

**Integrating light-level geolocation with activity tracking reveals unexpected  
nocturnal migration patterns of the tawny pipit**

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## Abstract

Migratory birds complete their seasonal journeys between breeding and non-breeding sites with a series of migratory flights that are separated by prolonged stopovers. While songbirds are the most common taxa among migratory birds, empirical data on flight and stopover behaviour along their entire migratory journeys are still rare. Here, we integrate activity and barometric pressure tracking with classical light-level geolocation to describe migration behaviour of tawny pipits *Anthus campestris* breeding in Central Europe. Surprisingly, tracked pipits used, on average, as many as 10 stopover sites during their six week, >5000 km long autumn migration. This conforms to a typical hop-type pattern of migration. In contrast to common knowledge which considers the tawny pipit as a typical diurnal migrant, our data revealed that more than 2/3 of all migratory movements were carried out at night. Nocturnal departure times were highly variable within individuals and spread across the entire night while landing most often took place within the first few hours after sunrise. Consequently, there was a negative relationship between departure timing relative to sunset and flight duration. Short flights of up to 2 h were most common and median flight duration was 4.5 h. There was a hyperbolic relationship between flight duration and maximum flight altitude and flight altitudes during night were two times higher compared to daytime. The overall ratio of flight vs stopover duration during migration was on average 1:6.5. This closely matches predictions from theoretical models. We show that multi-sensor tracking has the potential to provide unprecedented details on migratory behaviour of individual birds along their entire migratory journeys, and it also improves the precision of geographical locations derived from light-level geolocators.

**Keywords:** accelerometer, annual cycle, bird migration, departure, flight performance, nocturnal migrant

## 41 Introduction

42 Migratory journeys of birds comprise flight phases when distance is covered through energy  
43 consumption, and stopover phases when energy reserves are usually replenished. Piersma (1987)  
44 outlined three general travel schemes that are shaped by the relationships between fuel loads,  
45 stopovers and flight bouts: (1) *jump migration* that relies on high fuel loads, few long endurance  
46 flights and few lengthy stopovers, (2) *skip migration* with intermediate fuel loads, and several  
47 stopovers and flights of intermediate duration, and (3) *hop migration* that is characterized by low  
48 fuel loads, frequent and short flight phases and multiple short stopovers. The overall duration of the  
49 movement phase of migration (between the first departure and arrival at the final destination) is  
50 directly dependent on the travel scheme employed as fuel load upon the initial departure will  
51 determine how far the bird can fly on its first flight phase (Lindström et al. 2019). In small and  
52 medium sized passerines, theoretical models predict that the total duration of migration is divided  
53 between flight and stopover phases at a ratio of 1:7, with disproportionally more time spent on  
54 stopovers, which include the initial fuelling before first migratory flight (Hedenström and Ålerstam  
55 1997). Despite passerines being by far the most numerous taxon among migratory birds (Hahn et al.  
56 2009), empirical data to support these theoretical predictions still remain limited.

57       Because most time of migration is spent on stopovers for refuelling, fuel deposition rate  
58 largely underpins the total migration duration (Lindström et al. 2019). Most passerines, however, do  
59 not feed at night, hence using nighttime for migratory flights do not interfere with fuelling and can  
60 potentially reduce the total migration duration. As the current knowledge on Afro-Palearctic  
61 migrants suggest, 63% of species are assumed to migrate during the night (nocturnal migrants), while  
62 only a handful of species – 16%, mainly aerial foragers, are assumed to migrate during daytime  
63 (diurnal migrants; Dorka 1966, Adamík et al. 2016). The remaining pool of species are thought to  
64 exercise a mixed strategy. However, it is to be pointed out that the distinction between nocturnal  
65 and diurnal migrants is not always unequivocal and many species that predominantly migrate at, e.g.

daytime, have also been recorded to migrate during the night or vice versa (Hansen 1954, Adamík et al. 2016). Under what exact circumstances this happens, remains largely unknown.

The majority of nocturnal migrants are known to depart within the first few hours after the sunset (Liechti et al. 1997, Bulyuk and Tsvey 2006, Schmaljohann et al. 2011). This allows for compass calibration at twilight for orientation (Moore 1987, Muheim et al. 2006) and for longer nocturnal flights when larger distances can be covered. Landing typically occurs around sunrise (Bruderer and Liechti 1999) giving a maximum nocturnal flight duration of ca. 12 h during autumn migration in the Northern hemisphere in September and ca. 10 h during spring migration in April (Bauchinger and Klaassen 2005). There is, however, a considerable spectrum in both departure and landing times relative to sunset/sunrise among individuals (Bolshakov et al. 2007, Schmaljohann et al. 2013) which can vary seasonally (Bolshakov et al. 2007). Much of our current understanding about nocturnal departure and landing times of migrants comes from studies conducted at a single location along the migration route (e.g. Bolshakov and Bulyuk 1999, Bolshakov et al. 2003) or at ecological barriers where long flight duration with early nocturnal onset may be the prevailing pattern (Adamík et al. 2016, Ouwehand and Both 2016, Jiguet et al. 2019). Similarly, many of these studies have been conducted using radar observations (e.g. Schmaljohann et al. 2006), which does not allow for distinguishing species-specific behaviours, as species identification in radar signals remains a challenging issue (Bauer et al. 2019). As a result, studies done so far provide only snapshots at specific points in time and space, and we are still missing information on departure and landing behaviour of individual birds along their full migration cycles.

