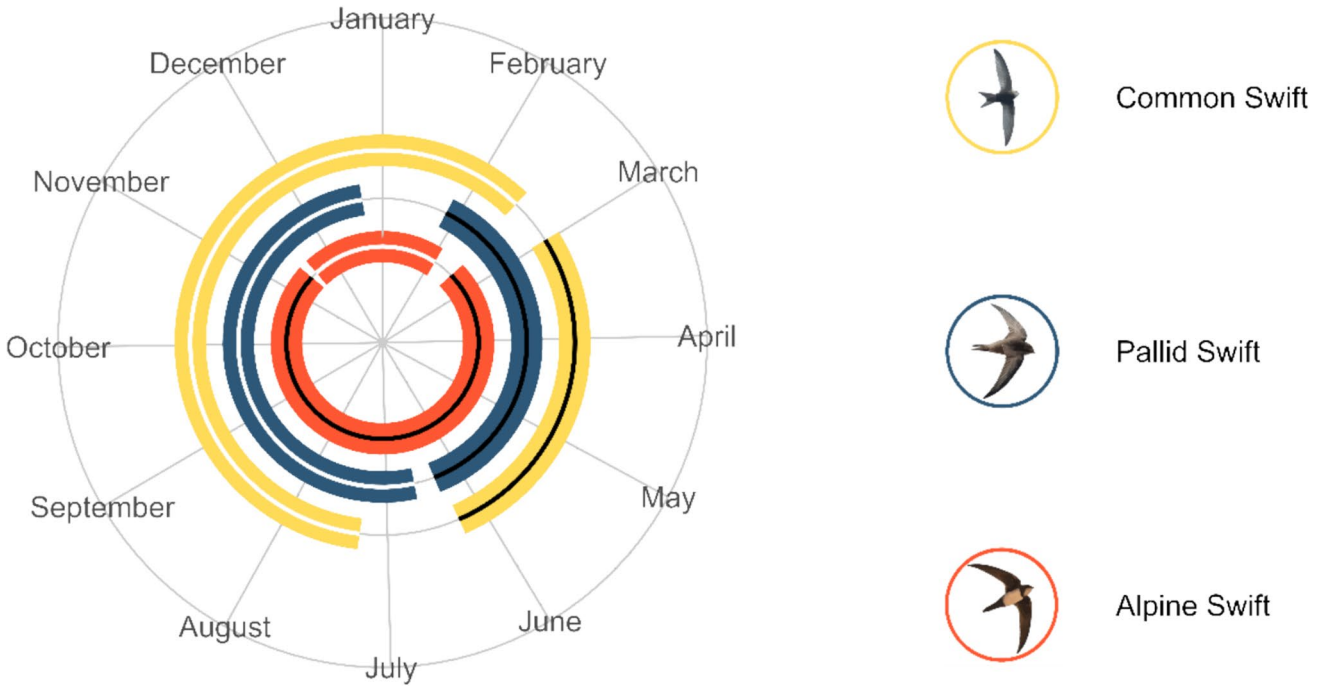

Fig. 1 Phenology over a full annual cycle of Common Swifts (*Apus apus*, yellow, $n=10$), Pallid Swifts (*A. pallidus*, blue, $n=10$), and Alpine Swifts (*Tachymarptis melba*, red, $n=5$) breeding in Israel, with the mean period at the breeding range in black and mean period at the non-breeding range in white

Swifts differed intraspecifically in their migration speed between autumn and spring migration (Table S2). While Common Swifts migrated faster during the spring migration ($p=0.040$), Pallid Swifts migrated slower ($p=0.001$; Fig. 3). Both species had a significantly different number of stopover days between autumn and spring (respectively for Common and Pallid Swifts, $p=0.011$ and 0.002). Most Common Swifts (eight out of ten) interrupted their migratory flight with a stopover during the autumn and most Pallid Swifts (seven out of ten) did so during the spring migration. Conversely, Alpine Swifts had no stopovers during either migration season. The ratio between stopover and travel days for Common Swifts was 1:0.7 and 1:6.5, respectively, in autumn and spring migration. For Pallid Swifts there was no stopover in autumn, and during spring the stopover-to-travel days ratio was 1:0.5. Pallid Swifts also had a significantly higher travel speed ($p=0.015$, Table S4) during the autumn migration, compared to the spring migration. The travel speed during migratory flights did not significantly differ from movements at the non-breeding range in Common or Pallid Swifts (Table S3–4). In contrast, Alpine Swifts had a significantly lower travel speed at the non-breeding range compared to the autumn migration ($p=0.029$, Table S5). Male and female Common and Alpine Swifts did not show any significant differences in their timing of migration or in the length of their migratory movements (Table S6). Common and Alpine Swifts showed no significant relationship between body size and timing of migration or migratory movements (Table S7 and S9). However, larger Pallid Swifts had a significantly larger detour ($p=0.044$) from a direct route, with significantly slower travel speeds ($p=0.049$) and departing earlier from the non-breeding range ($p=0.046$, Table S8).

After departing from their breeding range in Israel, most tracked Common Swifts stopped-over in the Sahel zone before continuing their migration to their first non-breeding site in central, tropical Africa (Fig. 4). During September, most individuals (nine out of ten) exhibited southward movements and some (three out of ten) continued southward into November and December with extensive movements to non-breeding sites in South-eastern Africa. Along their spring migration, only a few individuals (two out of ten) stopped over in the Sahel zone and for significantly fewer days than during the autumn migration ($p=0.007$). Pallid Swifts migrated along the western coast of the Red Sea southwards and from the southern border of Sudan towards the first non-breeding site in the Sahel zone between the Republic of Chad and Sudan. While only a few individuals (two out of twelve) performed West–East movements along the Sahel zone in August and September, most (ten out of twelve) moved to non-breeding sites in the South-eastern parts of Sudan in November to January. During their spring migration, most individuals (eight out of twelve) stopped over on the eastern coast of the Red Sea

