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Research article

Migration strategies, performance and annual activity budget in a short-distance migrant, the common starling *Sturnus vulgaris*

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Migratory birds typically separate energetically demanding parts of the annual cycle like breeding, moult and migration with some species engaging in so-called moult-migration. Moult-migration is known to occur in starlings from the northern breeding populations, however, little is known about the dynamics of this phenomenon and the costs and benefits for the involved individuals. Here, using state-of-the art multi-sensor geolocators we gathered information about the annual cycles of 10 starlings from two breeding sites in Latvia. We used a novel analytical approach based on atmospheric pressure measurements to reveal that all but one of the tracked individuals migrated to wintering sites in the British Isles. Tracking data exposed two separate migration strategies – 1) departure from the breeding grounds in mid-June soon after chick fledging with long stationary periods at moulting sites approx. 900 km westward (n = 5 of 10); 2) residing in close vicinity of the breeding sites up until the end of October (n = 5 of 10). Accelerometer data revealed significantly higher activity budgets during moult for the individuals exhibiting moult-migration. Furthermore, birds that underwent moult-migration arrived at the breeding sites in the following year on average 10 days later and showed significantly higher activity levels during the pre-breeding period compared to birds without moult-migration. Activity tracking also showed that 67% of all migratory flights were performed during the night, contradicting previous assumptions of starlings being predominantly diurnal migrants. Maximum recorded flight altitudes reached 2500 m a.s.l. and the longest uninterrupted flight lasted 22.5 h. Our results highlight energetic trade-offs of moult-migration in starling, but their downstream consequences remain to be tested.

Keywords: activity budget, barometric pressure, bird migration, geolocation, moult-migration, short-distance migrant



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Introduction

Annual cycles of migratory birds consist of various life history phases that are linked in a unified sequence and a great variety of strategies exist for balancing these phases temporarily and energetically. As a general pattern, birds have evolved to temporally separate energetically demanding events like breeding, moult and migration (Wingfield 2008). For birds living in seasonal environments and thus, seasonal differences in food availability, such management of time in relation to ecological conditions and annual cycle processes is especially crucial (Hedenström 2006). While the timing of breeding in seasonal environments seems to be fixed to match chick provisioning with peak food availability (Visser and Both 2005) scheduling migration and moult within the annual cycle provides larger flexibility as implied from the great diversity of strategies found across species.

Numerous bird species, notably short-distance migrants, undergo complete moult in their breeding grounds during the post-breeding period prior to autumn migration (Tonra and Reudink 2018). In order to gain enough time to breed and moult during the short summer, birds must perform either a rapid moult or partially overlap moulting with breeding or migration (Orell and Ojanen 1980). Many waterfowl and passerine species have evolved a so-called moult-migration – movement from the breeding grounds to a special moulting area before commencing migration to winter quarters (Salomonsen 1968, Jehl 1990).

Moult-migration allows birds to take advantage of the ample food availability in selected geographic regions, thus easing the growth of new feathers (Jenni and Winkler 2020, Pageau et al. 2020). A hypothesis proposed by Rohwer et al. (2005) stated that poor conditions on the breeding grounds during the post-breeding period would push birds to depart prior to moult, while productive stopover locations would pull them. The combination of good conditions at moulting sites and unfavourable conditions on the breeding grounds would mean that birds performing moult-migration could energetically benefit in comparison with staying in the vicinity of the breeding sites. At a moulting site where food is abundant, time and energy spent foraging would be lower. However, empirical data supporting this hypothesis are missing. Additionally, while it is widely accepted that autumn migration in short-distance migrants is more influenced by environmental conditions whereas in long-distance migrants it is mostly guided by circannual clocks (Berthold and Helbig 1992, Åkesson et al. 2017), factors that prompt moult-migration remain scarcely studied (but see Bridge et al. 2016).

Strategies of moult-migration vary among orders and species and travelled distances during these movements can range from tens to several hundreds of kilometres (Newton 2008). Among north temperate waterfowl, which during moult partly or completely lose their ability to fly, moult-migration is often not consistent with the direction of autumn migration (Little and Furness 1985, Boiko and Kampe-Persson 2012). These northward movements in part can be explained by birds taking advantage of the ample food

availability necessary for moult that the northern region provide during summer (Jenni and Winkler 2020). Moult-migration is also known to be widespread in North American landbirds with variable movement distances and directions among species (Pyle et al. 2018). In Europe, common starlings *Sturnus vulgaris* (hereafter, starling) from various parts of the breeding range are known to perform moult-migration (also referred to as ‘Zwischenzug’ in German literature meaning ‘intermediate migration’) shortly after the completion of breeding (Newton 2008). Thus, the post-breeding movements in these populations occur in two well separated waves where the first wave in summer (i.e. moult migration) mostly constitutes of juvenile birds while the second wave in autumn represents movement to wintering sites and involves all individuals of the population (Svårdson 1953). While the geographic patterns of moult-migration in starlings have been described for several central European populations using ring recovery data (Studer-Thiersch 1969, Fliege 1984, Bairlein et al. 2014), the proportion of adults taking part in it remains unknown and both the proportion of involved individuals as well as geographic patterns may differ between different breeding populations.

The ongoing technological advances and state-of-the-art tracking solutions readily provide the capacity for tackling these questions. Recently, a lightweight (approx. 1.4 g) multi-sensor data loggers were developed enabling tracking species as small as 50 g of body mass (Liechti et al. 2018). These novel tracking devices measure ambient light intensity, atmospheric pressure, ambient temperature, acceleration and magnetism (Liechti et al. 2018). Combined, they can provide information on movement and flight behaviour (e.g. migration timing, location, number of flight bouts and their duration, flight altitude, etc.) of the tracked individual, allowing for unprecedented insights into movement patterns of small-bodied birds (Dhanjal-Adams et al. 2018, Meier et al. 2018). This enables not only detailed documentation of current migration patterns and strategies of species and populations but also provide information on activity budget of the tracked birds across the annual cycle (Bäckman et al. 2017).