State-of-the-art multi-sensor tracking devices that integrate measurements of ambient light, activity and barometric pressure have the potential to bridge this gap in our knowledge and to provide novel insights into species- and individual-specific migratory behaviour along their entire migratory journeys (Bäckman et al. 2017a, b, Dhanjal-Adams et al. 2018, Liechti et al. 2018, Sjöberg et al. 2018). Here we use multi-sensor individual tracking to describe migratory patterns and flight behaviour over the entire journey of tawny pipits (*Anthus campestris*) breeding in Central Europe.

The tawny pipit is among the few Afro-Palearctic migratory species that are characterized as a 'typical diurnal migrant' (Dorka 1966, Alerstam 1990, Schmaljohann 2019), however, conclusive evidence is still missing. We employ novel analytical tools to test this long-standing assumption with a particular focus on describing flight and stopover behaviour and take-off and landing times of pipits in relation to sunset/sunrise throughout the migration journey. Furthermore, we integrate classical light-level geolocation with activity and barometric pressure measurements allowing for more detailed and precise estimates of migration timing and geographic positions of stationary sites and migration routes.

## Methods

### Field work

We studied tawny pipits breeding in open lignite mines in western Czech Republic (50.5° N, 13.83° E). During the breeding season in 2018, we captured 13 adult birds using mist-nets and perch traps and equipped them with multi-sensor geolocators (GDL3-PAM, Swiss Ornithological Institute; Liechti et al. 2018) that were mounted on the birds' backs using flexible silicone harness. The loggers accommodated sensors for measuring ambient light intensity, atmospheric pressure 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 was measured along the Z-axis for 3.2 s at 10 Hz frequency every 5 min storing the sum of the absolute differences between consecutive measures (31 values). Atmospheric pressure recordings were set to 30 min intervals.

In 2019, we successfully recaptured and retrieved geolocators from 5 of the 13 previously tagged individuals. One more bird was seen in the study area, but we failed to recapture it, amounting the total return rate to 46%. One of the retrieved geolocators contained data encompassing the full annual cycle. Two devices stopped recording during spring migration before

the birds had returned to the breeding area and two more devices stopped recording while the birds were still in their non-breeding residency sites in sub-Saharan Africa.

## Data analyses

Geolocator data analyses were carried out using the R-packages ‘TwGeos’ (Lisovski et al. 2015), ‘SGAT’ (Wotherspoon et al. 2013), and ‘PAMLR’ (Dhanjal-Adams et al. 2020). Location data were analysed using a threshold approach following general guidelines described in Lisovski et al. (2020) and integrating activity and atmospheric pressure recordings for more precise designation of migration timing, i.e. movement and stationary phases (flight, migratory stopovers and long residency periods).

For distinguishing between movement and stationary phases during the annual cycle, we used accelerometer and atmospheric pressure recordings. Because tawny pipits use flapping flight for migration, we used the flapping flight classification from the R-package ‘PAMLR’ and set the threshold to 1 h (equals to 12 consecutive readings of flapping activity at 5 min recording intervals) to classify migratory flights. Thus, activity measures that were classified as flapping and lasted for at least 1 h were regarded as migration episodes. A visual inspection of the atmospheric pressure readings revealed that some migratory flights when individuals clearly changed their location were, however, missed. Therefore, we performed a second classification based on atmospheric pressure recordings and cross-validated the two approaches. Atmospheric pressure is not expected to change rapidly when the bird is stationary (weather related changes) but can vary considerably as the bird takes altitude or covers substantial distance in flight (Liechti et al. 2018, Sjöberg et al. 2018). Because background variation in air pressure linked to weather rarely exceeded  $1 \text{ hPa } 30 \text{ min}^{-1}$ , we used a threshold of atmospheric pressure change  $>1.5 \text{ hPa } 30 \text{ min}^{-1}$  for identifying flight phases within the dataset. This approach allowed for identification of start times of migratory flights and their length with an accuracy of 30 min. If the bird was stationary for at least 24 hours, we considered this a stopover. To derive geographic positions, we first log-transformed the recorded light values and

