

Research Article

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Debora Arlt, Peter Olsson, James W Fox, Matthew Low, Tomas Pärt

Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird

Abstract: Stopover behaviour is a central element of migration strategies. But in recent geolocator studies, despite now being able to track individual songbirds during their entire migration, their stopover behaviour has received little attention. We used light-sensitive geolocators to identify the migratory routes and schedules of 12 northern wheatears (*Oenanthe oenanthe*) breeding in Sweden. Three geolocators collected temperature data complementing inferences from light data by providing additional information on behaviour during migration. The wheatears performed a slow migration with considerable stopover time (84%/76% of autumn/spring migration), with short stops while traveling through Europe, and a prolonged stopover period in both autumn and spring in the Mediterranean region. Spring migration was faster than autumn migration, mainly because of decreased stopover time. Migration routes and time schedules were similar to those from a German breeding population. Compared to wheatears breeding in Alaska with a three-fold migration distance, Swedish wheatears spent more time during stopovers during autumn and spring migration, suggesting less time constraints and potential flexibility in migration schedules. The finding of prolonged stopovers, similar to other recent geolocator studies, shows that temporary residency periods may be common. This changes our current view on stopover ecology to one where temporary residency periods are part of spatio-temporal strategies optimising resource use during the entire annual cycle.

Keywords: geolocator; light geolocation; stop-over; annual cycle; *Oenanthe oenanthe*; temporary residency;

migration schedule; time constraint; migratory connectivity; wintering area

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1 Introduction

Migration is usually viewed as the *movement* between two places, for migratory animals typically between the breeding and wintering grounds [1]. This idea has prevailed, largely due to the difficulty of tracking individuals during their entire migration. Tracking individuals throughout their annual life-cycle has been particularly difficult for small migratory passerine birds leaving many aspects of their migration obscured. During migration birds make stops, with stopover sites usually defined as locations where the birds' main activity is to refuel for the next migratory flight. Stopovers are generally thought to involve a trade-off between number of stopovers and their duration (optimal migration theory [2,3]). Because we have not been able to track individuals, until recently we had a poor idea of how often and how long many birds stopover during migration [4]. Recent studies reveal complex spatio-temporal strategies of migratory animals, and show that rather than simply moving between the breeding and wintering grounds birds may make prolonged stopovers that seem to extend beyond the time necessary for refuelling [5]. Such findings, which do not conform to optimal migration theory, will help shed new light on what constrains the rate of migration and drives stopover duration.

With the development of lightweight geolocators – *i.e.* data loggers that record light intensity and provide year-round positional information based on the timing of sunrise and sunset – there are now increasing opportunities to follow individuals during migration and during their entire annual life-cycle (e.g. [6]). This opens up possibilities for studying individual trade-offs

*Corresponding author: Debora Arlt: Swedish University of Agricultural Sciences, Sweden, E-mail: debora.arlt@slu.se

Peter Olsson: Lindmätaregatan 2, 218 38 Bunkeflostrand, Sweden

James W Fox: Migrate Technology Ltd, PO Box 749, Cambridge, CB1 0QY, UK

Matthew Low, Tomas Pärt: Department of Ecology, Swedish University of Agricultural Sciences, Box 7004, 75007 Uppsala, Sweden

and spatio-temporal strategies (residency places, periods and purpose) throughout the year, as well as variation between individuals and populations. Populations that differ in migration distance, migration routes, length of the breeding season and/or ecological conditions during different stages of their annual cycle (e.g. seasonality of food availability) experience different timing and, potentially, energetic constraints, leading to differences in selection on e.g. arrival time and migration rate. Populations with a greater migration distance and shorter duration of the breeding season are predicted to experience constraints (in terms of time and energy), and hence show less flexibility in their migration time schedule. Those populations may be predicted to start migration earlier (or, because start of migration is relative, may be predicted to spend less time at the breeding and/or wintering area), and/or migrate faster (higher flight speeds, or fewer and shorter stopovers). Hence, comparisons between populations on large geographical scales will allow investigations of the constraints on migration (e.g. [7]).

Currently geolocators are developed that collect additional data, e.g. acceleration data for inferences about an animal's activity [8]. Also temperature can provide information about an animal's behaviour. In seabirds, for example, temperature data reflecting sea surface temperature have been used to reveal activity patterns [9] and habitat use [10]. For terrestrial birds, changes in temperature could indicate when birds move between locations with different microclimates, e.g. protected resting places vs. exposed places during their daily routines, or locations differing in altitude, e.g. at the ground vs. at flight altitude. Because most passerine birds usually fly at altitudes of about 700 m when migrating over land or up to about 3000 m when migrating over water [http://www.birds.cornell.edu/AllAboutBirds/studying/migration/pathways] they experience generally lower temperatures at flight altitude than at the ground. We therefore predict that periods in flight are reflected by lower recorded temperature. The magnitude of this temperature difference will, however, depend on ambient temperatures at the ground, such that, e.g., during cold periods at more northerly stopover sites during migration in early spring flight periods will be more difficult to separate from drops in ambient temperature.

Northern wheatears (*Oenanthe oenanthe*, hereafter wheatear) are long-distance migrants breeding across Europe, North Africa, northern Asia, Alaska, north-eastern Canada and Greenland, and wintering in tropical Africa south of the Sahara desert. The aims of our study are threefold. First, the migration and wintering

area of wheatears breeding in Northern Europe are currently unknown. Of all wheatears that have been ringed in Sweden, only a few have been found during migration, and none have been found in their assumed wintering area [11]. Here, we report on migration routes and schedules for 12 wheatears breeding in central Sweden, with a particular focus on stopover behaviour during migration. We also investigate sex- and seasonal differences in migration strategy, and the flexibility of timings during migration. Second, we compare our data to data from breeding populations of wheatears in Germany and Alaska (all three populations wintering in the Sahel zone [12,13]) as a first step to relate migration schedules to migration constraints. Third, we present data from a new generation of geolocators that concurrently collect temperature information. We discuss the utility of the temperature data in terms of their potential to be used as a complement to inferences from light data and to provide additional information on migration behaviour.

2 Methods

We applied light-sensitive geolocators to track northern wheatears (hereafter wheatears) from a breeding population in southern central Sweden (59°50'N, 17°50'E). We have studied the breeding ecology of this population since 1993. In our study area wheatears arrive in mid-April to mid-May, the first pairs start egg laying in early May, and the majority of nestlings fledge before mid-June (details in [14-16]). After post-breeding moult the birds start their migration to Africa in August. Each year we monitored all sites potentially suitable for breeding wheatears from early April to the end of June.