To describe the annual cycle of short-distance migratory starlings, in this study, we tracked individuals from two breeding sites in Latvia using multi-sensor geolocators (Liechti et al. 2018). We integrated classical light-level geolocation with activity and barometric pressure measurements, which allowed for more detailed and precise estimates of migration timing, geographic positions of stationary sites, migration routes and inter-population differences in overall migration strategies. We took advantage of the year-round activity measurements to compare activity budget within and among individuals across different stages of the annual cycle. While there are several occurrences in scientific literature where starling is described as a mainly diurnal migrant (Cramp and Perrins 1994, Thorup and Rabøl 2007), conclusive evidence to categorise starlings migratory behaviour (more diurnal/nocturnal) is missing as they are well known to migrate both during the day and night (Dorka

1966, Glutz von Blotzheim and Bauer 1993, Kosarev 1995). We tried to clarify these assumptions with a particular focus on describing flight and stopover behaviour and take-off and landing times of starlings in relation to local sunset/sunrise throughout the migration journey.

Methods

Field work

In 2020, we set up two new study sites in Latvia to study starlings. One in eastern Latvia in Zeltaleja (57.19°N 26.86°E) consisting of 100 nest boxes and the second in western Latvia near Lake Engure (57.27°N 23.10°E) consisting of two plots ca 8 km apart with 100 nest boxes each. The distance between the two study sites was 230 km. During the breeding season from mid-April until mid-June all nest boxes were monitored at least once every four days and adult birds and chicks were ringed. Onset of egg laying at both study sites were highly synchronized among individuals with 90% of all recorded broods ($n=181$) started between 19 and 29 April. No second brood were recorded at either of the two study sites. In 2020, we fitted 70 adult breeders (35 at each site; 34 males, 36 females) with multi-sensor archival data loggers (model: GDL3-PAM, Swiss Ornithological Inst., Liechti et al. 2018), which were attached on bird's back using nylon cord leg-loop harness. Adult birds were predominantly captured with traps inside the nest boxes. To avoid nest abandonment the trapping and deployment of loggers was carried out during the late stages of the breeding between 17 and 26 May when the chicks were more than 10 days old. The geolocator including the harness on average weighed 1.90 ± 0.04 g, which represents less than 3% of the body mass of starling (80.4 ± 3.93 g, $n=107$), falling under recommended ethical threshold (Barron et al. 2010, Brlík et al. 2020). The loggers accommodated sensors for ambient light intensity, atmospheric pressure, ambient temperature and acceleration. The light sensor was equipped with a 7 mm long light guide and light intensity was measured every minute storing maximum values in 5 min intervals. Acceleration/activity was measured along the Z-axis for 3.2 s at 10 Hz frequency every 5 min. Atmospheric pressure and temperature recordings were set to 30-min intervals (Briedis et al. 2020).

In 2021, we acquired nine full tracks (5 males, 4 females) and two incomplete tracks (1 male, 1 female). One of the incomplete tracks (male) had recorded data up until 10 December, thus, including information about the autumn migration and the first half of the wintering period, while the others (female) barometric pressure data were unusable due to malfunction of the sensor. Overall recapture rate for birds with loggers was 15.7% (11/70), 20% (7/35) in Engure and 11% (4/35) in Zeltaleja. To see whether loggers had any impact on return rates we used Chi-square test comparing return rates of logger birds with those of control groups ($n=18$; birds undergoing the same handling procedure except fitting the loggers). Results showed no significant

difference between the two groups ($\chi^2=0.02$, $p=0.88$; males only: $\chi^2=4.77$, $p=0.21$; females only: $\chi^2=1.08$, $p=0.84$).

Data analyses

For distinguishing between movement and stationary phases during the annual cycle, we used accelerometer and atmospheric pressure recordings. Because starlings use flapping flight for migration (Rayner et al. 2001), we used the flapping flight classification from the R-package 'pamlr' (Dhanjal-Adams et al. 2022) and set the duration threshold to 1 h (equals to 12 consecutive readings of flapping activity at 5 min recording intervals). Thus, activity measures that were classified as flapping and lasted for at least 1 h were regarded as migratory flights (Briedis et al. 2020). Using 1 h as the cut-off threshold for the identification of migratory flights may left some shorter duration flights unnoticed. However, lowering the threshold increases the risk of misidentifying extended commutes to and from roosting sites or lengthy murmurations (King and Sumpter 2012) as migration. From the classified migratory flights, we could invertedly identify stopover periods in-between migration flights. Longer periods exceeding 45 days were regarded as residency sites. We considered long stationary phases during winter months (November–February) as the main wintering grounds.

To derive geographic locations of stationary sites, we used atmospheric pressure as it is not expected to change rapidly when the bird is stationary (weather related changes; Liechti et al. 2018, Sjöberg et al. 2018). Throughout the analyses, we followed general procedure outline in Nussbaumer et al. (2022a). The recorded pressure data were compared with surface-level atmospheric pressure data (ERA5 hourly surface-level pressure data) at 0.25×0.25 -degree grid cells available at The Copernicus Climate Change Service (Hersbach et al. 2018). Based on pre-analyses of light data, we defined an area between 60°N, 45°N, 10°W and 30°E where all birds had resided throughout the annual cycle and further location estimates were rendered in this pre-defined area to save computational time. To avoid birds' behaviour (e.g. flying, foraging, etc.) potentially influencing the recorded pressure data, only recordings during night (light recording=0) and while the bird was not in motion (acceleration < 5 units on the arbitrary scale; max recorded value across all birds=101) were used for location estimation. First, we excluded all the cells where recorded pressure data did not match the range of air pressure between lowest and highest elevation points within a cell at a given hour. To calculate this range, we combined remotely sensed elevation data at 90×90 m resolution available from SRTM DEM Digital Elevation Database (Jarvis et al. 2008) and the ERA5 data. Second, to further refine possible locations we calculated the maximal distance starlings could have travelled from the previous stopover/residency site assuming flight duration as per flight classification analyses and maximum average ground speed of 110 km h^{-1} (we deliberately chose a very high ground speed value to account for potential effects of strong tailwind support). Consequently, we excluded all cells outside the

potential flight range. Third, we derived longitudinal boundaries of the stopover/residency sites from recorded light intensity data using R-package, 'GeoLight' (Lisovski et al. 2012). Longitude in contrary to latitude estimates are more reliable throughout the year as they are not influenced by calibration and equinox times (Lisovski et al. 2012). After integrating these steps, we ran a correlation analysis of pressure recorded on the geolocator and ERA5 data in all remaining grid cells. Higher correlation coefficient here indicates a higher likelihood that a bird was residing at a given grid cell. Finally, we checked residuals between the recorded pressure data from geolocators with the ERA5 data from the cell with the highest correlation coefficient. This procedure allowed for detection of changes in roosting sites and potential migratory flights that were shorter than 1 h. If such flights were discovered, we split the stationary period accordingly and rerun the analyses (see section Labelling tracks from the user manual for GeoPressureR, Nussbaumer et al. 2022a, 2022b). Final maps illustrate grid cells with correlation coefficients within the 95th percentile (pressure data) of the potential residency/stopover area.