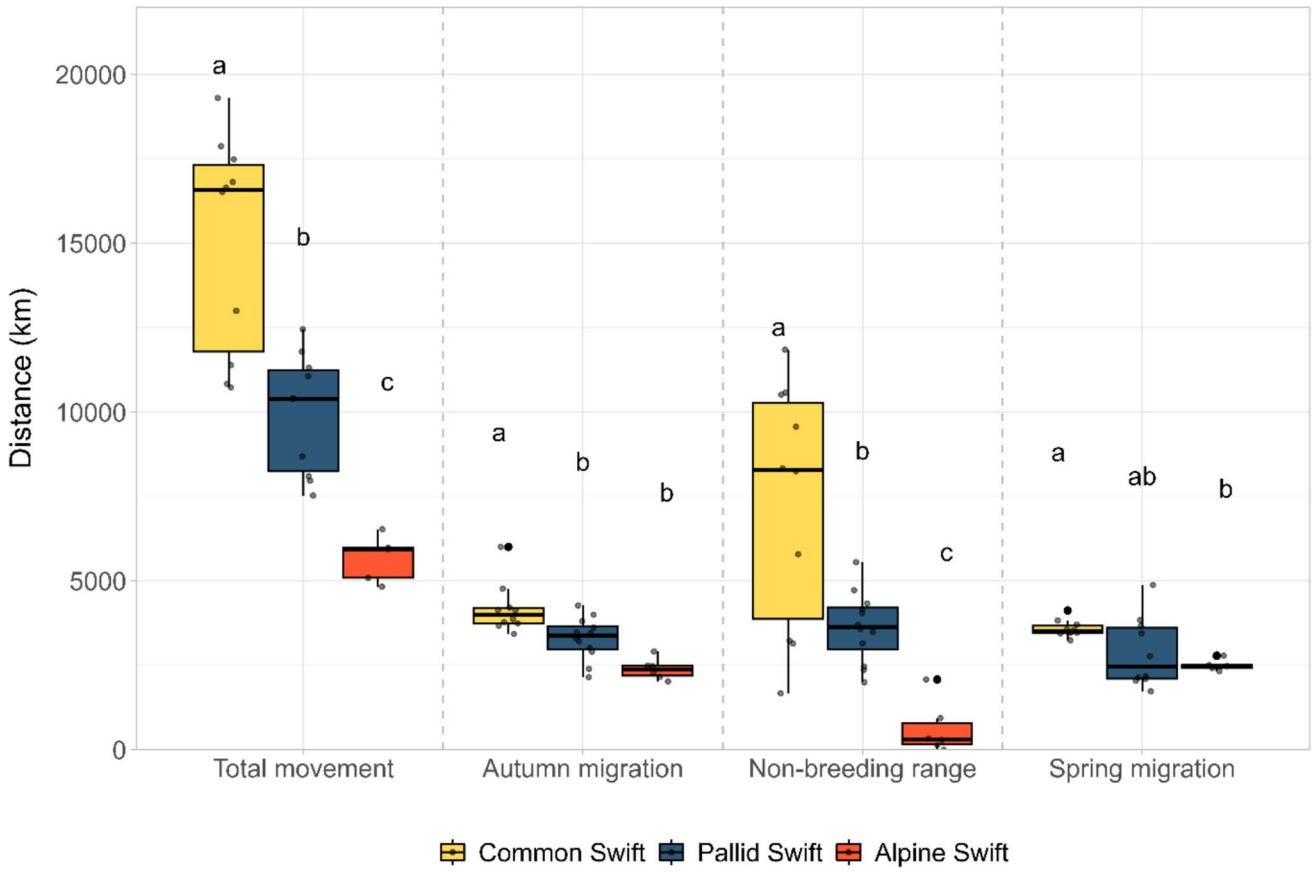

Fig. 2 Boxplots showing the distance (in km) of the movements during the total annual non-breeding season, autumn migration, at the non-breeding range and spring migration for Common Swifts (*Apus apus*, yellow, $n=10$), Pallid Swifts (*A. pallidus*, blue, $n=12$ in autumn and $n=10$ throughout the full annual cycle), and Alpine Swifts (*Tachymarptis melba*, red, $n=6$ in autumn and $n=5$ throughout the full annual cycle) with different labels indicating significant ($p<0.05$) differences between the species following post-hoc comparisons

for prolonged periods of up to 54 days. In contrast, all the tracked Alpine Swifts flew directly to their rather confined non-breeding range between South Sudan and Ethiopia. In their non-breeding range, all individuals remained relatively stationary until they migrated directly back to their breeding range in spring.

Discussion

Timing of the annual cycle

We found substantial differences in the annual cycle of three migratory swift species from Levant breeding populations, with respect to their movements and timing of different annual cycle stages. While Common and Pallid Swifts only spend around three and four months in their breeding range, respectively, Alpine Swifts spend nearly nine months in Israel. Unlike Common and Pallid Swifts from Northern Italy (Boano et al. 2020), the extended breeding period of Pallid Swifts in Israel resulted from their earlier return rather than a delayed departure from the breeding range. Generally, the variation in duration at the breeding range can reflect the species-specific breeding biology and moult. More specifically, the one-month longer breeding period of Pallid compared to Common Swifts may result from the former having up to two broods (Cucco et al. 1992) and moulting up to five primaries at the breeding range in Central Europe (Boano et al. 2015; Demongin 2016). In contrast, Common Swifts only have one brood (Lack 1956) and complete their post-breeding moult entirely at the non-breeding range (Demongin 2016). Nevertheless, in Israel, similar breeding starts in March and fledging peaking in May was reported, and only single broods were observed for both species (Shirihai 1996). Surprisingly, most studies on Alpine Swifts also found only one brood per breeding period (Cramp et al. 1985; Bize et al. 2008; Meier et al. 2020), including studies from Israel, although this is based on a small sample size of only two nests (Shirihai 1996). For a few breeding pairs in Bulgaria, second broods were