Over three years we deployed geolocators on a total of 66 wheatears (2010: 6 males, 4 females, 2011: 13 males, 16 females, 2012: 15 males, 12 females; see also [17]). In 2010 and 2011 we used British Antarctic Survey (BAS, Cambridge, UK) geolocators types Mk12S (2010: 15 mm stalk at 30° angle) and MK20ASLT (2011: 10 mm stalk at 25° angle). In 2012 we used Migrate Technology (http://www.migratetech.co.uk/) geolocators type Intigeo-P65C2-7 (7 mm stalk at 40° angle). We used geolocators with a stalk to minimise shading effects caused by the bird's plumage. The geolocators sampled light intensity at 1 min intervals and recorded the maximum light every 2 min (BAS Mk12/Mk20) or every 5 min (Intigeo, Mode 1).

Birds were trapped when feeding young in the nest during early and mid-June, covering the variation of breeding times from early to late breeders. We chose birds of both sexes, excluding birds known to be >4 years old

because they have a lower survival rate between years. Geolocators were attached using a leg-loop harness (Rappole-Tipton style [18]) made from 1 mm elastic EPDM rubber cord (Polymax, <http://www.polymax.co.uk/>) and leg-loop length was adjusted individually to each bird. Weights of geolocators including the harness were 1.3 g (2010), 1.0 g (2011) and 0.95 g (2012). Those weights corresponded to a mean load (proportion of body mass at the time of deployment) of 5.7%, 4.4% and 4.1% respectively (see also [17]). All previously unringed males and 84% of the females could be aged as either young (one year old) or old (at least two years old) based on plumage characteristics (see [14]). All tagged individuals were observed at the same site after deployment, usually until the end of breeding (end of June). Geolocators were retrieved after wheatears returned in the subsequent year, either shortly after arrival or later when provisioning nestlings.

Of 66 tagged wheatears 15 returned to our study area. Of those 15 we could download data over the entire annual cycle from 12 birds: 4 in 2011 (1 male, 3 females), 5 in 2012 (2 males, 3 females), and 3 in 2013 (3 males). In 2011 we were unable to retrieve the geolocator from a male bird. In 2012 two females were carrying a geolocator that had stopped recording data, one after 3 days, and the other on 23 October during or just before the Sahara passage. Return rates were low compared to those from individually marked (ringed) control individuals (5%, 11% and 30% lower in the three different years), and carrying a geolocator also slightly delayed time of arrival at the breeding area, and timing of breeding (see Arlt et al. [17] for a detailed assessment of geolocators effects).

2.1 Geolocator analysis

Geolocators record light intensity over time and information on twilight times (sunrise and sunset) allows derivation of latitude (based on day length) and longitude (based on time of midday). Analyses of geolocator light data were done based on established methods, *i.e.* employing a light level threshold to identify twilight times, and using a calibrated sun elevation angle (SEA) to calculate geographical fixes (positions) (see [19]). Geographical positions were analysed only during stationary periods, *i.e.* when the birds most likely remained stationary at one location.

Light data processing. – All data processing was performed in program R [20]. Twilight events (sunrise and sunset times) were identified as the times that the light signal crossed the chosen threshold value of 1 (BAS geolocator arbitrary scale) or 2 (Intigeo lux scale) of the

measured light level. The light data contained disturbances from shading leading to repeated increases and decreases of measured light level during a sunrise or sunset, with multiple light level peaks and hence multiple crossings of the chosen threshold value. Rather than manually removing multiple crossings we applied a filter that for each day curve performed a peak-hold-forward to midday (*i.e.* following the light level until a peak and keeping it stable at the peak light intensity until the light level increased again resulting in a monotonically increasing light curve) for sunrise identification, and the reverse between midday and midnight for sunset identification. Sunset events were then advanced by 1 minute (BAS geolocators) or 4 minutes (Intigeo geolocators), as both geolocator types only record the maximum light value every 2 minutes (BAS) or 5 minutes (Intigeo). We did not manually remove any (subjectively deemed noisy) sunrise and sunset events.

Identification of stationary periods. – Stationary periods were identified by a change-point analysis using the function `changeLight` in the R package `GeoLight` [21]. For each resulting stationary period we then calculated the period-specific SEA using `GeoLight`, and its standard error by bootstrapping ($n = 1000$). We verified the estimation of the start/end of stationary periods by comparing estimated arrival time at the breeding site (start of period) with observed arrival time (Appendix 1 Table A1).

Estimation of geographical positions. – For each stationary period we computed geographical positions using `GeoLight`, and using the period-specific SEA. We computed median longitude and latitude estimates because, in most cases, latitudes and longitudes within periods were not normally distributed. Closer to equinox, when daytime and night are of approximately equal duration around 20 March and 22 September at all latitudes, differences in day length become smaller. Because calculated latitude estimates depend on day length they are highly uncertain close to equinox and `GeoLight` does not output latitudes 10 days before and after equinox. Here, we also calculated latitudes from the light data close to equinox, using standard astronomical algorithms [22, see also Ekstrom [23] for details and background on geolocation], and included them when computing the median latitude estimates within periods. To check the general performance of those astronomical algorithms we checked their output against `GeoLight` output using input data away from equinox and found calculated positions nearly identical (up to two decimal places). Including latitudes close to equinox will essentially increase the error for the calculated latitude positions. In contrast to latitude, calculations of longitude

are no less reliable around equinox than at any other time and help determine whether birds remain stationary or move, provided that any movement contains a significant longitudinal component. All positions are given in decimal degrees.

To estimate precision errors of all positions we used Monte Carlo error propagation. Median position errors should reflect SEA uncertainty because SEA and estimated position (latitude) are dependent variables. Monte Carlo error propagation allows propagating the errors from the SEA calibration. We assumed a normal distribution for the calibrated SEA estimate. From the distribution we drew 2000 random SEAs and used those to estimate latitude and longitude during the period from each pair of sunrise and sunset. We used the quantiles of the distribution to estimate the median and errors (99% interval). Accuracy for calculated positions is possible to calculate only by ground-truthing during periods with known position of the birds. We calculated accuracy during stationary periods at the breeding site as a mean error distance between calculated and known positions for all individuals (Appendix 1 Table A2).

Temperature data. – Intigeo-P65C2-7 geolocators also sampled ambient temperature. The temperature sensor was located at the centre of the geocator, thus measuring temperature close to the body and temperature measurements being influenced by body temperature. Temperature was sampled at 5 min intervals and the maximum and minimum value every 4 hours was recorded. We retrieved data from three Intigeo geolocators in 2013.

Northern wheatears are nocturnal migrants. Therefore, we analyse temperatures recorded during the 4-hour periods covering night hours. Those 4-hour periods differed in timing between geolocators because the start of the recording interval depended on the time when the geocator was activated. Since air temperatures are lower at flight altitude than at the ground we assumed that periods in flight are reflected by cold recorded night temperatures, at least during some time periods of the annual cycle. During spring migration, however, birds likely also experience cold ground temperatures at European sites; hence, cold nights may also indicate cold ground temperatures rather than flight.