derived sunrise and sunset times in the R-package 'TwGeos' using a light intensity threshold of 1 unit on the log-transformed scale. Recorded twilight times were then calibrated against the actual sunrise and sunset times at the breeding sites of the birds prior to the start of the autumn migration (i.e. in-habitat calibration; Lisovski & Hahn 2012). Further, we used the R-package 'SGAT' to model the most likely migration path, stopover and residency locations along with their confidence intervals. For this, we used a grouped Estelle model where location estimates coming from the same site (based on acceleration and pressure classification) were grouped together. This procedure increases the overall accuracy of the stationary positions (Lisovski et al. 2020). We applied a spatial mask that confined stationary sites to terrestrial habitats only while movement was allowed to cross over oceans and seas. The twilight error distribution was assumed to follow Gamma distribution as based on the parameters inferred from the in-habitat calibration. The final model also included a movement model – birds were allowed to move only when preceding activity and pressure analyses had detected migratory flights and movement duration was restricted to the duration of migratory flight hours at the specific day (*dt* parameter in the *groupedThresholdModel* function). Speed distribution for the movement model followed a Gaussian distribution (shape = 30, scale = 0.6) with the highest probability of ground speeds between 40–60 km h<sup>-1</sup> during the movement phase. The start of all tracks and the end of the single complete track were fixed to the known tagging/breeding location. To initiate the model, we first ran a *modifiedGamma* model with relaxed assumptions for 1000 iterations. Then the resulting model was tuned five times (300 iterations each) with all assumptions/priors (*Gamma* model) before initiating the final run with 2000 iterations to ensure convergence. We present the most likely migration tracks and stationary locations as inferred from median location estimates along with 95% probability distributions of location estimates.

We calculated the ratio between the duration of flight and stopover phases as the total number of flight hours vs the total number of stationary hours between the initial departure flight and final arrival flight. Thus, our estimated do not include the initial fuelling before departure (Hedenström and Ålerstam 1997). Departure (i.e. take-off) and landing times were compared to

169 sunset and sunrise times as derived from the data recorded by the geolocators light-sensor. In-  
170 habitat calibration revealed that sensitivity of the light-sensors was on average higher than Sun's  
171 azimuth of 0° relative to the horizon (actual sunrise/sunset) at  $-4.8^\circ \pm 0.5$  (mean  $\pm$  SD). Thus, the  
172 migratory flight timing here is expressed relative to the approximate start of civil twilight (centre of  
173 the Sun 6° below the horizon) rather than sunrise/sunset when the centre of the Sun is at 0° relative  
174 to the horizon.

175         Maximum flight altitude (measured in m above sea level, m asl) during each flight was  
176 calculated applying the hypsometric equation to the atmospheric pressure measurements assuming  
177 standard atmospheric conditions (Stull 2016, Liechti et al. 2018). We compared flight altitudes during  
178 diurnal and nocturnal migratory phases using linear mixed effects model accounting for random  
179 effects of individual identity in R-package lme4 (Bates et al. 2014). The precision of altitude estimates  
180 of the used loggers is described in Liechti et al. (2018); rarely under extraordinary atmospheric  
181 conditions it can exceed 200 m (approx. 25 hPa).

## 183 Results

184 Throughout the year, the start and end of the daily activity patterns coincided with sunrise and  
185 sunset times as recorded by the geolocators light sensor in such a manner that the tracked birds  
186 were immobile (resting or sleeping) during the dark hours of the night. The only exception to this was  
187 migratory flights, most of which took place at night. Actogram summarizing annual activity patterns  
188 of the individual 22BK, the single individual with a full annual track, is shown in Figure 1, actograms  
189 of the remaining four individuals are given in Supplementary materials Figure S1. Pipits were often  
190 most active during the early morning hours after sunrise and in the evening a few hours before  
191 sunset (Figure 1, Figure S1). The time period in the middle of the day was often spent  
192 resting/sleeping.



### Migration timing, distance, stopovers

In autumn, all birds migrated along the western flyway to their non-breeding sites in West Africa (Figure 2; see Supplementary materials Figure S2 for comparison of location estimates their CIs and migration timing estimates when using classical light-level geolocation where data analyses are performed using only the light data). Migration started in the second half of August and birds arrived in sub-Saharan Africa about six weeks later (average migration duration = 43 days) in late September – early October. A summary of autumn migration parameters for each individual is given in Table 1. Two birds (20NT & 22BN) spent long periods (>40 days in total) at multiple intermediate stopover/non-breeding sites in sub-Saharan Africa before they arrived at their final non-breeding residency site in the second half of November – these movements were not considered as part of the autumn migration. Overall, during the autumn migration, tracked pipits used on average 10 different stopover sites where birds stopped for at least 24 hours. Longer stopovers of more than 3 days, however, were scarce, averaging at 3.2 per individual. Interestingly, the ratio of flight to stationary days during the movement phase of autumn migration (from departure until arrival) was on average 1:1 (21.4 flight days vs 21 stationary days; Table 1). From the total migration duration (measured in hours), the proportion of time spent in migratory flight was 13.3% while the remaining 86.7% of time was spent on stopovers, which includes all stops of any length. Thus, the ratio of flight vs stopover duration was on average 1:6.5. Pipits on average migrated more than 5000 km reaching an average travel speed of 125 km day<sup>-1</sup>.

### Flight performance

Tracked pipits completed their autumn migration with an average of 23.8 individual flights. The total number of flight hours ranged between 121 and 146 h for the five individuals (Figure 3). During barrier crossing, flights were prolonged into the day lasting on average  $14 \pm 3.8$  h (SD; n = 11 from a total of 132 tracked flights) and up to 20 h for two of the five tracked individuals (Table 1). Average ground speed along the most likely migration track (orange lines in Figure 2) was estimated at 39.5 km h<sup>-1</sup> (Table 1).