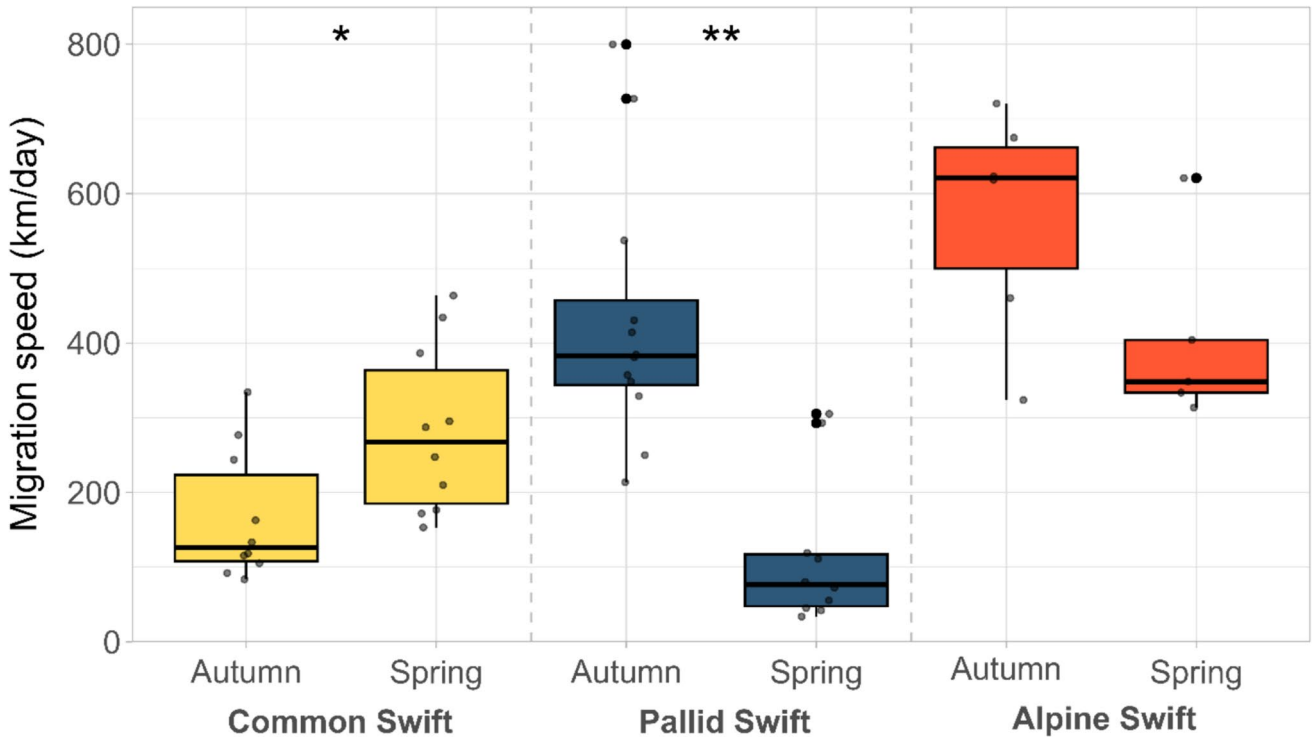

Fig. 3 Boxplots showing the migration speed (km/day) of autumn and spring migration for Common Swifts (*Apus apus*, yellow, $n=10$), Pallid Swifts (*A. pallidus*, blue, $n=12$ in autumn and $n=10$ in spring), and Alpine Swifts (*Tachymarptis melba*, red, $n=6$ in autumn and $n=5$ in spring) with significance level indicators (*$0.05>p>0.01$, **$0.01>p>0.001$, ***$p<0.001$)

observed, yet, at a low frequency (Antonov and Atanasova 2001). Thus, Alpine Swifts in general, remain at their breeding range substantially longer than required for reproduction (Meier et al. 2020). Particularly in Israel, where fledging was observed in June (Shirihai 1996), roughly five month before their departure. This extended period spend in the breeding range could be partly due to their complete post-breeding moult at the breeding range; only a few individuals have been observed to suspend their flight feather moult (Demongin 2016). In addition, Alpine Swifts might experience better food supply at the breeding range than elsewhere, or reduce energy costs and predation risk by night roosting in the colony (Meier et al. 2020). Further studies must explore the breeding biology of Alpine Swifts, specifically with regard to their number of broods, breeding behaviour, and activity budget during the breeding period and prior to autumn migration.

Common Swifts in Israel breed at the southern edge of their distribution range (Billerman et al. 2022), which likely results in a longer breeding period compared to Common Swifts in Northern Europe (Åkesson et al. 2012). Their phenology is also shifted, with earlier departure for autumn migration than in Northern (Åkesson et al. 2012; Hedenström et al. 2016) and even Southern Europe (Boano et al. 2020). The Pallid Swifts breeding in Israel also differ markedly in the timing of their annual cycle and arrive three to four months earlier at the breeding range compared to other conspecifics from the northern distribution range (Boano et al. 2015; Hedenström et al. 2019). Insufficient data from populations of Pallid Swifts breeding further to the south or east on the Arabian Peninsula limit the understanding of potential geographic gradients in the timing of their annual cycle. In Alpine Swifts, Meier et al. (2020) found a latitudinal gradient in the length of their breeding period. Following this trend, the Alpine Swifts breeding in Israel, one of the most southern migratory populations (Billerman et al. 2022), were observed to stay two months longer at the breeding range than birds from Spain and Turkey (Meier et al. 2020).

The non-breeding season of Common Swifts is similar in length to that described in studies from Europe (Åkesson et al. 2012; Hedenström et al. 2016), yet, the birds spent more time at their non-breeding range and less on migration compared to birds from Northern Europe (Åkesson et al. 2012). Pallid Swifts breeding in Israel spent around three months longer away from their breeding range (Hedenström et al. 2019), and Alpine Swifts around half as long at the non-breeding range compared to conspecifics from Central Europe (Liechti et al. 2013; Meier et al. 2020). Intriguingly, the species-specific period spent at their non-breeding range