Because geolocators recorded maximum and minimum temperature during a 4-hour period we can compare the change in both temperatures to derive further details on behaviour. For example, a drop in minimum temperature that is paralleled by a drop in maximum temperature would indicate a change in behaviour linked to a change in microclimate (ambient

temperature) lasting during at least the entire 4-hour period. A drop in minimum temperature only would indicate a change in behaviour during less than the 4-hour period (*i.e.* a short-time drop in temperature shows up in the recorded 4-hour minimum while it does not affect the recorded 4-hour maximum). Such short behavioural changes could be short flights, or short visits away from protected resting places. Wheatears rest in cavities, *e.g.* under rocks, that are sheltered and where temperature is buffered against air temperatures, *i.e.* warmer relative to cold air temperatures and cooler relative to high air temperatures.

To evaluate how temperatures recorded by the geolocators reflect ambient air temperatures we compared air temperature recorded at the Ultuna Climate Station (59°82' N, 17°65' E; http://grodden.evp.slu.se/slu_klimat/index.html) with temperatures recorded by the geolocators (1) while not mounted on bird, *i.e.* before deployment in 2012 and after retrieval in 2013, and (2) while mounted on bird and when the bird was known (confirmed by sightings) to be stationary at its breeding site. While not mounted on bird the geolocators were placed on a roof at about 5 m above ground level at about 200 m from the climate station. On bird the distance to the climate station was 9-14 km. From the hourly minimum and maximum air temperature recorded at the climate station we used the minimum and maximum value, respectively, during 4 hours most closely matching the 4-hour recording period of each geocator.

To illustrate how temperature can be used to confirm or adjust periods when birds are determined stationary or moving from light data alone we plotted minimum and maximum temperature during two 4-hour periods spanning night hours alongside estimated latitude and longitude.

2.2 Migration and travel speed

We measured migration distance by the great-circle distance, *i.e.* the shortest distance between two points measured along on the surface of the Earth. We calculated migration rate as the great-circle distance divided by the total time (whole days) between the breeding site and the wintering site (using the first wintering site for autumn and last for spring migration). We calculated travel speed as the great-circle migration distance divided by the total time on the move (whole days), *i.e.* total migration time (whole days) minus total stationary period time (whole days). We expect these calculations give a general estimate of the minimum speed as birds did not move strictly along straight great-circle lines.

2.3 Statistical analyses

Differences in timings (departure dates) or durations during migration between the sexes or between seasons were analysed using mixed models with sex or season as fixed factor and year as random factor (to account for variation among years) using function `lme()` in the R package ‘nlme’. Mixed models and the function `lme()` were also used to analyse time flexibility during annual cycle: as the relationship between timings or duration during subsequent autumn migration and the timing of breeding (lay date of first egg), or as the relationship between different timings and duration during autumn and spring migration. Those models included sex as fixed factor and year as random factor.

2.4 Ethics statement

Birds were captured with permission from the Swedish Bird Ringing Centre, Swedish Museum of Natural History (permit no. 509). This study was carried out in accordance to the legal and ethical requirements for animal research and approved by the regional Swedish ethical committee (permit Uppsala djurförsöksetiska nämnd Dnr C117/8).

3 Results

3.1 Migration route

After leaving the breeding site all birds followed a southerly route (Fig. 1, Appendix 2 Fig. A1) and then moved through Central Europe with several flight legs, interrupted by short stopovers lasting only up to a few days (range 1-8, median 2). Three birds appeared to have left the breeding site relatively early and then made longer stops of ≥ 10 days south of the breeding area with estimated median positions in Sweden or Poland (bird 5: dates 30-Aug – 15-Sep, latitude/longitude median [99% error interval] = 51.7/12.0 [49.6-53.9/12.0-12.1]; bird 8: 21-Aug – 31-Aug, 53.5/19.0 [52.9-54.1/19.0-19.0]; bird 11: 30-Aug – 09-Sep, 53.3/18.2 [51.6-55.3/18.1-18.2]). Due to latitudinal uncertainty it was not possible to distinguish whether birds crossed the Alps or circumvented them (Fig. 1, Appendix 2 Fig. A1). The birds then moved through northern/central Italy, or south-eastern France, and northern Algeria (Fig. 1, Appendix 2 Fig. A1). While latitude estimates are associated with large errors (because of short stationary periods and/or stationary periods close to the equinox, 99% error intervals up to 2000 km, see also Appendix 3 Table A3), estimates of longitude (99% error intervals up to 210 km) show that most of our wheatears

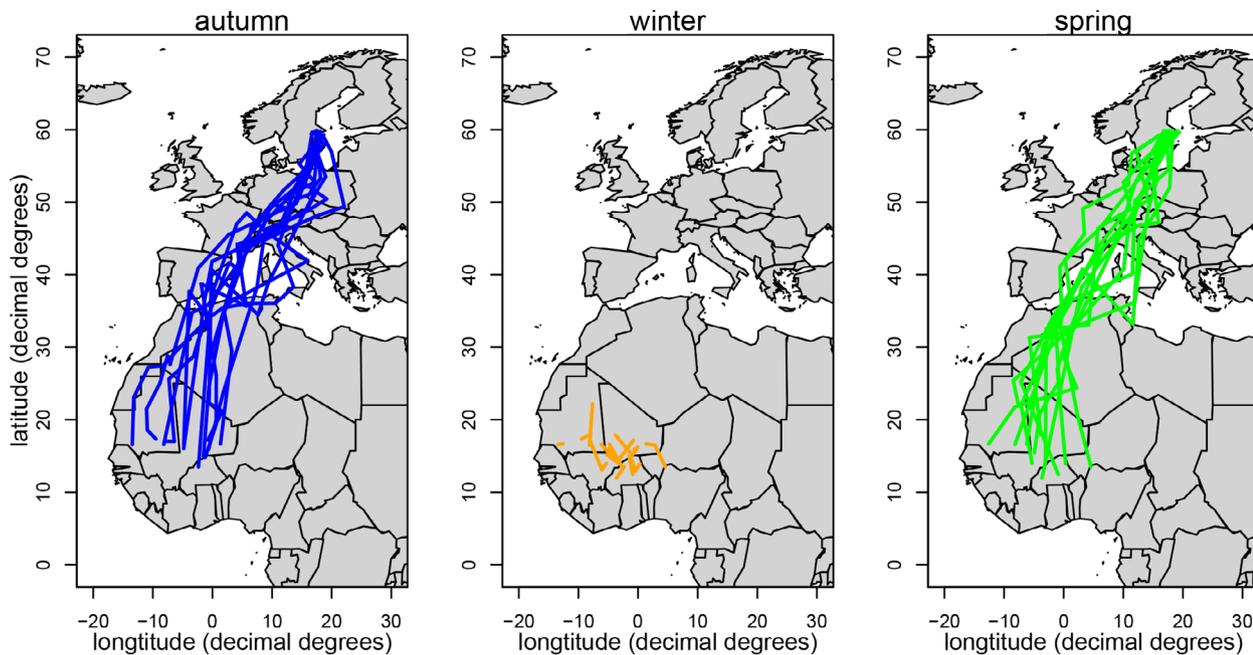


Fig. 1. Migration tracks and winter locations for 12 wheatears. Latitude and longitude are given in decimal degrees. Lines connect median position estimates of stationary periods during autumn migration (blue), spring migration (green), and winter locations (orange).

crossed the Mediterranean Sea on a rather central route, whereas four or five individuals may have followed a more westerly route moving through Spain (Fig. 1, Appendix 2 Fig. A1).