To evaluate precision of this method, we used breeding period when the bird was at a known location and calculated the distance between the best-match ERA5 cell centre (i.e. most likely location of the bird based on analyses) and the known breeding site of the birds. For this evaluation we used two periods when birds were present in the vicinity of the breeding site: 1) from 1 June (approx. end of breeding season) up until the first migratory flight; 2) from the last migratory flight in spring (arrival at the breeding site) up until 20 May. While the length of the periods for each bird differed and fluctuations associated with short-distance flights after the breeding season were not excluded from the analyses, error of the estimated locations was minimal (mean = 13.7 ± 12.2 km (SD); Supporting information) indicating high spatial accuracy for location estimates derived using pressure data (Nussbaumer et al. 2022a).

Recorded light intensity data were used to identify sunrise and sunset times, which allowed us to distinguish between diurnal and nocturnal migratory flights. To better understand the migratory behaviour of starlings, this data was also used to compare departure and landing times to local sunrise and sunset. Also, individual migratory flight durations were compared with take-off times relative to local sunset. Further, for each individual we calculated cumulative flight duration, migration distances, average ground speed and migration speed in summer/autumn and in spring. Migration distance was calculated as a great circle distance between the breeding site and the most likely location estimates across the annual cycle. Here, 'migration speed' (km day^{-1}) describes speed at which a bird travelled from breeding site to the main wintering grounds and back, including stopover time. 'Ground speed' (km h^{-1}) describes flight speed between individual stationary points along the migratory track.

Application of hypsometric equation to the atmospheric pressure measurements allowed us to calculate flight altitudes of each individual flight at 30 min temporal resolution

('pamlr' function *calculate_altitude*; Dhanjal-Adams et al. 2022). Flight altitudes were later compared between autumn and spring, as well as between diurnal and nocturnal flights using two-tailed Student's t-test.

We calculated daily activity across the annual cycle of all tracked birds as the sum of registered accelerometer records within a given day ($n = 288$ records per 24-h period at 5-min recording interval). Further, we used linear mixed effects models (LMM) to compare average daily activity across various annual cycle stages between individuals of different migration strategies. To account for the non-independence of hierarchy, we included individual ID as a random factor in the models. LMM analyses were run with the R-package 'lme4' (Bates et al. 2015) and p-values were obtained using R-package 'lmerTest' (Kuznetsova et al. 2017).

Results

Migration timing, distance and stopovers

All tracked birds migrated west, with stopover/residency sites near the coastline of the Baltic and the North Seas and wintering grounds in the British Isles ca 2000 km away from the breeding site (Fig. 1, individual migration maps are given in the Supporting information). One individual (bird ID: 24YH), however, spent the winter months on the continental part of Europe near the Wadden Sea (Fig. 1b). Analysis of migratory timing showed that half of the tracked individuals (5 out of 10) started migration in mid-June, 14 ± 2.4 days after chicks fledging. Four individuals from this group spent long periods (> 100 days) at residency (presumed moulting) sites near the southwestern coast of the Baltic Sea and the Wadden Sea (approx. 900 km from the breeding sites) up until departure to wintering grounds at the beginning of November, while one individual spent the same period at the western part of Latvia (approx. 300 km from the breeding site). The other group (5 individuals) did not perform long migratory flights in summer and stayed close to breeding sites up until the end of October. We did not find any indications of 2nd breeding attempts in the recorded geolocator data in either of the tracked individuals. Thus, birds breeding in Latvia exhibit two distinct migratory strategies: 1) the classic autumn–spring migration and 2) a three-phase summer–autumn–spring migration, where the summer phase corresponds to moult-migration (Fig. 1).

Birds with the three-phase migration strategy arrived at the main wintering grounds on the first week of November (mean: 6-Nov), while the late departing group reached their destination almost two weeks later (mean: 19-Nov; Table 1). For both strategies spring migration was carried out in March with most of the birds leaving their main wintering grounds on the second week of March (mean: 11-Mar) and arriving at their respective breeding sites ca two weeks later (mean: 25-Mar, Table 1). There was a 10-day difference in average arrival time between birds of different migration strategies (three-phase: 20-Mar, two-phase: 30-Mar). In contrary to the