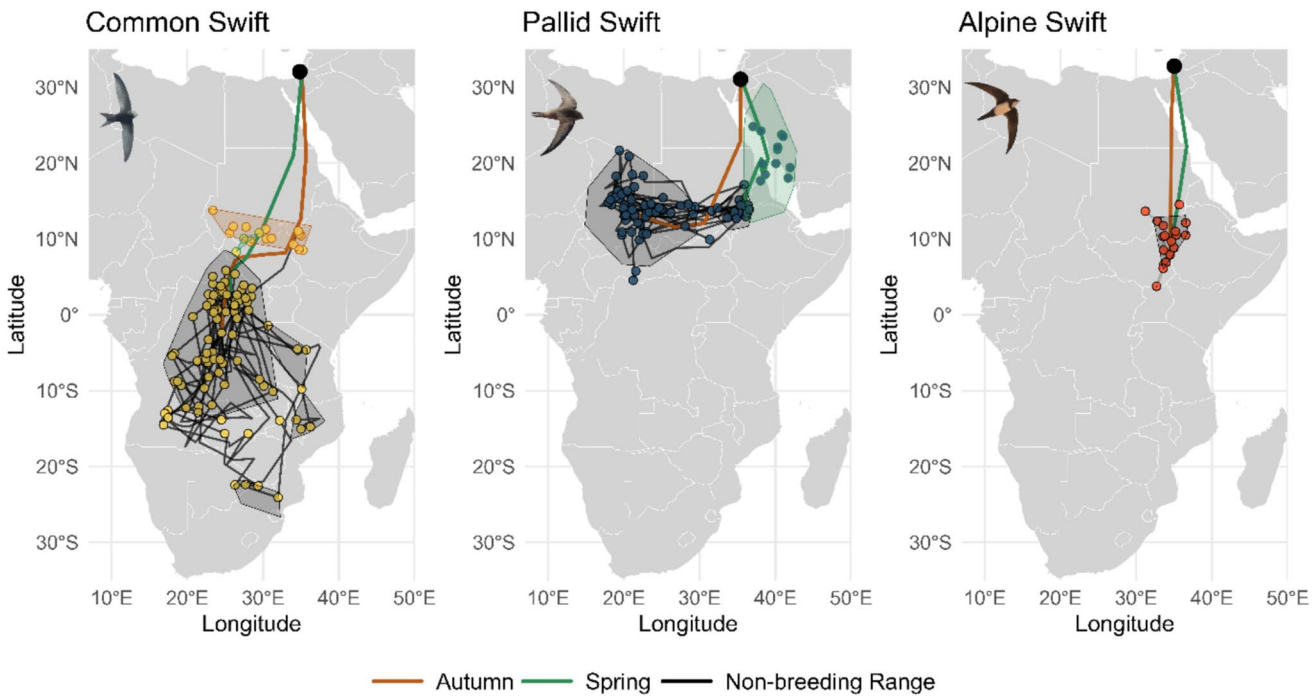

Fig. 4 Annual movements of Common Swifts (*Apus apus*, $n = 10$), Pallid Swifts (*A. pallidus*, $n = 12$ in autumn, $n = 10$ throughout the full annual cycle), and Alpine Swifts (*Tachymarptis melba*, $n = 6$ in autumn, $n = 5$ throughout the full annual cycle). Maps show the smoothed autumn and spring migration routes and movements between stationary non-breeding sites. Points indicate individual mean locations during stationary periods, and polygons represent species-specific 95% minimum convex polygon (MCP) home ranges at stopover and non-breeding sites. Monthly movements are shown in more detail in Figs. S1 and S2

was equal to the time the given species required to complete its moult. For Common Swifts, this was the full flight feather moult, while for Alpine Swifts it was the partial moult among individuals that suspended their post-breeding moult (Demongin 2016; Brighten et al. 2025). The studied swifts also differed in their total annual movement distance, which was linked to the ratio of time spent in the breeding and non-breeding ranges (Winger et al. 2024). Common Swifts, with the shortest breeding period, had the longest total annual migration distance of about 15,000 km. Pallid Swifts showed medium to long-distance movements of about 10,000 km, while Alpine Swifts, which spent a particularly long period at the breeding range, migrated only about 5,700 km during their annual cycle.

Migration speed and routes

Our with light-level geolocation tracked swifts showed high travel and migration speeds, which are in line with other tracking and radar studies of aerial feeding birds, such as swifts and swallows (Hedenström and Alerstam 1998; Bruderer and Boldt 2001; Åkesson et al. 2012; Norevik et al. 2019). Due to their fly-and-forage migration strategy, these birds can keep up a significantly higher migration speed for prolonged periods, leading to speeds of over 200 km/day, well above the normal migration speed for small birds with flapping flight (Hedenström and Alerstam 1998). Noteworthy, some Pallid and Alpine Swifts, showed astonishingly high travel speeds of over 700 km/day, suggesting directed migratory flights over 18 and 15 h, respectively. Nevertheless, this is still within the daily maximum time of 75% that swifts are expected to be able to fly with respect to their maximum metabolic scope (Hedenström and Alerstam 1998). Interestingly, Alpine Swifts not only had higher travel speeds than the other species, as expected from their larger size (Bruderer and Boldt 2001), but our results also suggest that they minimise the time of migration more than the other swifts. The mean travel speed of our tracked Alpine Swifts corresponds to 10.3 h of flight per day, in respect to the species-specific mean flight speed measured by radar (Bruderer and Boldt 2001). Conversely, Common and Pallid Swifts' travel speeds suggest only 8.2 and 8.9 h of flight, respectively. Consequently, Alpine Swifts spend more time on directed migratory flight and less time presumably foraging at slower flight speeds. This is in contrast to the expected pattern of long-distance migrants showing a faster individual migratory pace (Nilsson et al. 2014; Winger et al. 2024). Furthermore, our tracked Common and Pallid Swifts had lower travel speeds compared to conspecifics from Central and Northern Europe, which breed further away from their

non-breeding range compared to swifts from Israel (Åkesson et al. 2012; Norevik et al. 2019; Åkesson and Bianco 2021).

Only Common Swifts, the species with the longest migration distance in our study, migrated significantly faster during spring than autumn. This pattern is consistent with results from conspecifics in northern populations (Åkesson et al. 2012, 2016; Åkesson and Bianco 2021) and reflects the expected pattern for most migrants (Pearson and Lack 1992; Hedenström and Alerstam 1998; Nilsson et al. 2013). In contrast to this expected pattern and findings in Pallid Swifts from Central Europe (Norevik et al. 2019), our tracked Pallid Swifts had a significantly higher migration speed during autumn than in spring migration. Alpine Swifts showed a non-significant trend of higher mean migration speed during autumn migration which is in line with their other populations (Meier et al. 2020). Notably, the migration of Alpine Swifts from our study, and from other populations (Meier et al. 2020) was particularly short and suggests a non-stop migration during both seasons. The significantly different migration speeds between both seasons in Common and Pallid Swifts is largely related to the difference in the number of stopover days. Stopovers were not obligatory in both species and a few individuals performed both migrations without any prolonged stops (more than three days), in contrast to Common Swifts from Northern Europe (Åkesson et al. 2012, 2016). The stopover-to-travel ratio of 1:0.7 in our tracked Common Swifts during autumn migration is similar to that reported from Central and Northern European populations (Åkesson et al. 2012; Klaassen et al. 2014a; Wellbrock et al. 2017). In spring, however, our Common Swifts had a lower number of stopover days than in other populations, with a ratio of 1:6.5, possibly suggesting time minimisation during spring migration (Alerstam and Lindström 1990). Conversely, Pallid Swifts exhibited a slower spring migration (1:0.5 ratio) due to a prolonged stopover at the Red Sea coast, while autumn migration was direct without stopovers. Notably, Pallid Swifts from Central Europe migrated directly in both seasons (Norevik et al. 2019).