Before crossing the Sahara (a distance of about 1500-2000 km) wheatears spent a longer time period (~30 days) at one or two sites with position estimates indicating locations in northern Algeria (or north-eastern Morocco; “Mediterranean” stopover, Table 1, Appendix 2 Fig. A1, Appendix 4 Table A4). When data indicated a move between two locations that were located in the same area in the Mediterranean region and at which birds spent more than just a few days (typically >10 days) we deemed those locations to belong to a common stopover

“Mediterranean” period (see also Appendix 4 Table A4). Those longer stopovers typically overlapped with the time period spanning two weeks of either side of the equinox, when estimates of latitudes have large errors. Nevertheless, the data indicate that during those longer stopovers the birds made no long-distance movements, *i.e.* stayed in the same area: in those cases when at least part of the longer stopover extended the 14 days on either side of the equinox (total stopover duration indicated by stability in longitude) the estimates of latitude across the whole stopover period were similar. Because of the large latitudinal errors, however, we cannot say with certainty that the stopover location was south of the Mediterranean Sea.

Table 1. Durations during the annual cycle. Breeding duration is estimated number of days spent at the breeding site, *i.e.* time between the observed arrival date in the year of geolocator deployment and estimated departure dates as derived from geolocator data. Observed arrival date was the first day we observed a bird in the field, and all known and potential territory sites of wheatears in the study area were monitored every second to third day during the arrival period. MSO duration is the time spent stationary at the Mediterranean stopover (MSO) locations, and winter duration the time spent at winter locations (see also Appendix Table A4 for dates spent at separate MSO or winter locations). The time spent on migration between the breeding site and the MSO locations in autumn is Br-MSO, in spring MSO-Br. Sahara passage is given as the estimated number of nights between the last stop north and first stop south of the Sahara in autumn, and *vice versa* in spring.

individual	sex	breeding duration [days]	Br-MSO [days]	autumn MSO duration [days]	autumn Sahara passage [nights]	winter duration [days]	spring Sahara passage [nights]	spring MSO duration [days]	MSO-Br
<i>2010-2011</i>									
bird 1	M	101	17	44	4	142	4	20	11
bird 2	F	95	45	19	6	136	1	33	13
bird 3	F	109	22	41	3	158	3	21	6
bird 4	F	n.a. ¹	20	34	4	154	3	29	15
<i>2011-2012</i>									
bird 5	F	122	35	18	4	160	3	17	17
bird 6	F	121	12	44	4	144	3	9	13
bird 7	M	121	19	29	2	163	4	18	16
bird 8	F	119	26	25	3	160	4	27	4
bird 9	M	121	26	20	3	165	3	12	13
<i>2012-2013</i>									
bird 10	M	95	33	29	4	181	3	9	14
bird 11	M	128	33	25	3	145	5	19	10
bird 12	M	106	42	25	5	171	2	9	9
mean±SD	M	--	28.3±9.5	28.7±8.2	3.5±1.1	161.2±15.1	3.5±1.1	14.5±5.1	12.2±2.6
mean±SD	F	--	26.7±11.7	30.2±11.2	4.0±1.1	152.0±9.9	2.8±1.0	22.7±8.8	11.3±5.2
mean±SD	both	112.5±11.8	27.5±10.2	29.4±9.4	3.8±1.1	156.6±13.1	3.2±1.0	18.6±8.1	11.8±3.9

¹: Breeding duration could not be determined due to missing observed arrival date.

The first estimated position south of the Sahara was typically located south or slightly south-west of the last estimated position north of the Sahara. An exception was bird 1 that took a more westerly route to reach a rather westerly wintering area (Appendix 2 Fig. A1). All wheatears spent their winters in areas located in the Sahel belt at locations spreading across an area extending about 2000 km in a west-east direction (distance between individuals with the most distant estimated longitudinal positions), with the majority of wintering areas in southern Mauritania to Central Mali (Fig. 1, Appendix 2 Fig. A1). The data indicate that all but one bird made at least one distinct move in mid-winter. Estimated latitudes indicated moves to a more southern position for eight individuals, while for the other three estimated latitudes for the different wintering sites were similar (Fig. 1, Appendix 2 Fig. A1, Appendix 4 Table A4).

Also during spring migration the birds spent a prolonged time period (~20 days; Table 1, Appendix 4 Table A4) at one or two locations estimated for northern Algeria (or NE Morocco, “Mediterranean” stopover). Birds then continued generally through southern France, with some individuals taking a more westerly route (Fig. 1, Appendix 2 Fig. A1). Similar to autumn migration, spring migration through Central Europe was characterised by several flight legs interrupted by short stops.

3.2 Temperature data

Temperature data recorded by the geolocators while not mounted on bird were limited to short time periods, either before deployment on birds or after retrieval, in early spring (during May). Off-bird geolocator temperature closely reflected ambient air temperature recorded by the local climate station (Appendix 5 Fig. A2), showing that geolocator temperature sensors measured temperature correctly. Temperature data recorded by the geolocators while mounted on bird and when the birds were known to be at the breeding site close to the climate station were also limited to short time periods (mainly during June in 2012, or also early May in 2013). On-bird geolocator temperature correlated to ambient temperature but was clearly influenced by body temperature and buffered against fluctuations in ambient air temperature. For ambient temperatures between 5-20°C on-bird temperature generally varied between 30-37°C (Appendix 5 Fig. A3). On-bird evaluation also shows that in some nights on-bird minimum temperatures are lower than in nights with similar ambient air temperature with a maximum difference in temperature between nights of similar ambient air temperature of about 10°C (Appendix 5 Fig. A3).