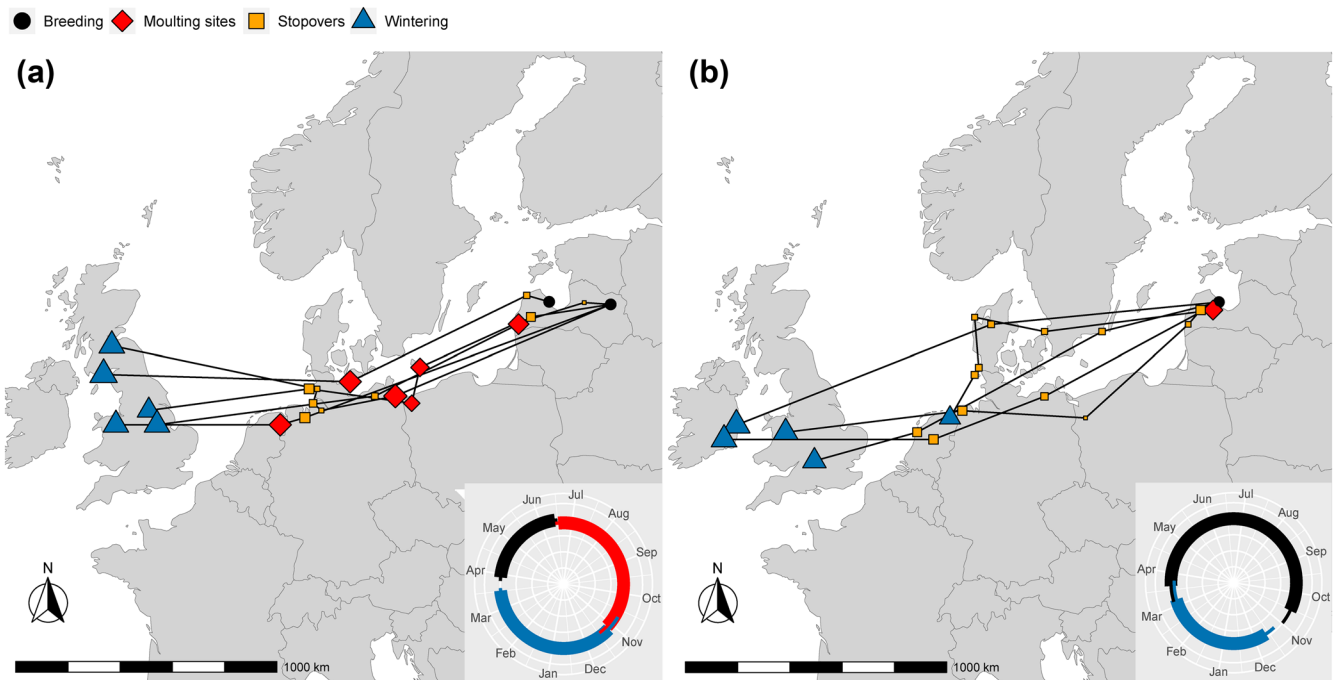


Figure 1. Migration routes (spring migration excluded) in two groups of common starlings breeding in Latvia: (a) three-phase migration strategy (summer–autumn–spring) including moulting, (b) classic two-phase strategy (autumn–spring). In both panels different symbols indicate different annual cycle stages (circles – breeding sites, squares – stopovers, diamonds – presumed moulting sites (long residency periods > 45 days), triangles – wintering grounds). The size of the symbols indicates length of the stationary period where smaller size corresponds to a shorter period. Please see Supporting information for uncertainties of location estimates. Circular diagrams indicate the average periods ($\pm$ SD) of birds residing at specific locations during the annual cycle (black – breeding sites, red – moulting sites, blue – wintering grounds).

rest, bird 24YH (wintering on the continental part of Europe) left wintering grounds already in the beginning of February and arrived at the breeding site on 25th of February – more than two weeks ahead of the second earliest arrival (Table 1). The spread of breeding site arrival across all individuals was 45 days.

Birds that engaged in moulting-migration on average spent ca. one month more at the wintering sites compare to birds without moulting-migration (two-phase: 136 ± 12 days, three-phase: 108 ± 26 days). Among the birds with two-phase strategy, migration period in autumn was longer (mean: 32 ± 14 days) than in spring (mean: 13 ± 7 days). During the annual migration cycle birds travelled on average 3889 ± 564 km (Table 1).

Activity budget

Throughout the year daily activity patterns coincided with sunrise and sunset times as recorded by the geolocators light sensor showing no activity during the night, except for migratory flights. Actograms summarizing annual activity patterns of birds with three-phase (moulting-migration) and two-phase migration strategies are shown in Fig. 2 (actograms of all individuals are given in the Supporting information). Starlings on average were most active during the migratory stages with spring migration being the period of highest activity (Fig. 3). Birds exhibiting moulting-migration showed

significantly higher average daily activity during summer/autumn stationary period compared to birds without moulting-migration ($\beta = -168.6$, $t = -2.84$, $p = 0.02$). Similarly, during the pre-breeding period birds with moulting-migration showed significantly higher activity levels than those without moulting-migration ($\beta = -167.9$, $t = -3.13$, $p = 0.02$). Across all annual cycle stages, the mean daily activity rate was the lowest during the wintering period (Fig. 3). However, when compared relative to available daylight hours, wintering period was the third most active period of the entire annual cycle falling short only to autumn and spring migration (Supporting information). Breeding period (from the onset of laying of eggs up until chick fledging) showed a wide spread of daily activity due to the large differences in recorded activity between incubation and chick provisioning stages while the period shortly after the chick fledging (first week of June) had one of the highest activity rates of the whole annual cycle (Fig. 3).

Flight performance

Tracked starlings completed their annual migration cycle with an average of 13.3 ± 4.8 individual flights distributed equally between post-breeding and pre-breeding migrations (Table 1). The total number of flight hours for the nine individuals with full information about their migratory cycles ranged between 43.8 and 64.0 h. Group of birds performing

Table 1. Summary data of migration and flight characteristics of 10 starlings depending on their migration strategy. Note that departure date is always given as the date of the evening of the night when the first migratory flight occurred. Arrival is given as the date of the morning when the last migratory movement occurred. Autumn migration speed of the three-phase strategy group is excluded due to inability to precisely distinguish start/end times of summer and autumn migration stages.