Pipits predominantly travelled during the night (on average 68.6% of all migratory movements; Table 1). Time of nocturnal departures were spread across the entire night with an average departure time  $4:25 \pm 5:17$  h (SD,  $n = 132$ ) after the sunset (Figure 4a). Longer flights (including Sahara crossing flights) typically started shortly before or after sunset and there was a general decline in flight duration with increasingly later nocturnal departure times (Figure 4c).

Landing most often occurred around sunrise (average landing time:  $0:45 \pm 3:41$  h (SD),  $n = 132$ , Figure 4b). Median migratory flight duration across all five birds was 4:30 hours (Table 1) and short flights of up to 2 hours were the most common accounting for 30% of all recorded flights (40/132; Figure 4d). Maximum flight altitudes ranged between 2600 and 3200 m asl for different individuals and there was a positive hyperbolic relationship between individual flight duration and the maximum altitude reached (Table 1, Figure 5). Flight altitudes during night were higher compared to daytime (night:  $1090 \pm 728$  m asl (SD); daytime:  $498 \pm 428$  m asl;  $\beta = 590 \pm 38$ ,  $t = 15.7$ , random effects variance: bird identity 2417 (49.2 SD)).

### Spring migration

The departure date for spring migration could only be estimated for three birds which showed a variation of more than one month: 22BP = 18 Feb, 22BN = 12 Mar, 22BK = 22 Mar. Loggers 22BP and 22BN stopped recording shortly after the birds departed while 22BK recorded until the bird arrived at the breeding site on 24 Apr. Spring migration of this individual started with a 20 h long non-stop flight across the Sahara and compared to autumn migration spring migration was overall shorter (both in distance – 11.6%, and duration – 17.5%), the migration speed was higher (7.4%), the total number of flight hours was lower (24.5%), while the maximum flight altitude reached was 500 m higher (3662 m asl) (see Table 1 for all migration parameters).

## Discussion

Our results of activity and barometric pressure tracking revealed that tawny pipits predominantly migrate at night contradicting the earlier notion of the species as a typical diurnal migrant (Dorka 1966, Alerstam 1990, Schmaljohann 2019). We found that landing most often occurred within the first four hours after sunrise, which could explain the earlier observation-based assumption of diurnal migration by tawny pipits. Similarly, barrier crossing flights over the Sahara often stretched into the daytime as shown in other long-distance migrants (Adamík et al. 2016, Ouwehand and Both 2016, Jiguet et al. 2019, Schmaljohann et al. 2006). Departure times of migratory flights were spread across the night, contrasting the commonly shown pattern of departures being clustered shortly after sunset (Kerlinger and Moore 1989, Liechti et al. 1997, Bruderer and Liechti 1999, Bolshakov et al. 2003). Departure times relative to sunset were highly variable within and across individuals during the migration season. Thus, it is likely that environmental settings and individual body condition, rather than an inherent circadian clock, are the main drivers of departure time (*cf.* Bulyuk and Tsvey 2006, Müller et al. 2016).

During migration, tawny pipits employed a *hop migration* pattern with numerous short flights and stopovers (Piersma 1987). Our conclusion of the pipits conforming to a *hop migration* is clearly dependent on the high temporal resolution of our data making it possible to identify 24–72h long stopovers. The number of longer stopovers (>3 days) varied from 1–5 between different individuals and in many cases prolonged stopovers were associated with Sahara crossing which was completed with long endurance flights (Figure 2, Figure 3). Such co-occurrence is likely attributed to prolonged fuelling to build energy stores necessary for crossing ecological barriers (Schaub and Jenni 2000, Fransson et al. 2006). The ratio between the duration of flight and stopover phases was on average 1:6.5 which is slightly lower than the predicted ratio of 1:7 based on theoretical models (Hedenström and Alerstam 1997). However, our estimates of the total stopover duration did not include the fuelling period before the initial departure for migration (Lindström et al. 2019). It is likely

that with this period included, the ratio of flight vs stopovers would match the theoretical predictions (Hedenström and Ålerstam 1997).

Overall, exercising a *hop migration* pattern may have energetic benefits for individuals. Birds can save energy on reduced transport costs if they migrate in short flight steps and low fuel levels (Ålerstam 2001). Consequently, birds need to spend less time on stopovers refuelling and reduction in total energy requirements will also enable to reduce the total duration of migration. Such migration strategy is, however, possible only if resources along the migration routes are widespread and settling costs at new stopover sites are small. The observed difference in flight altitudes between night and day may suggest that birds employ a fly-and-search migration when prolonging the flight into the day. Flight of short duration and diurnal flights were most commonly carried out at altitudes below 500 m asl which may allow the birds to search for favourable landing sites where food for refuelling may be found. This may also explain why pipits prefer late night/early morning flights where new stopover sites may be visually located after sunrise. Thus, *hop migration* may be inevitably linked with fly-and-search migration strategy and hence, late night departure times and landing times after sunrise.