Geolocator temperature records were useful to confirm departure dates, flight nights for the Sahara passage, and stationary periods during migration. Temperature was clearly lower during nights for which light data indicated that birds crossed the Sahara (during spring; Fig. 2, for autumn see Appendix 5 Fig. A4 & A6). Both minimum and maximum temperatures were distinctly lower than during the preceding winter period (spring) or preceding prolonged Mediterranean stopover (autumn). In particular minimum temperature usually deviated during both 4-hour night periods, thus indicating a long period during which birds experienced cold ambient temperature. Because departure from the winter area was often close to the equinox when estimates of latitude are highly uncertain temperature data was particularly useful during those time periods when temperatures clearly indicated behavioural changes. This is exemplified by bird 10 for which light data suggests departure from the winter area during the equinox period but a return to a location south of the Sahara before departing on spring migration about two weeks later (Appendix 4 Table A4). Recorded temperatures suggest that the bird indeed spent several nights in flight after the first departure and again after the second departure, and the temperature pattern between the two departures was matching the pattern during the winter period (Fig. 2) suggesting similar behaviour and location as during the winter. Equinox periods also often overlapped with the time periods during which birds were determined stationary at their Mediterranean stopover (see above). Those prolonged stopover periods are also largely corroborated by the temperature data showing periods with fairly stable minimum and maximum temperatures (Fig. 2, Appendix 5 Fig. A4-A6). Temperature data also confirmed winter movements. Temperature was generally very stable during the winter period (Fig. 2, Appendix 5 Fig. A4 & A5). Minimum temperature dropped, however, during single nights corresponding to shifts in both latitude and longitude as determined from light data (Fig. 2, Appendix 4 Table A4, Appendix 5 Fig. A4).

While birds were moving through Europe (as determined from light data) minimum temperature varied strongly between nights (Fig. 2, Appendix 5 A4-A6). Maximum temperature deviated for only a few nights, and often only during one of the two 4-hour periods. While deviations for both maximum and minimum temperatures during the same night suggest a flight period, deviations in minimum temperature only must be interpreted more cautiously. During this part of the migration birds often experience cold temperature at the ground, and lower minimum temperature may also result from birds leaving their shelter during short time intervals (similar to lower temperature during some nights during the on-bird evaluation period, see above).

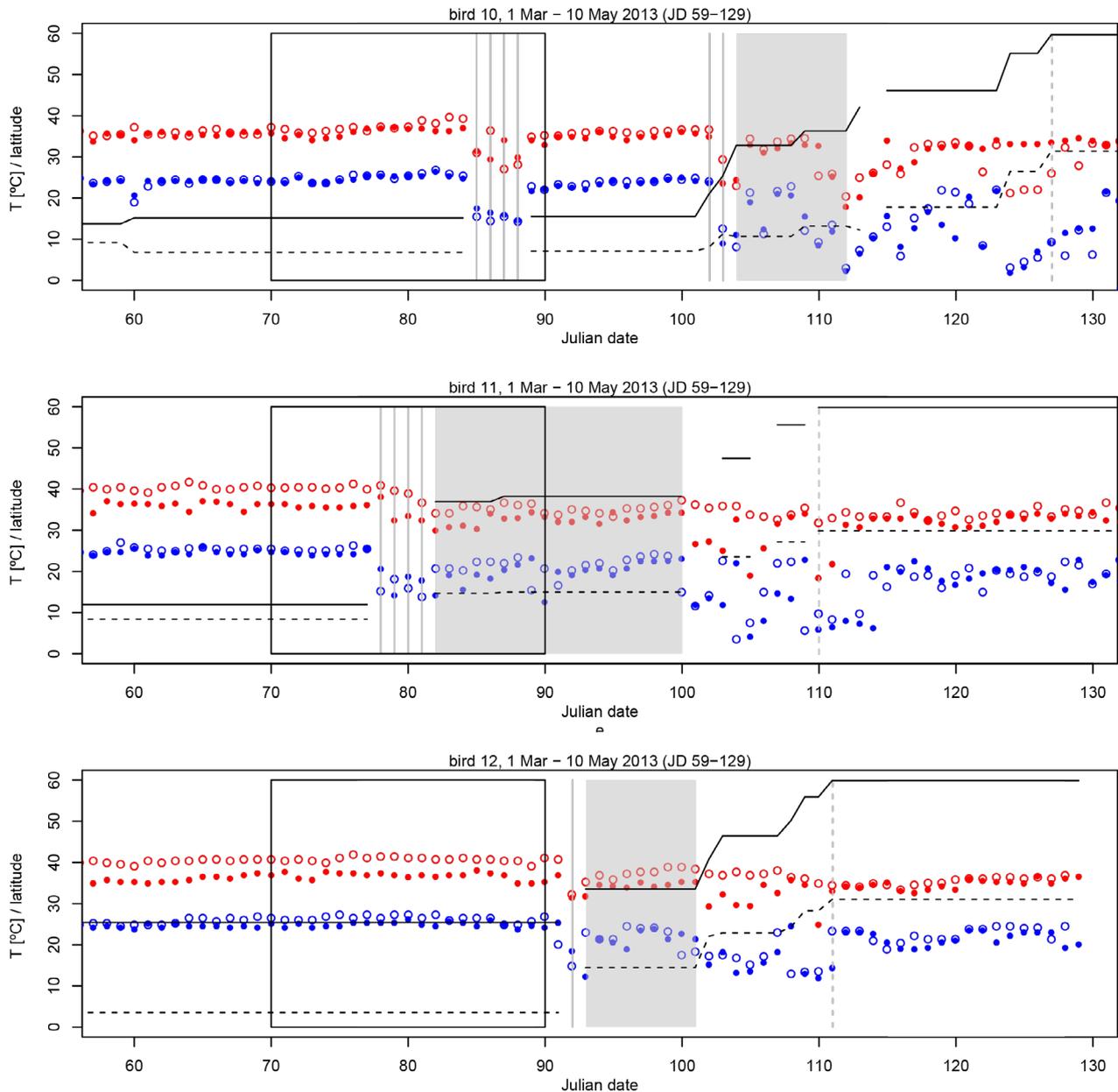


Fig. 2. Temperature during spring migration 1 March – 10 May 2013. Minimum (blue) and maximum (red) temperature recorded by the three Integeco geolocators are shown along median latitude (solid line) and median longitude (dashed; in decimal degrees) as determined from the light data. Temperature data are shown for two 4-hour recording intervals (see Methods) that coincide (at least partly) with hours during early (open symbol) or late (filled) night. The 4-hour recording periods were for bird 10: 22:08-02:08 and 02:08-06:08, bird 11: 23:49-03:49 and 03:49-07:49, bird 12:18-04:18 and 04:18-08:18. For better viewing minimum temperature is shown as recorded value-10, and longitude as median longitude+15. The open rectangle shows the time period spanning from 10 days before to 10 days after equinox on 20 March. Vertical grey lines mark dates determined for Sahara crossing (solid lines) and arrival at the breeding area (dashed). The grey rectangle marks the time period when birds were determined stationary during their Mediterranean stopover (see Results).