	Three-phase strategy including moult-migration						Two-phase (autumn–spring) migration strategy						Average (total)
	24XE	24VR	24VE	24WA	24VF	AVERAGE	24YJ	24YK	24YH	24YN	24XB	AVERAGE	
Migration characteristics													
Departure from breeding grounds	15-Jun	13-Jun	10-Jun	16-Jun	16-Jun	14-Jun	31-Oct	29-Oct	25-Oct	08-Oct	30-Sep	18-Oct	16-Aug
Arrival at wintering grounds	14-Oct	07-Nov	07-Nov	10-Nov	26-Nov	06-Nov	28-Nov	09-Nov	25-Nov	30-Nov	06-Nov	19-Nov	13-Nov
Departure from wintering grounds	16-Mar	19-Mar	15-Mar	20-Mar		17-Mar	02-Mar	30-Mar	07-Feb	18-Mar	07-Mar	07-Mar	11-Mar
Arrival at breeding grounds	26-Mar	01-Apr	02-Apr	01-Apr	30-Mar	30-Mar	26-Mar	10-Apr	25-Feb	24-Mar	14-Mar	20-Mar	25-Mar
Annual migratory track distance (km)	3649	3995	4177	3974		3949	3484	4156	2940	3650	4980	3842	3889
Wintering grounds (great circle distance km)	1662	1862	1960	1809	1815	1822	1635	1912	1126	1750	1989	1682	1752
Flight characteristics													
No. of flights (summer/autumn)	3	11	11	8	7	8.0	5	4	9	4	7	5.8	6.9
No. of flights (spring)	6	9	7	7		7.3	11	4	6	4	10	7.0	7.1
Proportion of migratory flight at night	77.3%	59.0%	53.7%	67.4%	49.1%	61.3%	77.6%	77.7%	76.7%	68.5%	61.1%	72.3%	66.8%
Cumulative flight hours summer/autumn (hh:mm)	16:30	27:40	22:50	26:50	30:35	24:53	31:39	27:55	29:45	26:10	30:20	29:09	27:01
Cumulative flight hours spring (hh:mm)	27:15	29:40	29:00	24:35		27:37	23:44	36:05	16:05	25:20	27:30	25:44	26:34
Longest flight summer/autumn (hh:mm)	8:55	11:05	4:55	10:10	22:30	11:31	7:10	13:20	8:40	12:55	12:10	10:50	11:10
Longest flight spring (hh:mm)	10:15	9:45	11:25	7:40		9:46	5:35	16:00	10:00	13:05	7:55	10:31	10:11
Ground speed summer/autumn (km h ⁻¹)	104.0	76.1	89.5	67.2	56.6	78.7	52.1	68.4	43.4	69.4	69.0	60.5	69.6
Ground speed spring (km h ⁻¹)	67.8	65.4	71.5	82.8		71.9	74.7	60.4	84.6	68.7	75.6	72.8	72.4
Migration speed autumn (km day ⁻¹)							61.8	180.7	42.5	32.9	54.2	74.4	74.4
Migration speed spring (km day ⁻¹)	180	185.6	112	152.3		157.5	71.5	183.6	72.4	310.9	299.5	187.6	174.2
Maximum flight altitude summer/autumn (m a.s.l.)	1515	852	1314	870	549	1020	1400	1239	375	843	1889	1149	1085
Maximum flight altitude spring (m a.s.l.)	2509	2071	1457	1467		1876	1044	1563	2163	1333	1025	1426	1626

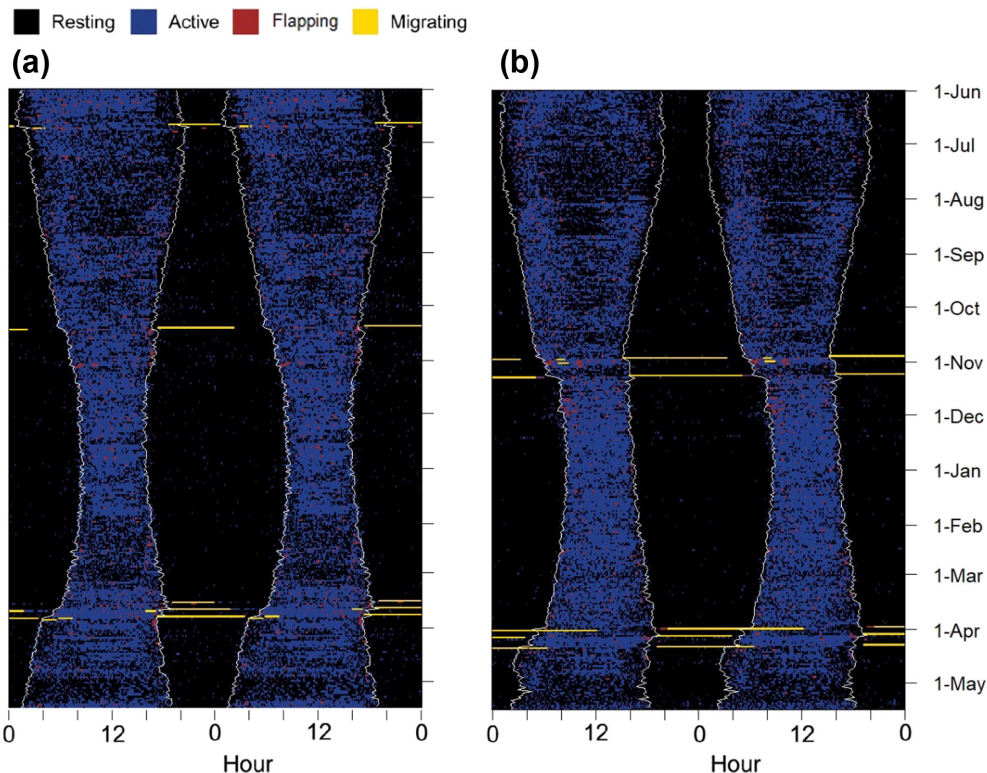


Figure 2. Actograms showing classified annual activity patterns (from 1 June 2020 until 20 May 2021) of two common starlings with different migratory strategies: (a) three-phase strategy with moult-migration in summer (bird ID: 24XE), (b) two-phase strategy with departure in autumn (bird ID: 24YK). Activity data is classified into 4 categories – resting, active, flapping and migrating. In both panels each horizontal line represents the activity data of two consecutive days, where the second day is repeated as the first day on the next line. White lines in the actograms represents sunrise and sunset times as recorded by the geolocator's light sensor.

moult-migration spent similar time in flight during the summer/autumn migration as during spring migration ($t = -1.02$, $p = 0.349$; Table 1). Consequently, differences among ground speed were not significant between summer/autumn migration and spring migration ($t = 0.25$, $p = 0.807$; Table 1). For the two-phase migration group the differences in flight hours were also not significant between the seasons ($t = 1.02$, $p = 0.358$; Table 1), as well as there was no significant difference in ground speed ($t = -1.84$, $p = 0.106$; Table 1). However, the overall migration speed for both groups was significantly faster during spring migration compared to summer/autumn migration ($t = -2.75$, $p = 0.017$; Table 1). For the whole annual cycle, the average migration speed was estimated at 137 ± 86.5 km day⁻¹ (Table 1).