Our tracked Common Swifts stopped over in the Sahel zone after crossing the Sahara Desert during the autumn, likely to refuel after crossing a wide ecological barrier, as documented in swifts (Åkesson and Bianco 2021) and other trans-Saharan migratory insectivorous (Stach et al. 2012; Tøttrup et al. 2012; Norevik et al. 2017). Before returning to their breeding range, our Pallid Swifts stopped over at the eastern coast of the Red Sea of the Arabian Peninsula, a detour also observed in other insectivorous migrants (Tøttrup et al. 2012; Koleček et al. 2016; Briedis et al. 2018; Meier et al. 2020). Since the Pallid Swifts had an overall slower migration due to their prolonged stopover of up to 54 days (mean of 25.7 days), it is unlikely that they took advantage of favourable winds to increase their migration speed, such as Barn Swallows (*Hirundo rustica*; Briedis et al. 2018). Regional peaks in food availability are a likely explanation for this detour (Pearson and Lack 1992; Tøttrup et al. 2008); however, the eastern coast of the Red Sea is not known as a highly important stopover site for fuelling (Shobrak 2011). The swifts may track sea breeze fronts, like those found at their non-breeding range in West Africa, that produce weather conditions that locally increase the abundance of airborne insects (Kearsley et al. 2022). Nevertheless, further studies are needed to reveal why Pallid Swifts use this area for prolonged stopovers.

Interestingly, the detour of the spring migration route significantly increased, and travel speed significantly decreased, with the body size of Pallid Swifts. Since we did not have enough individuals with known sex, we were unable to test for sex-specific differences in Pallid Swifts. Yet, both the wing length and body mass are slightly higher in males (Cramp et al. 1985; Demongin 2016), suggesting a sex-specific migration strategy during spring migration. In contrast to the expected pattern of more direct and faster spring migration in males (Morbey and Ydenberg 2001), larger birds, presumably males, left the non-breeding range earlier to move more and at lower travel speeds near the eastern coast of the Red Sea. This could suggest that this area is a high-quality stopover site for Pallid Swifts, more extensively used by the larger, and possibly more dominant (Shelley et al. 2004), males, that fuel up to arrive to the breeding range in optimal condition (Holzschuh and Deutschlander 2016). Alternatively, males may have stopped over to wait for specific environmental cues prior to their arrival at the breeding range, to prevent potential negative fitness consequences from arriving too early (Lerche-Jørgensen et al. 2018). In line with results from another aerial insectivorous migrant, the Barn Swallow (Liechti et al. 2015), Common and Alpine Swifts did not show any sex-specific timing or migration routes.

In contrast to their Central and Northern European conspecifics, our tracked swifts had more direct and shorter migration routes, without seasonal differences in length or detour of their route (Åkesson et al. 2012; Norevik et al. 2019; Åkesson and Bianco 2021). All three studied swift species crossed the Sahara Desert in a direct south-north oriented route, likely to minimise the time crossing this wide ecological barrier (Alerstam et al. 2003). The direct migratory route along the western coast of the Red Sea during autumn migration in all three species suggests that this flyway may be favourable, e.g. in terms of wind assistance (Erni et al. 2005). Selection of routes with tailwind support during the Sahara Desert crossing was previously shown for Common Swifts (Åkesson et al. 2016; Åkesson and Bianco 2021). All of our tracked Common and Alpine Swifts took a direct spring migration route along the western coast of the Red Sea. Conversely, some Common and Alpine Swifts in other tracked populations (Åkesson et al. 2016; Meier et al.

2020) and Pallid Swifts in our study performed detours over the Arabian Peninsula during spring.

Movements at the non-breeding range

While the migratory routes are similar between the swift species, their movements in the non-breeding range differ significantly. Common Swifts in particular, and to a lesser extent Pallid Swifts, performed long movements between two or more sites at their dynamic non-breeding range. In contrast, Alpine Swifts had a well-confined static non-breeding range in a restricted area between South Sudan and Ethiopia, such as conspecifics from other populations, particularly from Turkey (Meier et al. 2020; Hufkens et al. 2023). This specific area in East Africa is a known area utilised by a variety of insectivorous migrants (Horns et al. 2016; Thorup et al. 2017; Rime et al. 2025), that track local peaks in vegetation (Thorup et al. 2017) and rainfall (Rime et al. 2025). Yet, the temporal niche of Alpine Swifts in East Africa does not completely overlap with the other studied insectivorous migrants as the Alpine Swifts arrived slightly later, during November (Horns et al. 2016; Thorup et al. 2017; Rime et al. 2025). Alpine Swifts differ in their diet composition from the Common and Pallid Swifts, preferring larger prey items (Cramp et al. 1985; Collins et al. 2009). As insect species differ in their distribution in relation to environmental conditions (Schoener and Janzen 1968), dietary preferences could partly explain how the swifts' interspecific movement patterns evolved. The non-breeding range of Pallid and Alpine Swifts overlapped for a couple of months in East Africa. Presumably, these species forage at different altitudes (Hufkens et al. 2023) and select different prey items (Cramp et al. 1985; Collins et al. 2009). Analogously, the spatiotemporal locations of Common and Pallid Swifts did not overlap for the entire non-breeding season (Norevik et al. 2019), possibly reflecting the 'ghost of competition past' (Connell 1980) because of their similar dietary preferences (Cramp et al. 1985).

Most of our tracked Common and Pallid Swifts moved from their first non-breeding site to one or more further sites within their dynamic non-breeding range. These movements between stationary non-breeding sites were performed at comparable travel speeds to the migratory journeys during autumn and spring (Table S3–5), suggesting a pattern of itineracy rather than foxtrot migration (Pokrovsky et al. 2024). The itinerancy pattern of Common Swifts, moving from their first non-breeding site at the Congo basin to sites further south and/or eastwards, was observed for most populations across Europe (Klaassen et al. 2014b; Wellbrock et al. 2017; Boano et al. 2020). Only the Swedish population spent the entire non-breeding period at the Congo basin (Åkesson et al. 2012, 2016; Hedenström et al. 2016; Åkesson and Bianco 2021). Our results provide further evidence for a chain-migration pattern (Holmgren and Lundberg 1993) in Common Swifts, since some individuals from the Levant moved even further south than swifts breeding in Southern Europe (Boano et al. 2020), to areas south of latitude 20°S. Interestingly, the itinerancy was not consistent among all individuals, and the extent of their non-breeding movements substantially varied between individuals. While one individual remained relatively stationary at its first non-breeding site, the other Common Swifts travelled progressively further south to additional stationary non-breeding sites. Some Common Swifts (three out of ten) performed particularly long-distance movements in November and December to non-breeding sites in Botswana and South Africa. High variance in isotope ratios previously suggested a large geographic non-breeding range for Common Swifts breeding in Israel (Evans et al. 2012). Furthermore, other tracked Common Swifts showed similar marked variation between individuals from the same colony; yet, Wellbrock et al. (2017) also observed that Common Swifts are consistent in their individual-specific migration between two successive years and surprisingly faithful to their individual non-breeding sites. Our data did not allow a statistical study between years to examine the within-individual variation of these properties. Notably, the single Pallid Swift individual (20MX) that was tracked over two successive years had similar spatiotemporal localisations.