Our estimates of the average ground speed of  $39.5 \text{ km h}^{-1}$  along the most likely migration track is slightly lower than the ground speed measurements of  $\text{ca } 50 \text{ km h}^{-1}$  for passerines obtained using tracking-radar (Bruderer and Boldt 2001). Such discrepancy is not surprising, because geolocators provide positions only twice per day and the migration path between them is smoothed. Therefore, with a positional frequency averaging at 12 h intervals, we cannot account for small in-flight detours of the birds when estimating ground speed. Consequently, both ground speed and travel speed (average of  $125 \text{ km day}^{-1}$ ) are likely underestimated.

Tawny pipits' migration routes via the Iberian Peninsula and non-breeding sites in the Sahel zone in West Africa were largely similar to an earlier tracking study of this population (Briedis et al. 2016). Integration of activity and barometric pressure tracking into the classical light-level geolocation, however, opens a new avenue in the details we can reveal about migration patterns.

This includes a detailed description of the seasonal flight and stopover behaviour as well as their interrelationship which can then be tested against theoretical predictions for different migratory strategies. Developing algorithms that can translate activity recordings into daily, seasonal and year-round energy budgets have the potential to further our understanding on the linkages between particular evolutionary and behavioural strategies we observe in the wild and their energetics.

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## Authors' contributions

MB, PA, and SH conceived the idea and study design; VB carried out fieldwork; MB performed data analyses and drafted the manuscript with inputs from all other authors.

## Data accessibility

Bird tracking dataset will be uploaded to an open repository (Zenodo, Dryad or MoveBank) providing the manuscript is accepted for publication.

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412

## 413 Tables & Figures

414 **Table 1.** Summary data for each bird. Note that departure date is always given as the date of the  
 415 evening of the night when the first migratory flight occurred. Arrival is given as the date of the  
 416 morning when the last migratory movement occurred. Total duration, however, is given as the  
 417 number of days (rounded to full days) between the precise time of departure and arrival, thus in  
 418 some instances creating a discrepancy in the numbers given in the table and the absolute difference  
 419 in days between departure date and arrival date.

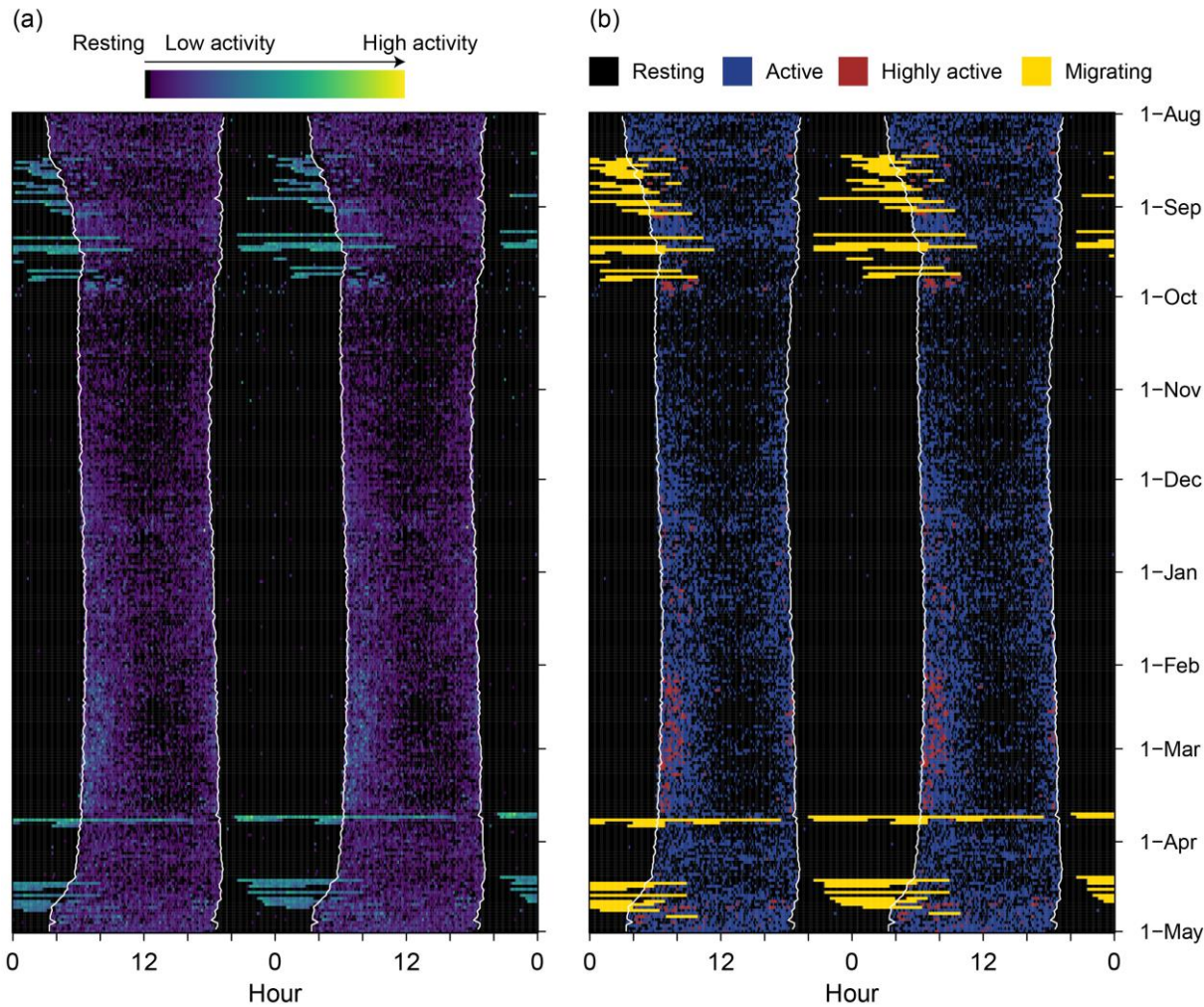
<i>Migration</i>	Autumn						Spring
<i>characteristics</i>	22BK	20NT	22AU	22BN	22BP	<i>Average</i>	22BK
Departure	15-Aug	18-Aug	28-Aug	28-Aug	26-Aug	<i>23-Aug</i>	22-Mar
Arrival	25-Sep	2-Oct	6-Oct	10-Oct	11-Oct	<i>5-Oct</i>	24-Apr
Total duration (days)	40	45	39	42	46	<i>43</i>	33
Migratory track distance (km)	5440	5290	5340	4890	5370	<i>5266</i>	4810
Great circle distance (km)	4480	4740	4390	4410	4450	<i>4494</i>	4480
Travel speed (km day <sup>-1</sup> )	136	118	137	116	117	<i>125</i>	146
Travel speed great circle distance (km day <sup>-1</sup> )	112	105	113	105	97	<i>106</i>	136
No. flight days	26	19	22	17	23	<i>21</i>	13
No. stopover days	14	26	17	25	23	<i>21</i>	20
No. stopovers	12	10	11	7	9	<i>10</i>	5
No. stopovers (>3 days)	1	5	3	4	3	<i>3.2</i>	1
Proportion in flight	13.1%	12.3%	15.8%	11.9%	13.3%	<i>13.3%</i>	12.2%