Most migratory flights were carried out during the night (on average $67\% \pm 10.7$ of all migratory movements; Table 1). Time of nocturnal departures were widely distributed with majority of departures happening right around sunset or a few hours before dawn (average departure time $00:35 \pm 07:10$ h before sunset; $n = 141$ flights, Fig. 4a). Longer flights typically started shortly before or after sunset with a general decline in flight duration for flights departing later in the night (Fig. 4d).

Landings typically occurred around sunrise (average landing time relative to sunrise: $1:31 \pm 5:38$ h, Fig. 4b). Migratory

flight duration on average was $3:48 \pm 3:52$ h, with short one to two-hour flights being the most prominent accounting for 53% of all recorded flights (Fig. 4c). Remarkably, one individual (ID: 24VF) during the autumn migration performed a migratory flight lasting 22:30 h. Maximum flight altitudes varied between 600 and 2500 m a.s.l., with significantly higher altitudes reached during spring migration (spring: 488 ± 538 m a.s.l., autumn: 160 ± 326 m a.s.l., $t = -10.08$, $p < 0.001$). On average migratory flights during the day were carried out at significantly lower altitudes (166 ± 288 m a.s.l.), than during the night (359 ± 519 m a.s.l., $t = 7.9$, $p < 0.001$). Nocturnal flights were also significantly higher during the spring compared to autumn migration (spring: 555 ± 608 m a.s.l., autumn: 188 ± 348 m a.s.l., $t = -9.71$, $p < 0.001$).

Discussion

Our study provides the first insight into the spatiotemporal organization, migration performance and activity budget of the entire annual cycle of a short-distance migrant, the common starling. Our findings reassure the assumption that starlings perform a moult-migration (Schüz 1932, Kosarev 1995, Rost 2021), however, it is not unequivocal among all adult birds

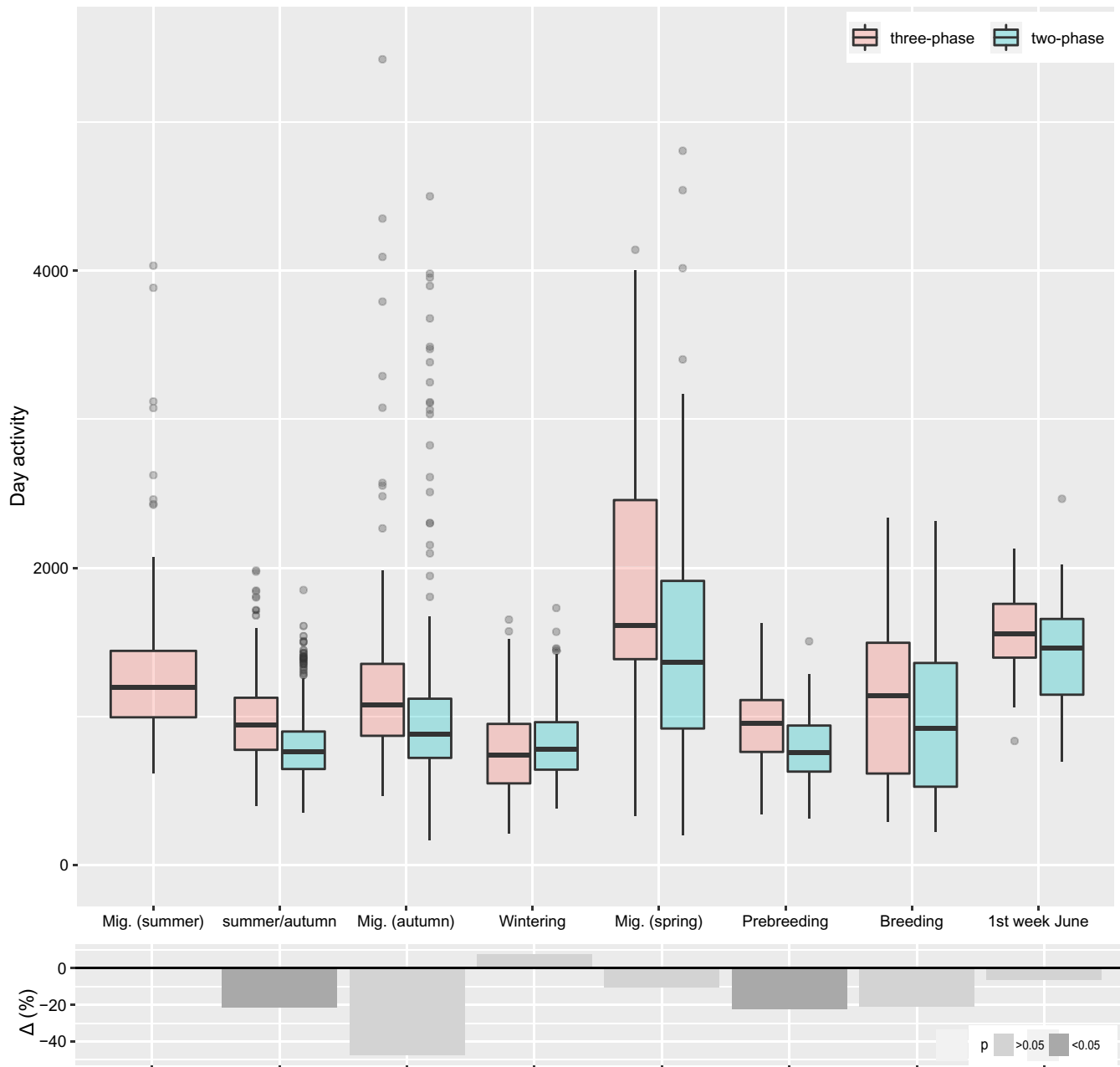


Figure 3. The average daily activity of all tracked common starlings with two different migration strategies (three-phase strategy – red, two-phase strategy – blue) at each of the annual cycles stage. Each box shows the median (line), interquartile range (boxes), data span without outliers (whiskers) and outliers (points). Differences in the mean activity between three-phase and two-phase strategy groups are given as % of two-phase group in the lower panel.

as half of the birds from our study with retrieved geolocators stayed close to the breeding sites up until the end of October. The remaining five birds performed a moult-migration in mid-June soon after breeding season and spent long residency periods at moulting sites near the south-western coast of the Baltic Sea and the Wadden Sea (approx. 900 km from the breeding sites), with one individual spending the same period at the western part of Latvia (approx. 200 km from the breeding site). Summer moult of starlings lasts from 98 to 108 days

(Jenni and Winkler 2020), which corresponds with our results as the five starlings performing moult-migration in summer spent on average 116 ± 11.5 (SD) days at a single residency site without long migratory flights in between.