3.3 Annual cycle

Wheatears left the breeding area in mid-August (Appendix 4 Table A4). They made several (5-8, median 6) short movements and stopovers through central Europe (in total 17-45 days in the autumn) before their stopover in the

Mediterranean region. Here they stayed 18-44 days before crossing the Sahara during 2-6 nights (mean=3.8±1.1 SD; Table 1, Appendix 4 Table A4). In spring, wheatears crossed the Sahara during 1-5 nights (mean=3.8±1.0 SD, Table 1, Appendix 4 Table A4), spent 9-33 days at the Mediterranean stopover, and moved with short stopovers

to the breeding area during 4-16 days. The total time spent on migration during the autumn was 49-72 days, and 20-48 days in spring.

Since the longer stopover in the Mediterranean region was often close to or overlapping with the equinox estimated stopover durations have to be treated cautiously; the data indicate, however, that the birds made no long-distance movements (see above). Temperature data from at least two of the three birds that were carrying Intigeo geolocators show distinctly lower temperatures (expected during flight nights) during the few days preceding and following, but generally not during, the determined stationary period (see above).

Individuals reached the wintering location between early and late October, with some individuals clustering around similar dates within the same year (Appendix 4 Table A4). The birds started spring migration departing from the wintering location between early March and early April (Appendix 4 Table A4). Spring departure from the wintering location was close to equinox (Appendix 4 Table A4) but clear shifts in longitude allowed confident determination of departure dates. The temperature data from the three individuals tagged with the Intigeo geolocators show that a long period with fairly constant temperature during the night hours was followed by a few nights with clearly reduced minimum temperature, indicating nights during which birds migrated (Fig. 2; see above).

Over the full annual cycle the wheatears spent on average 113 ± 12 SD days (31% of a year) at the breeding site, 157 ± 13 SD days (43% of a year) at the wintering location(s), and 61 ± 8 SD days on migration in autumn and 33 ± 9 SD days in spring (total migration time: 26% of a year, data on durations for each individual can be found in Table 1, Appendix 4 Table A5).

Sex differences: Males and females did not significantly differ in migration duration in either autumn or spring although estimates indicate that there was a tendency for males to migrate faster (time between the breeding area and the Mediterranean stopover, autumn: estimate(male) = -0.36 ± 6.28 SE, $df=8$, $t=-0.05$, $p=0.95$, spring: 0.83 ± 2.37 SE, $df=8$, $t=0.635$, $p=0.73$; the Mediterranean stopover duration, autumn: -1.50 ± 5.67 SE, $df=8$, $t=-0.27$, $p=0.08$, spring: -6.60 ± 4.14 SE, $df=8$, $t=-1.59$, $p=0.15$; total migration duration, autumn: -4.69 ± 4.31 SE, $df=8$, $t=-1.09$, $p=0.31$, spring: -6.18 ± 4.66 SE, $df=8$, $t=-1.32$, $p=0.22$; Table 1, Appendix 4 Table A5). Similarly, departure and arrival times were not significantly different among those 12 individuals (departure from breeding grounds: estimate(male) = -2.67 ± 4.48 SE, $df=8$, $t=-0.56$, $p=0.57$; arrival at winter area: estimate(male) = -5.30 ± 3.90

SE, $df=8$, $t=-1.36$, $p=0.21$; departure from winter area: estimate(male) = -1.67 ± 5.02 SE, $df=8$, $t=-0.33$, $p=0.75$; arrival at breeding area: estimate(male) = -3.50 ± 4.52 SE, $df=8$, $t=-0.78$, $p=0.46$).

Seasonal differences: There were clear differences between the seasons, with spring migration being faster than autumn migration. During spring migration all durations were shorter (time between breeding area and Mediterranean stopover: estimate(spring) = -15.75 ± 3.16 SE, $df=20$, $t=-4.99$, $p<0.001$, Mediterranean stopover: -10.83 ± 3.18 SE, $df=20$, $t=-3.41$, $p=0.003$, total migration duration: -27.83 ± 3.06 SE, $df=20$, $t=-9.10$, $p<0.001$; Table 1, Appendix 4 Table A5), as was the time spend travelling (total number of days during migration - number of days of estimated stationary periods; estimate(spring) = -3.17 ± 0.98 SE, $df=20$, $t=-3.24$, $p=0.004$; Appendix 4 Table A5).

Time flexibility during annual cycle: Birds breeding late in the season may be expected to depart relatively late from the breeding ground if the time needed to prepare for migration (e.g. time for complete post-breeding moult) is relatively inflexible, or migrate more slowly if later breeders are of lower quality or have lower body condition due to spending more parental effort when seasonal conditions had deteriorated. We did not find a relationship between the timing of breeding (lay date of first egg) and timings during subsequent autumn migration ($y \sim \text{lay date} + \text{sex} + (1|\text{year})$): departure time from the breeding ground (lay date estimate = -0.27 ± 0.37 SE, $df=7$, $t=-0.73$, $p=0.490$), Mediterranean stopover duration (0.17 ± 0.47 SE, $df=7$, $t=0.36$, $p=0.727$), or total autumn migration duration (-0.08 ± 0.35 SE, $df=7$, $t=-0.23$, $p=0.828$). All geocator birds successfully raised fledglings in the deployment year, which means that those relationships are not affected by variations in termination of breeding and/or duration of parental effort spent.

Birds departing late may be expected to migrate faster if it is important to arrive early at the wintering ground (e.g. competition for sites). In autumn the wheatears showed some flexibility in the speed of migration, showing shorter migration duration after a late departure; although this seemed not enough to compensate fully for a late departure from the breeding ground as there was a tendency that a later departure also meant a later arrival at the wintering grounds (Table 2). Autumn migration duration was, however, not related to duration of the long Mediterranean stopover, but the Mediterranean stopover was shorter after a longer time spent since the departure from the breeding ground (Table 2).

The birds seemed to be more flexible in adjusting spring migration duration: later departing individuals had shorter migration duration, without a relationship

between departure from the wintering grounds and arrival at the breeding ground (Table 2). Variation in spring migration duration was clearly related to Mediterranean stopover duration (Table 2).

3.4 Migration distance and speed

Calculated distances are only indicative of the general pattern as they do not account for uncertainty in position estimates and exact routes travelled between two locations are unknown. The birds travelled a total great-circle distance of 5162 ± 139 SD km between their Swedish breeding area and their wintering area (distance to first winter stop). This corresponded to an average migration rate of 86 ± 12 SD km/day during the autumn, and 167 ± 39 SD km/day during the spring (Appendix 4 Table A5). When only considering travel nights, *i.e.* excluding number of days determined stationary from migration duration, travel speeds were calculated as 492 ± 132 SD km/day during the autumn and 711 ± 192 SD km/day during the spring.