Most Pallid Swifts (eleven out of twelve) moved during their non-breeding season from a first stationary site in the Central Sahel zone between Niger and Chad, further eastwards to south-eastern Sudan. This longitudinal movement within the Sahel is a novel pattern of itinerancy for Pallid Swifts, as it differs from the known movements within the Sahel in West Africa (Norevik et al. 2019; Kearsley et al. 2022; Hufkens et al. 2023) where birds moved southward, as expected for most Afrotropical migrants (Heckscher et al. 2011; Renfrew et al. 2013; Liechti et al. 2015). Generally, aerial insectivorous birds, such as swifts and swallows, are underrepresented among migrants that spend their entire non-breeding season in the Sahel zone due to the highly seasonal resource abundance in a generally dry landscape (Morel 1973). The two patterns of itinerancy documented in the western and eastern populations of Pallid Swifts likely reflect adaptations to local peaks in food resources, e.g., the gradual progressing Intertropical Convergence Zone or local vegetation greenness (Norevik et al. 2019; Kearsley et al. 2022). Resource-tracking likely also explains the movements of Common Swifts as they might exploit the seasonal peaks in the northern and southern hemispheres through their continuous non-breeding season movements (Alerstam et al. 2003).

Conclusion

Our results advance the understanding of annual movement patterns of Common, Pallid, and Alpine Swifts from the understudied Levant, revealing species- and population-specific differences in distribution, timing, and movements at the non-breeding range. The hitherto undescribed longitudinal itinerancy of Pallid Swifts underlines the need for better geographic coverage in studying species-specific movements. Nevertheless, our sample size (ten Common, ten Pallid, five Alpine Swifts) is too small to generalise to the entire Levant population. Therefore, future studies should track more birds from multiple colonies across the Levant and neighbouring regions (e.g. Arabian Peninsula, Turkey). Additional meta-studies, such as Meier et al. (2020), should also incorporate the Levant and other understudied populations (e.g. North Africa, Arabian Peninsula, Eastern Palearctic) to test: (i) whether Common Swifts follow a chain migration pattern; and (ii) whether itinerancy varies among populations. Generally, we need a better understanding of swifts' movement ecology, testing whether specific environmental factors shape movements and timing along migration routes and at non-breeding sites. This could clarify: (i) the drivers of extensive non-breeding movements in Common Swifts; (ii) why Pallid Swifts stop over at the arid Red Sea coast (Shobrak 2011); and (iii) why Alpine Swifts reach East African non-breeding sites later than other insectivores (Horns et al. 2016; Thorup et al. 2017; Rime et al. 2025). In addition to ultimate drivers, proximate mechanisms must be investigated to explain intra-specific variation (Schmaljohann 2018), such as (i) why Common Swifts from the same colony differ markedly in non-breeding movements; and (ii) why some Pallid Swifts make extended spring stopovers. Such knowledge is crucial for predicting responses to environmental change and for effective conservation across the species' distribution ranges and throughout the annual cycle (Sala et al. 2000).

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Data availability The light-level geolocation tracking data used for the figures and results, as well as the R code for the statistical analysis are publicly available on figshare.com via the following link: https://doi.org/10.6084/m9.figshare.28581752.v2.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval To attach light-level geolocation loggers on swifts, we obtained permits from the Israel Nature and Parks Authority (No. 2017-41691, 2018-41862, 2019-42174).

References

Adams WM, Small RDS, Vickery JA (2014) The impact of land use change on migrant birds in the Sahel. Biodiversity 15:101–108. https://doi.org/10.1080/14888386.2014.931822

Åkesson S, Bianco G (2021) Wind-assisted sprint migration in northern swifts. iScience 24:1–8. https://doi.org/10.1016/j.isci.2021.102474

Åkesson S, Klaassen R, Holmgren J et al (2012) Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. PLoS ONE 7:1–9. https://doi.org/10.1371/journal.pone.0041195

Åkesson S, Bianco G, Hedenstrom A (2016) Negotiating an ecological barrier: crossing the Sahara in relation to winds by Common Swifts. Philos Trans R Soc Lond B Biol Sci 371:1–15. https://doi.org/10.1098/rstb.2015.0393

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E (ed) Bird migration. Springer Verlag Berlin, Heidelberg, pp 331–351

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Antonov A, Atanasova D (2001) Second clutches in the Alpine Swift *Apus melba*. Ardea 89:543–544

Bäckman J, Alerstam T (2001) Confronting the winds: orientation and flight behaviour of roosting swifts, *Apus apus*. Proc R Soc B Biol Sci 268:1081–1087. https://doi.org/10.1098/rspb.2001.1622

Bairlein F (2016) Migratory birds under threat. Science 354:547–548. https://doi.org/10.1126/science.aah6647

Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (2022) Birds of the world. Cornell Laboratory of Ornithology, Ithaca

Bize P, Devevey G, Monaghan P et al (2008) Fecundity and survival in relation to resistance to oxidative stress in a free-living bird. Ecology 89:2584–2593. https://doi.org/10.1890/07-1135.1

Boano G, Pellegrino I, Cucco M (2015) Moult and morphometrics of the Pallid Swift *Apus pallidus* in Northwestern Italy. Ardeola 62:35–48. https://doi.org/10.13157/arla.62.1.2015.35

Boano G, Pellegrino I, Ferri M et al (2020) Climate anomalies affect annual survival rates of swifts wintering in sub-Saharan Africa. Ecol Evol 10:7916–7928. https://doi.org/10.1002/ece3.6525

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83. https://doi.org/10.1038/nature04539

Briedis M, Kurlavičius P, Mackevičienė R et al (2018) Loop migration, induced by seasonally different flyway use, in northern European barn swallows. J Ornithol 159:885–891. https://doi.org/10.1007/s10336-018-1560-1

Brighten AL, Bize P, Payo-Payo A et al (2025) Stable isotope evidence for suspended moult and age-related differences in moult location in the trans-Saharan migratory Alpine Swift. Ibis. https://doi.org/10.1111/ibi.13389

Brlík V, Koleček J, Burgess M et al (2020) Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. J Anim Ecol 89:207–220. https://doi.org/10.1111/1365-2656.12962