Interestingly all four birds from the study site in eastern part of Latvia performed the moult-migration, while only one of five birds from study site in western Latvia did. These results correspond to the latest information from eBird modelled abundance maps which indicate that summer movements

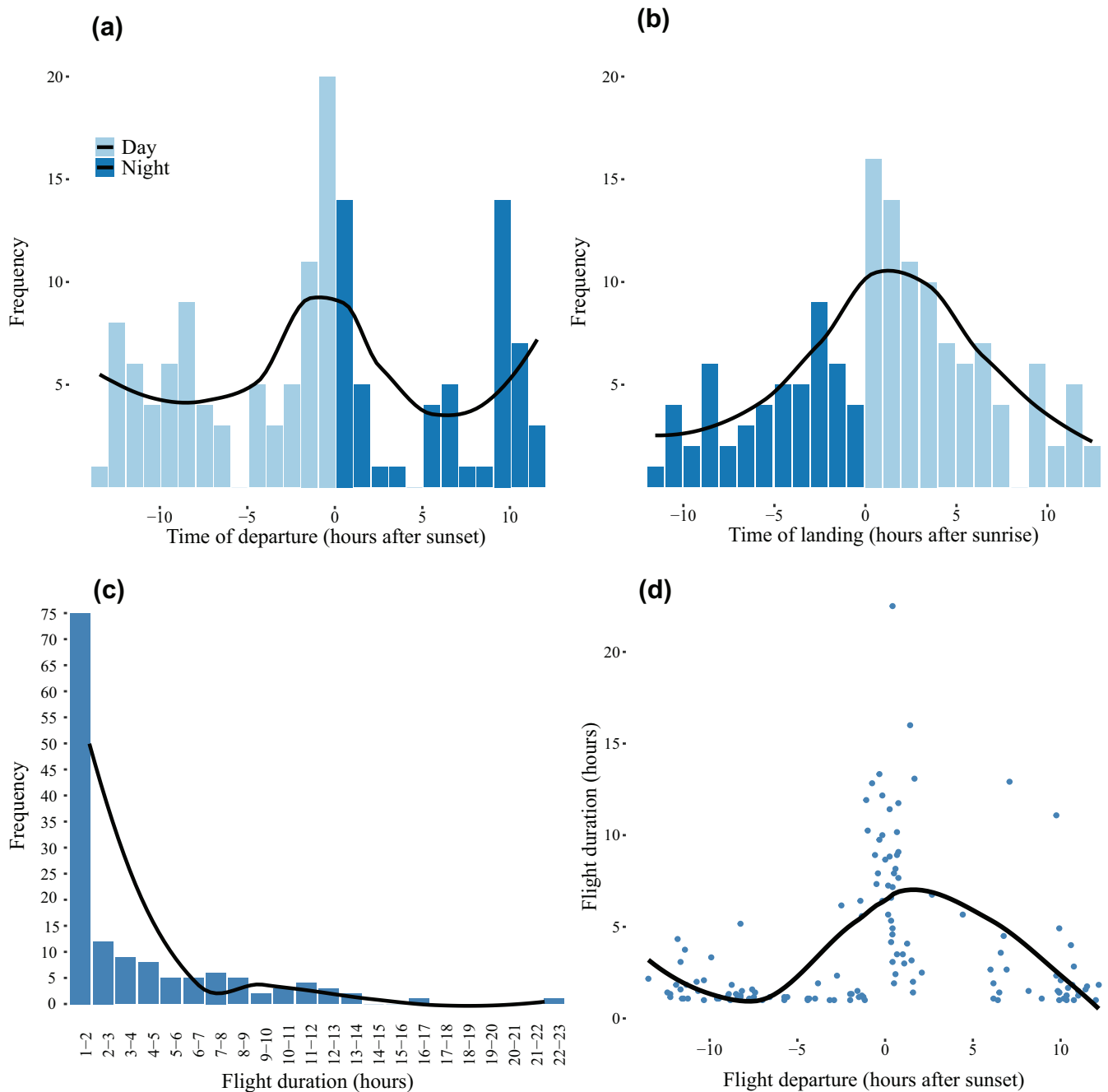


Figure 4. Characteristics of migratory flights of common starlings. (a) Frequency distribution of departure time relative to sunset, (b) landing time relative to sunrise, (c) frequency distribution of flight duration, (d) relationship between flight duration and departure time relative to sunset. Black lines in panels are estimated density curves.

of starlings in Europe have a geographic NE to SW gradient (Fink et al. 2021). This might be connected to large-scale climatic conditions as in northeast Europe the weather is more continental and the average temperatures during autumn months are lower than further southwest, potentially affecting foraging conditions in August–October before the autumn migration. If so, this would support the ‘push’ aspect of the ‘push–pull hypothesis’ driving moult-migration (Rohwer et al. 2005). Pageau et al. (2020) concluded that

moult-migration in North American passerines is driven by aridity of the breeding grounds that ‘pushes’ birds to engage in moult-migration. Distances travelled during moult-migration by the tracked starlings appear to be relatively large in comparison to most other passerines (Pyle et al. 2018). However, the direction of these movements in starlings are in the general direction of autumn migration and thus, bear minimal costs for movement displacement relative to location of the wintering grounds.