Proportion stationary	86.9%	87.7%	84.2%	88.1%	86.7%	86.7%	87.8%
<i>Flight characteristics</i>							
No. flights	27	25	25	19	23	23.8	15
Median flight duration (hh:mm)	3:30	3:00	5:30	6:00	4:30	4:30	5:00
Cumulative flight hours (hh:mm)	126:30	132	146	121	144:30	134	95:30
Longest flight (hh:mm)	14:30	20	16	11:30	20:30	16:30	21:00
Proportion of migratory flight at night	75.4%	64.2%	73.7%	75.7%	54.2%	68.6%	70.4%
Flight speed along migratory track (km h <sup>-1</sup> )	43	40.1	36.6	40.4	37.2	39.5	51.6
Maximum flight altitude (m asl)	3159	2611	2978	3182	2912	2968	3662

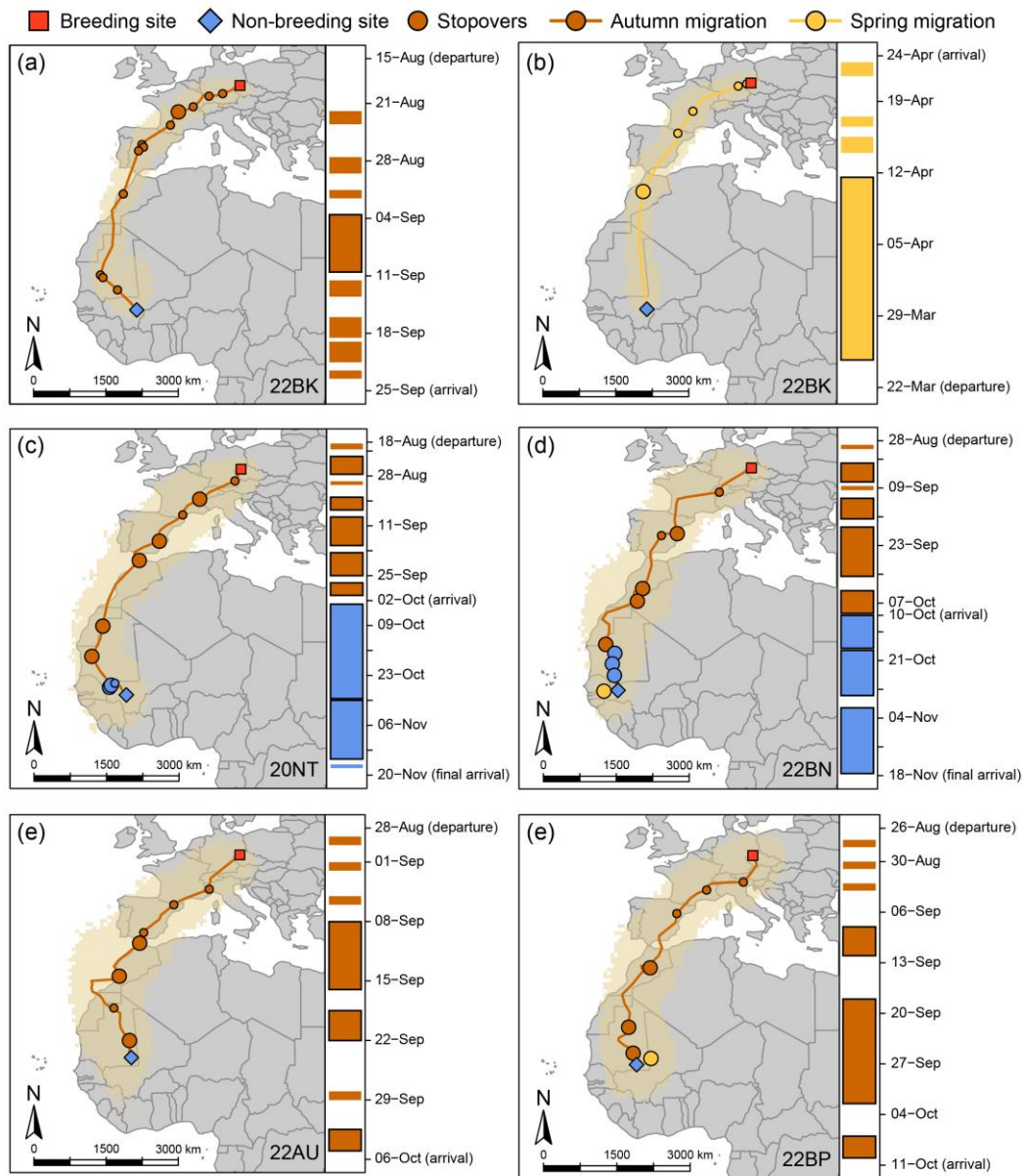
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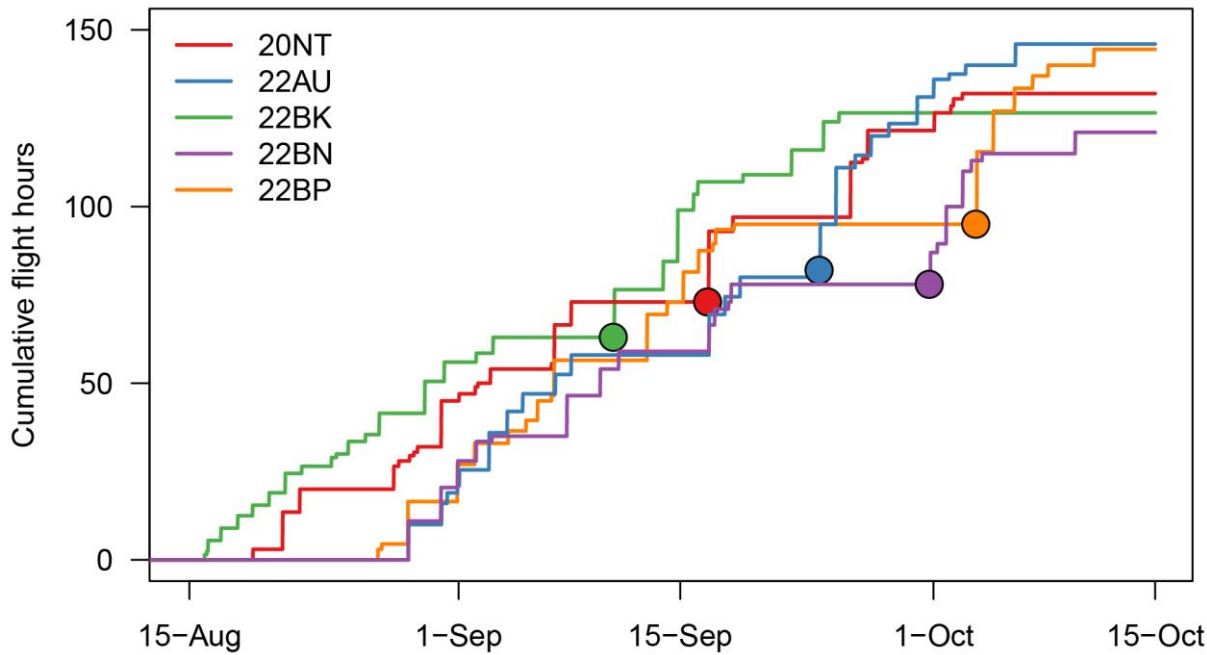
**Figure 1.** Actograms showing the annual activity pattern of a tawny pipit (bird ID: 22BK) from 1-Aug 2018 until 1-May 2019. (a) Raw accelerometer measures, (b) activity data classified into 4 categories – resting, active, highly active, and migrating. In both panels, each horizontal line represents 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.