4 Discussion

4.1 Stopover duration

Recent geolocator studies have shown prolonged stopovers of durations that have been regarded as extending beyond the expected time needed for refuelling [5] and here we find similar results for wheatears from a Swedish population. During migration the wheatears

appeared to spend a long time stationary (on average in autumn: 51 of 61 days, spring: 25 of 33 days), including a several week-long period at one or two locations located in the same area in the Mediterranean region during both autumn and spring migration. Although latitudes of the locations of the lengthy Mediterranean stopover were highly uncertain, data from wheatears breeding in Germany [12] corroborate our data indicating stopovers in Africa north of the Sahara. Areas in northern Africa north of the Sahara are generally assumed to be used as stopover area for many species in both autumn and spring [24,25,26].

Geolocator data from the German breeding population indicate that those wheatears make similar prolonged stopovers [12], and also wheatears from an Alaskan breeding population spent about two weeks during autumn in a restricted area on their route to eastern Africa [13]. While some passerine species show fast migrations with no or only short stopovers (*e.g.* [27]), other species make longer stopovers of several weeks (autumn: [28-32], spring: [33,34]). Those stopovers may be needed to fuel up before, or recovering and refuelling after, a passage through inhospitable areas, but these long stops often exceed the time for migratory refuelling expected from energetic models [2], or the time likely to be forced staying by poor weather. Birds may partly make use of locally favourable conditions before continuing migration, and some authors have called these prolonged stopovers short-term residency periods [30,35].

A large portion of the Mediterranean stopover duration in autumn (18-44 days, average 29) is needed to prepare (fuelling) for the Sahara passage, as birds most

Table 2. Relationships between timing and duration during autumn and spring migration. Relationships were analysed by mixed models, all including sex as fixed factor and year as random factor to account for variation among years ($y \sim x + \text{sex}$, random= ~ 1 year) using function `lme()` in R package ‘nlme’. All $N=12$, $df=7$. arrival_w , arrival_b : arrival date at winter or breeding site, departure_w , departure_b : departure date from winter or breeding site, MSO duration: sum of number of stationary days at Mediterranean stopover, time to/from MSO: sum of number of days between departure from breeding site and arrival at Mediterranean stopover area, or *vice versa*.

model $y \sim x$	time or duration effect			sex effect (male)		
	estimate \pm SE	t	p	estimate \pm SE	t	p
<i>autumn</i>						
$\text{arrival}_w \sim \text{departure}_b$	0.44 \pm 0.22	2.01	0.084	-5.29 \pm 3.50	-1.51	0.174
migration duration $\sim \text{departure}_b$	-0.56 \pm 0.22	-2.52	0.040	-5.29 \pm 3.50	-1.51	0.174
MSO duration \sim time to MSO	-0.88 \pm 0.15	-5.86	<0.001	-2.36 \pm 3.08	-0.77	0.469
migration duration \sim MSO duration	0.23 \pm 0.22	1.07	0.321	-4.93 \pm 4.28	-1.15	0.187
<i>spring</i>						
$\text{arrival}_b \sim \text{departure}_w$	0.11 \pm 0.30	0.40	0.704	-3.30 \pm 3.74	-0.70	0.509
migration duration $\sim \text{departure}_w$	-0.64 \pm 0.22	-2.92	0.022	-8.23 \pm 3.49	-2.36	0.050
time from MSO \sim MSO duration	-0.07 \pm 0.19	-0.36	0.732	0.29 \pm 2.92	0.10	0.926
migration duration \sim MSO duration	0.98 \pm 0.17	5.80	<0.001	0.86 \pm 2.62	0.33	0.754

likely do not refuel during the passage [36]. To cross a similar barrier without possibility to refuel wheatears belonging to the Icelandic/Greenlandic subspecies *O. o. leucorhoa*, stopping over on Helgoland during spring migration and preparing for an oversea flight to reach Greenland, had a high rate of body mass increase (1.7 g/day) and more than half of those birds stayed for up to 12 days, regularly increasing their body mass by about 40-100% of their fat-free body mass [37,38]. The heavier of those birds matched wheatears departing from Greenland in autumn with an estimated flight range of at least 3400 km [39]. Wheatears without supplementary food during stopover are assumed to have somewhat lower rates of body mass increase [40] and according to [41] fuel deposition rate for passerines of the size of wheatears may be assumed about 1g/day. Assuming a rate of body mass increase of 1.0 g/day wheatears would need about 10-20 days to increase their body mass by about 50-100%. Thus, the time needed to fuel up before the autumn crossing of the Sahara (ca. 2000-2500 km, or up to 3000 km including the Mediterranean Sea) can be expected to be up to 20 days. This estimate matches the time needed for fuelling observed in the slightly smaller garden warbler *Sylvia communis* (fat-free body mass = 16 g) stayed 13-20 days on Crete to fuel up from small fuel loads before crossing the Sahara [42].

For spring migration it is less clear how much time the birds need to refuel and restore body condition after the Sahara passage. Intake rate may be physiologically limited upon arrival to a stopover site and birds may need to rebuild the digestive system (up to 2-3 days in blackcaps *Sylvia atricapilla*: [43,44], or white-crown sparrows *Zonotrichia albicollis*: [45]), although search and settlement costs (including potential recovery from physiological limitation) seem to be negligible in wheatears [13]. Moreover, wheatears are likely to be able to refuel on the way north in various habitats, and they move through Europe with frequent short stopovers not needing large fuel loads. Northern wheatears generally show low fuel loads at different stopover sites in Europe [46], and the majority of Scandinavian wheatears observed during spring migration on Helgoland had low fat scores, a body mass only slightly greater than fat-free body mass and departed quickly and irrespective of refuelling and weather conditions [37]. Similarly, in other species stopover time in spring seem less related to the bird's fuel stores (e.g. [47]).

Based on the above, it seems unlikely that all of the Mediterranean stopover duration is needed to either prepare for the Sahara passage in autumn, or to recover from the Sahara passage in spring. Prolonged stopovers

have been suggested to result from using an area providing important resources for fuelling subsequent rapid migration [34]. Alternatively, we suggest that the prolonged stopover may be partly a strategy of using areas with optimal foraging conditions at a time when foraging conditions in the wintering areas have deteriorated (in the Sahel 6-7 months after the last rain season [48]) but are still less favourable further north (see also [49]). Thus, prolonged stops may optimise resource use similar to the use of multiple winter sites where birds follow the rains (e.g. [35], see also [50]), or similar to following the "green wave" in geese [51], perhaps following a prior expectation about the spatial and temporal occurrence of resources (see also [3]). During autumn, although departure is favoured when autumn conditions (e.g. food availability) in the breeding area have deteriorated (see also [27]), it is less clear why earlier arrival at the wintering site is not favoured, given that foraging conditions in the Sahel deteriorate from October onwards. Future studies of stopover ecology at the stopover sites are needed to resolve those questions. Regardless, given that stopovers extend the time needed for refuelling they may allow adjustment of migration duration *en route* if conditions at breeding and/or wintering sites change.