Yet, analyses of accelerometer data showed significant differences among the two migration strategies – for birds with moult-migration the average daily activity was significantly higher during the time of moult in late summer–early autumn (Fig. 3). Raw accelerometer measurements, although difficult to link with specific behaviours, can be used to compare the general activity levels, i.e. movement frequency and intensity and resting time, among tracked individuals (Dhanjal-Adams et al. 2022). The observed differences between individuals that exhibit moult-migration and those that do not may indicate different environmental setting and possibly food availability under which moult takes place. Lower activity measurements of the individuals that remain close to the breeding sites for moult imply that this strategy may be more beneficial for individuals regarding their activity budget and energy acquisition to complete the moult. Thus, direct benefits from engaging in moult-migration by the north European population of starlings remain to be identified. However, these results need to be viewed with caution due to limited sample size in both groups.

Differences found in activity measurements during the pre-breeding period are, however, likely connected to different arrival times at the breeding grounds as birds that engaged in moult-migration arrived on average 10 days later than birds with two-phase migration. Thus, the late arrivals were probably under larger time constraints to both refuel after migration and establish territories as the onset of egg laying among starlings within the same population is well synchronized (Flux and Flux 1981, Tainen et al. 1989) and there is a strong decline in clutch size with each delayed day (Smith 2004). Therefore, late arrival in starlings may bear fitness costs that potentially may be linked to migration strategy and activity budget during earlier stages of the annual cycle. In a similar study, Pelletier et al. (2020) showed that different migration strategies and energy budgets have no obvious carry-over effects on the reproductive success in northern gannets *Morus bassanus*. This remains to be tested in our study population of starlings.

Analyses of flight performance revealed relatively high ground speed compared to the measurements obtained in earlier studies using tracking radar (Bruderer and Boldt 2001). These results suggest that starlings take advantage of tailwind support during long nocturnal flights (c.f. Liechti 2006). Conditions when birds are actively using wind currents are difficult to detect remotely and therefore were excluded from our analysis, but recent developments in modelling techniques could make it more accessible in the future (Nussbaumer et al. 2022b). Better tailwind conditions due to Europe's prevailing westerly winds – the westerlies – would also explain the recordings of higher ground speed, migration speed and higher migration altitudes during spring migration. In general, migration speed in starlings was higher than those measured for passerines in earlier geolocator studies (Schmaljohann 2018, 2019). Yet, it is important to note that most of earlier studies have been conducted on long-distance migrants, which are known to have longer migration periods with lengthy stopovers for

fuelling, consequently reducing the overall migration speed (Newton 2008, Schmaljohann and Both 2017).

Remarkably, one of the tracked starlings (ID: 24VF) performed a 22.5-h long flight during autumn migration. The bird departed on the 25 November from the coastline of Heligoland Bight in Germany and landed on the 26 November approximately 700 km further west near Leeds in United Kingdom. Some long-distance migrants are known to perform long endurance flights when crossing large ecological barriers, like the Sahara desert (Adamík et al. 2016, Liechti et al. 2018, Briedis et al. 2020) but this should not be the case in our study since the great circle route between the departure and landing site is relatively short given the recorded flight duration. Unfortunately, our method cannot provide an exact route of the flight, therefore reasons for such elongated flight with low ground speed are hard to tell, but it might be a result of unfavourable wind conditions during the flight and/or an elongated detour.

Our results of activity and barometric pressure tracking showed that starlings are predominantly nocturnal migrants contradicting some of the previous assumptions of starlings migrating mainly during the day (Cramp and Perrins 1994, Thorup and Rabøl 2007). Two thirds (67%) of all migratory flights were performed at night. Unfortunately, we were unable to precisely detect migratory flights shorter than 1 h and thus may have underestimated the total migratory flight duration. If such short flights would have happened predominantly at day or night, also the estimated proportion of nocturnal versus diurnal flights may be slightly different. However, given the cross validation in flight detection (Methods), only a small fraction of such flights could have been missed with negligible effects on our results. Birds generally departed in the time window between one hour before to one hour after the sunset, which does not conform with the general pattern noticed among small passerine nocturnal migrants, which typically depart after the sunset (Kerlinger and Moore 1989, Liechti et al. 1997, Müller et al. 2016). The pattern observed in our study of birds departing also before sunset might be typical for species that migrate both during the day and night. Landing typically happened within the first four hours after sunrise, which might explain the earlier observation-based assumption of starlings being diurnal migrants. The nocturnal flights were typically longer and higher in altitude than those performed during the day, as birds seemingly use the morning hours to fly lower and seek for good foraging/stopover grounds (Alerstam 2009). Due to the highly social behaviour of starlings, it would be interesting to know whether the high-altitude nocturnal flights are also performed in a flock formation. Since predator risk at night is miniscule, flock formation would be non-beneficial from this point of view (Powell 1974), however, flocking and social information obtained during nocturnal flights may be used for navigational purposes (Piersma et al. 2020).

Overall, integration of classical light-level geolocation with activity and barometric pressure measurements gives great insights into annual cycles of migratory birds (Liechti et al. 2018). Our approach in combining atmospheric pressure

recordings from geolocators with large-scale databases like ERA5 and SRTM DEM Digital Elevation Database looks especially promising enabling tracking even short-distance migrants at high spatiotemporal resolution. Further methodological developments show great promise in advancing this technique and obtaining additional insights in flight behaviour of migrants (Lathouwers et al. 2022, Nussbaumer et al. 2022a, b). Furthermore, year-round activity measurements of free flying birds will bring an in-depth understanding of activity and energy budgets during various annual cycle stages and their downstream consequences for individual performance and fitness.

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Author contributions

Viesturs Vigants: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Oskars KeiĶs:** Conceptualization (equal); Funding acquisition (lead); Investigation (lead); Project administration (lead); Supervision (equal); Writing – review and editing (supporting). **Ivo Dinsbergs:** Investigation (equal); Writing – review and editing (supporting). **Valts Jaunzemis:** Investigation (equal); Writing – review and editing (supporting). **Elza Zacmane:** Investigation (supporting); Writing – review and editing (supporting). **Ance Priedniece:** Investigation (supporting); Writing – review and editing (supporting). **Martins Briedis:** Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (lead); Supervision (lead); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (lead).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9s4mw6mmk> (Vigants et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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