Bruderer B, Boldt A (2001) Flight characteristics of birds: I. Radar measurements of speeds. Ibis 143:178–204. https://doi.org/10.1111/j.1474-919x.2001.tb04475.x

Casper RM (2009) Guidelines for the instrumentation of wild birds and mammals. Anim Behav 78:1477–1483. https://doi.org/10.1016/j.anbehav.2009.09.023

Collins CT, Tella JL, Colahan BD (2009) Food habits of the Alpine Swift on two continents: intra- and interspecific comparisons. Ardeola 56:259–269

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138

Cramp S, Brooks DJ, Dunn E et al (1985) Handbook of the birds of Europe the Middle East and North Africa—the birds of the Western Palearctic. Oxford University Press

Cucco M, Malacarne G, Orecchia G, Boano G (1992) Influence of weather conditions on pallid swift *Apus pallidus* breeding success. Ecography 15:184–189. https://doi.org/10.1111/j.1600-0587.1992.tb00022.x

Delmore KE, Fox JW, Irwin DE (2012) Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proc R Soc B Biol Sci 279:4582–4589. https://doi.org/10.1098/rspb.2012.1229

Demongin L (2016) Identification guide to birds in the hand, 1st edn. Beauregard-Vendon

Egevang C, Stenhouse IJ, Phillips RA et al (2010) Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. Proc Natl Acad Sci U S A 107:2078–2081. https://doi.org/10.1073/pnas.0909493107

Erni B, Liechti F, Bruderer B (2005) The role of wind in passerine autumn migration between Europe and Africa. Behav Ecol 16:732–740. https://doi.org/10.1093/beheco/ari046

Evans KL, Newton J, Mallord JW, Markman S (2012) Stable isotope analysis provides new information on winter habitat use of declining avian migrants that is relevant to their conservation. PLoS ONE 7:1–7. https://doi.org/10.1371/journal.pone.0034542

Gill RE, Piersma T, Hufford G et al (2005) Crossing the ultimate ecological barrier: evidence for an 11.000-km-long nonstop flight from Alaska to New Zealand and Eastern Australia by bar-tailed godwits. Condor 107:1–20. https://doi.org/10.1093/condor/107.1.1

Gow EA, Knight SM, Bradley DW et al (2019) Effects of spring migration distance on tree swallow reproductive success within and among flyways. Front Ecol Evol 7:1. https://doi.org/10.3389/fevo.2019.00380

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Heckscher CM, Taylor SM, Fox JW, Afanasyev V (2011) Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. Auk 128:531–542. https://doi.org/10.1525/auk.2011.10280

Hedenström A, Alerstam T (1998) How fast can birds migrate? J Avian Biol 29:424–432. https://doi.org/10.2307/3677161

Hedenström A, Norevik G, Warfvinge K et al (2016) Annual 10-month aerial life phase in the Common Swift *Apus apus*. Curr Biol 26:3066–3070. https://doi.org/10.1016/j.cub.2016.09.014

Hedenström A, Norevik G, Boano G et al (2019) Flight activity in Pallid Swifts *Apus pallidus* during the non-breeding period. J Avian Biol 50:1–8. https://doi.org/10.1111/jav.01972

Henningsson P, Hedenström A (2011) Aerodynamics of gliding flight in common swifts. J Exp Biol 214:382–393. https://doi.org/10.1242/jeb.050609

Henningsson P, Johansson LC, Hedenström A (2010) How swift are swifts *Apus apus*? J Avian Biol 41:94–98. https://doi.org/10.1111/j.1600-048X.2009.04850.x

Holmgren N, Lundberg S (1993) Despotic behaviour and the evolution of migration patterns in birds. Ornis Scand 24:103–109. https://doi.org/10.2307/3676359

Holzschuh JA, Deutschlander ME (2016) Do migratory warblers carry excess fuel reserves during migration for insurance or for breeding purposes? Auk 133:459–469. https://doi.org/10.1642/AUK-15-141.1

Horns JJ, Buechley E, Chynoweth M et al (2016) Geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) identifies key regions for migratory wetland specialists in the Middle East and sub-Saharan East Africa. Condor 118:835–849. https://doi.org/10.1650/CONDOR-16-63.1

Hufkens K, Meier CM, Evens R et al (2023) Evaluating the effects of moonlight on the vertical flight profiles of three western palaearctic swifts. Proc R Soc B Biol Sci 290:1–11. https://doi.org/10.1098/rspb.2023.0957

Kearsley L, Ranc N, Meier CM et al (2022) The aeroecology of atmospheric convergence zones: the case of Pallid Swifts. Oikos 2022:1–16. https://doi.org/10.1111/oik.08594

Klaassen RHG, Hake M, Strandberg R et al (2014a) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J Anim Ecol 83:176–184. https://doi.org/10.5061/dryad.ds388

Klaassen RHG, Klaassen H, Berghuis A et al (2014b) Trekroutes en overwinteringsgebieden van Nederlandse Gierzwaluwen ontrafeld met geolocators. Limosa 87:173–181

Knight SM, Gow EA, Bradley DW et al (2019) Nonbreeding season movements of a migratory songbird are related to declines in resource availability. Auk. https://doi.org/10.1093/auk/ukz028

Koleček J, Procházka P, El-Arabany N et al (2016) Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. J Avian Biol 47:756–767. https://doi.org/10.1111/jav.00929

Lack D (1956) Further notes on the breeding biology of the Swift *Apus apus*. Ibis 98:606–619. https://doi.org/10.1111/j.1474-919X.1956.tb01452.x

Lerche-Jørgensen M, Korner-Nievergelt F, Tøttrup AP et al (2018) Early returning long-distance migrant males do pay a survival cost. Ecol Evol 8:11434–11449. https://doi.org/10.1002/ece3.4569

Liechti F, Witvliet W, Weber R, Bächler E (2013) First evidence of a 200-day non-stop flight in a bird. Nat Commun 4:1–7. https://doi.org/10.1038/ncomms3554

Liechti F, Scandolara C, Rubolini D et al (2015) Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. J Avian Biol 46:254–265. https://doi.org/10.1111/jav.00485

Lisovski S, Hahn S (2012) GeoLight – processing and analysing light-based geolocator data in R. Methods Ecol Evol 3:1055–1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x

Lisovski S, Bauer S, Briedis M et al (2020) Light-level geolocator analyses: a user's guide. J Anim Ecol 89:221–236. https://doi.org/10.1111/1365-2656.13036