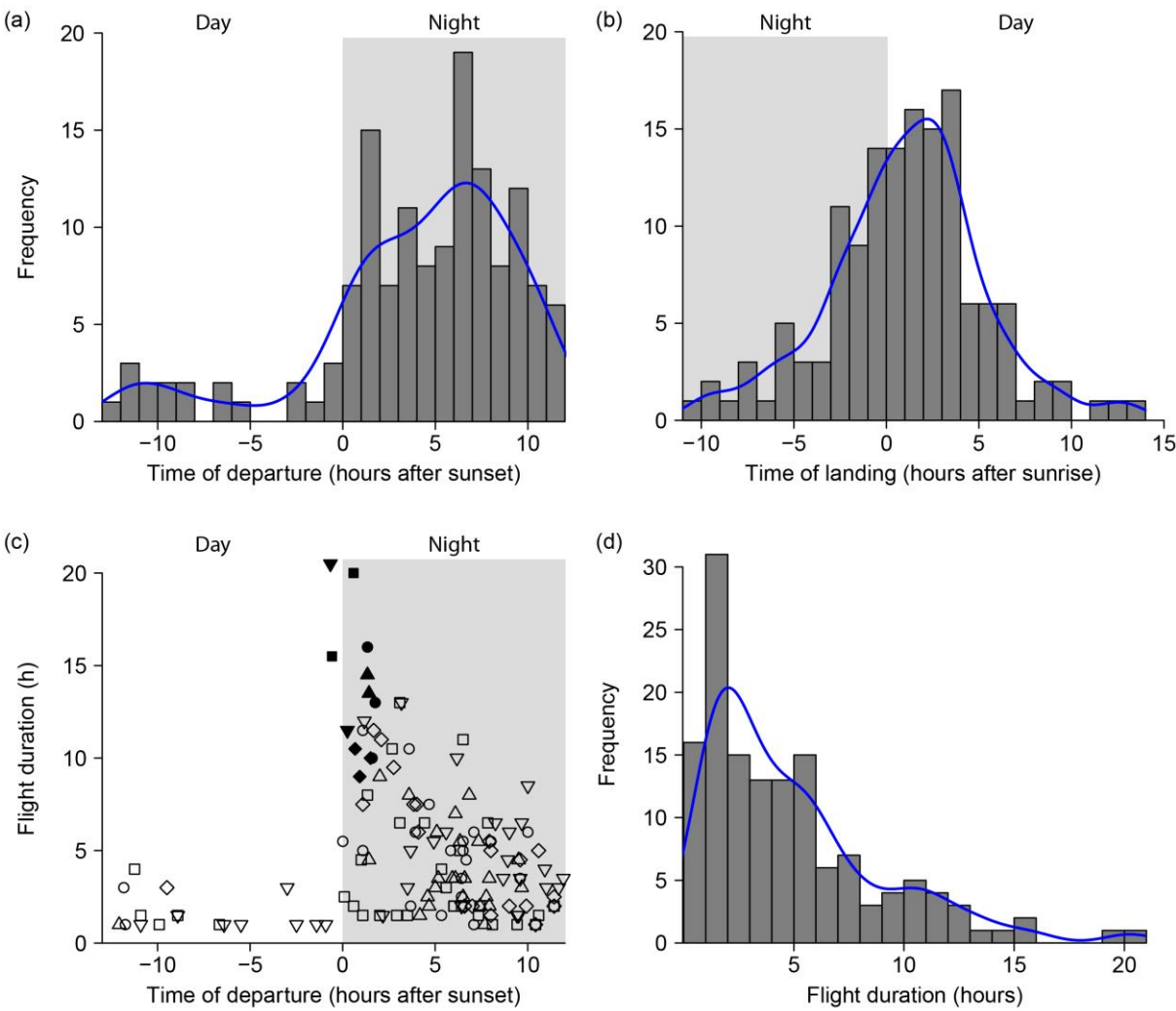
**Figure 2.** Migration routes, stopovers and non-breeding sites of five geolocator-tracked tawny pipits. Shaded areas show 95% probability distributions of location estimates. For each bird, timing and duration of migration is shown alongside the map where coloured bars indicate stopovers longer than 24 h (stopovers longer than 3 days are marked with black borders) and white spaces between them indicate movement periods between the stopovers. Please note that bars indicating migration timing have variable scales. Panels a and b represent autumn and spring migration of the same individual. Intermediate non-breeding sites are marked in blue for the two birds that showed non-breeding site itinerancy (panels c & d).



**Figure 3.** Cumulative flight hours of five tawny pipits during the autumn migration between 15-Aug and 15-Oct 2018. Start of Sahara crossing for each bird is indicated with a dot.



**Figure 4.** Characteristics of migratory flights of tawny pipits. (a) Frequency distribution of departure time relative to sunset, (b) landing time relative to sunrise, (c) relationship between flight duration and departure time relative to sunset. Different symbols denote different individuals (legend as in Fig. 5), filled symbols denote barrier crossing flights, (d) frequency distribution of flight duration. Blue lines in panels a, b and d are estimated frequency density curves. Note that sunrise and sunset times here are derived from geolocators' light recordings and approximately correspond to a sun's azimuth of  $-4.8^\circ$  (see methods).



**Figure 5.** Relationship between flight duration and the maximum altitude during autumn migration. Different symbols denote different individuals, filled symbol indicate Sahara crossing flights. Quadratic model fit is depicted by a solid line with 95% CI (shaded area).