Loss SR, Will T, Marra PP (2015) Direct mortality of birds from anthropogenic causes. Annu Rev Ecol Evol Syst 46:99–120. https://doi.org/10.1146/annurev-ecolsys-112414-054133

McKinnon EA, Love OP (2018) Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. Auk 135:834–856. https://doi.org/10.1642/AUK-17-202.1

Meier CM, Karaardıç H, Aymí R et al (2020) Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant. J Avian Biol 51:1–11. https://doi.org/10.1111/jav.02515

Morbey YE, Ydenberg RC (2001) Protandrous arrival timing to breeding areas: a review. Ecol Lett 4:663–673. https://doi.org/10.1046/j.1461-0248.2001.00265.x

Morel GJ (1973) The Sahel Zone as an environment for Palearctic migrants. Ibis 115:413–417. https://doi.org/10.1111/j.1474-919X.1973.tb01979.x

Newton I (2024) The migration ecology of birds, 2nd edition. Elsevier, London

Newton I, Dale LC (1997) Effects of seasonal migration on the latitudinal distribution of west Palaearctic bird species. J Biogeogr 24:781–789. https://doi.org/10.1046/j.1365-2699.1997.00153.x

Nilsson C, Klaassen RHG, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837–845. https://doi.org/10.5061/dryad.82d4q

Nilsson C, Bäckman J, Alerstam T (2014) Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. Behav Ecol Sociobiol 68:1799–1807. https://doi.org/10.1007/s00265-014-1789-5

Norevik G, Åkesson S, Hedenström A (2017) Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore—the European Nightjar *Caprimulgus europaeus*. J Avian Biol 48:738–747. https://doi.org/10.1111/jav.01071

Norevik G, Boano G, Hedenström A et al (2019) Highly mobile insectivorous swifts perform multiple intra-tropical migrations to exploit an asynchronous African phenology. Oikos 128:640–648. https://doi.org/10.1111/oik.05531

Pearson DJ, Lack PC (1992) Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. Ibis 134:89–98. https://doi.org/10.1111/j.1474-919X.1992.tb04738.x

Pokrovsky I, Curk T, Dietz A et al (2024) Foxtrot migration and dynamic over-wintering range of an Arctic raptor. Elife 12:1–17. https://doi.org/10.7554/eLife.87668

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing

Rakhimberdiev E, Saveliev A, Piersma T, Karagicheva J (2017) Flightr: an R package for reconstructing animal paths from solar geolocation loggers. Methods Ecol Evol 8:1482–1487. https://doi.org/10.1111/2041-210X.12765

Renfrew RB, Kim D, Perlut N et al (2013) Phenological matching across hemispheres in a long-distance migratory bird. Divers Distrib 19:1008–1019. https://doi.org/10.1111/ddi.12080

Rime Y, Osinubi ST, Liechti F et al (2025) Small intra-tropical long-distance migratory birds track rainy seasons across hemispheres. Proc R Soc B Biol Sci 292:1–11. https://doi.org/10.1098/rspb.2024.2633

Sachs G (2017) Energy saving of aerial roosting Swifts by dynamic flap-gliding flight. J Ornithol 158:943–953. https://doi.org/10.1007/s10336-017-1447-6

Sala OE, Chapin FS, Armesto JJ et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schmaljohann H (2018) Proximate mechanisms affecting seasonal differences in migration speed of avian species. Sci Rep 8:1–10. https://doi.org/10.1038/s41598-018-22421-7

Schoener TW, Janzen DH (1968) Notes on environmental determinants of tropical versus temperate insect size patterns. Am Nat 102:207–224

Shelley EL, Tanaka MYU, Ratnathicam AR, Blumstein DT (2004) Can Lanchester's laws help explain interspecific dominance in birds? Condor 106:395–400. https://doi.org/10.1093/condor/106.2.395

Shirihai H (1996) The birds of Israel. Academic Press, London

Shobrak M (2011) Bird flyways and stopover conservation sites in the Arabian Peninsula. Zool Middle East 54:27–30. https://doi.org/10.1080/09397140.2011.10648898

Signer J, Fieberg J, Avgar T (2018) Animal movement tools (amt): R-package for managing tracking data and conducting habitat selection analyses

Stach R, Jakobsson S, Kullberg C, Fransson T (2012) Geolocators reveal three consecutive wintering areas in the thrush nightingale. Anim Migr 1:1–7. https://doi.org/10.2478/ami-2012-0001

Stutchbury BJM, Siddiqui R, Applegate K et al (2016) Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. Am Nat 188:28–40. https://doi.org/10.5061/dryad.785sc

Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian estimation of animal movement from archival and satellite tags. PLoS ONE 4:1–13. https://doi.org/10.1371/journal.pone.0007324

Teitelbaum CS, Bachner NC, Hall RJ (2023) Post-migratory non-breeding movements of birds: a review and case study. Ecol Evol 13:1–14. https://doi.org/10.1002/ece3.9893

Thorup K, Tøttrup AP, Willemoes M et al (2017) Resource tracking within and across continents in long-distance bird migrants. Sci Adv 3:1–10. https://doi.org/10.1126/sciadv.1601360

Tøttrup AP, Thorup K, Rainio K et al (2008) Avian migrants adjust migration in response to environmental conditions en route. Biol Lett 4:685–688. https://doi.org/10.1098/rsbl.2008.0290

Tøttrup AP, Klaassen RHG, Strandberg R et al (2012) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proc R Soc B Biol Sci 279:1008–1016. https://doi.org/10.1098/rspb.2011.1323

Trierweiler C, Mullié WC, Drent RH et al (2013) A palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. J Anim Ecol 82:107–120. https://doi.org/10.1111/j.1365-2656.2012.02036.x

Van Bokhorst E, De Kat R, Elsinga GE, Lentink D (2015) Feather roughness reduces flow separation during low Reynolds number glides of swifts. J Exp Biol 218:3179–3191

Wellbrock AHJ, Witte K (2022) No 'carry-over' effects of tracking devices on return rate and parameters determining reproductive success in once and repeatedly tagged common swifts (*Apus apus*), a long-distance migratory bird. Mov Ecol 10:1–12. https://doi.org/10.1186/s40462-022-00357-y

Wellbrock AHJ, Bauch C, Rozman J, Witte K (2017) 'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years. J Avian Biol 48:897–903. https://doi.org/10.1111/jav.01251

Winger B, La Sorte FA, Hack MD, Pegan TM (2024) Joint evolution of the biogeography and phenologyof seasonal migration. PNAS Nexus 4:1. https://doi.org/10.1093/pnasnexus/pgaf247