4.2 Population comparisons

The annual cycle of our Swedish wheatears was very similar to that of wheatears from a German breeding population [12] with an about 1000 km shorter distance between the breeding and wintering locations. Leaving the breeding area at a similar time the Swedish birds reached the wintering location after a slightly longer time, left the wintering location somewhat later but had very similar spring migration duration (Table 3). They spent a similar time at the wintering grounds, and slightly shorter time at the breeding grounds (Table 3). They also showed similar migration rate (Table 3). Hence, the difference in migration distance (about 20% of the total distance for the Swedish population) did not seem to exert a noticeable constraint on the Swedish wheatears' time schedule.

In comparison to wheatears breeding in Alaska with a 3-fold migration distance, those wheatears breeding in Europe were, however, clearly less time limited. This was expressed in higher (about 2-fold) overall migration rate of the Alaskan wheatears in autumn and spring (Table 3, [13]). The time constraint was mainly expressed during spring migration: while during autumn estimated absolute stopover times for our Swedish wheatears were not very different from Alaskan wheatears (sum of days for shorter stopovers: about 22 vs. 20-25, lengthy stopover in Mediterranean region or close

to Caspian Sea, respectively: about 29 vs. 18-35 days), during spring migration Alaskan wheatears made shorter stopovers (only few short stopovers with longest lasting 8 days [13] vs. Swedish wheatears including a lengthy stopover of about 19 days). These comparisons indicate that in particular in spring there is a stronger selection for faster migration in the more time constrained population. These comparisons also show that Alaskan wheatears, covering several thousand kilometres without a longer stopover, can refuel during very short times, suggesting that shortening of stopover time for European wheatears is possible.

4.3 Migration schedule

As for many bird species [5,50], and the German and Alaskan wheatears [12,13], spring migration was faster than autumn migration. In spring it is expected that birds benefit from early arrival [52,53,54] and therefore increase their overall speed of migration by optimising fuel deposition rates to decrease total stopover time [55]. Indeed, our data indicate that the shorter migration duration in spring was mainly due to a decrease total stopover time. Shorter stopovers made spring migration on average faster than autumn migration also in several other species [30, 31,56], including Alaskan wheatears [13].

Spring migration duration seemed largely determined by the time spent at the Mediterranean stopover. Thus, individual adjustments of spring migration duration will be mainly possible by adjusting the Mediterranean stopover duration. Indeed, there was evidence for such flexibility as there was no correlation between winter departure and spring arrival dates (similar to [31]; but different to several studies where winter departure dates were the strongest predictor of spring arrival dates [5]). Further, late departing birds had shorter migration duration. Whether individuals can shorten the Mediterranean stopover

and therefore spring migration duration will, however, depend on what mainly determines stopover duration: physiological constraint determining the time needed to refuel (little flexibility), food availability determining the time needed to refuel (shorter duration with increased food availability), or limiting conditions further north (shorter duration with improved foraging conditions and hence lower cost of departing earlier, see also above).

A common pattern in many species is the earlier migration (arrival at the breeding ground) of males. Here we did not find a significant difference between the sexes, although our data weakly indicate that males may arrive earlier at the winter sites and have shorter migration duration. The sex difference in arrival time at the breeding ground is, however, relatively small for our population (males on average 3.6 days earlier [57]). Thus, finding significant differences either in departure times during migration or in migration duration will require larger sample sizes.

4.4 Temperature data

Temperature recorded by geolocators was a useful complement to light data, in particular during time periods close to equinox when estimates of latitude are highly uncertain. During equinox when latitude estimates are uncertain and when birds may move in a mainly north-southerly direction (*i.e.* no or only small change in longitude) temperature data indicate behavioural changes that may correspond to flight periods and can thus confirm shifts in position estimates.

When provided with sufficient temporal resolution temperature data can also inform about duration of behavioural changes. Here, colder temperatures during both night periods suggest flight durations of up to eight hours. However, one of the night periods partly overlapped with evening or morning hours when birds

Table 3. Population comparison of migration data. Summary of migration data from wheatears breeding Sweden (this study, $n=12$), Germany (Rhineland-Palatinate, $n=5$, [12]) and Alaska ($n=3$, [13]).

	Sweden	Germany	Alaska
approximate migration distance [km]	5000	4000	15000
time spent at breeding area [days]	mean=113	mean=130	ca. 87
departure dates from breeding area	05-Aug-29-Aug	15-Jul-20-Aug	18-Aug-20-Aug
autumn migration duration [days]	mean=61	mean=48	ca. 91
total autumn migration rate [km/days]	mean=83	mean=88	mean=160
time spent at winter area [days]	mean=157	mean=147	ca. 131-141
departure dates from wintering area	03-Mar-12-Apr	25-Feb-06-Mar	29-Mar-08-Apr
spring migration duration [days]	mean=33	mean=36	ca. 46-56
total spring migration rate [km/days]	mean=167	mean=126	mean=257

likely were resting on the ground, hence if temperature only dropped during one of the night periods (the one not overlapping with evening or morning hours) this does not necessarily mean that birds spent less time in flight. Furthermore, on-bird evaluation showed that recorded minimum temperature was lower during some nights despite similar ambient air temperature. This variation was likely due to changes in bird behaviour that exposed the bird to colder microclimate during at least a portion of the 4-hour recording period. During the on-bird evaluation period when birds were stationary at their breeding sites those temporarily lower temperatures unlikely reflect long-distance flights, instead such drop in minimum temperature may result from a bird temporarily leaving a sheltered resting place. This showed that separation of distance flights from short-time movements between different microclimate can be difficult, especially during time periods when birds experience locally cold ambient air temperatures (e.g. during spring and autumn while travelling through Europe). Clearly, records with a higher temporal resolution would be more informative, allowing to distinguish behavioural changes lasting short or longer time, and as such separation of likely distance flights from small local movements. Furthermore, calibration of temperature data against observed behaviours of the birds would help interpreting recorded temperature patterns. Alternatively, accelerometer data of high temporal resolution may provide more easily interpretable data to distinguish between different activities and their durations [8].

4.5 Wintering area

Wheatears from our population breeding in southern central Sweden spent the winter in similar areas in the Sahel as wheatears breeding in south-western Germany, the Netherlands and the Swiss Alps ([12,58], C. Meier, unpublished data). Individuals from different breeding populations overlapping in their wintering area is a common pattern (e.g. [59,60,61]; but see e.g. [62], nightingales *Luscinia megarhynchos* from separate breeding populations with limited overlap of wintering areas). As found for the wheatears from the German population [12] and from the Alps (C. Meier, unpublished data) our 12 birds wintered at locations spread out over a large area, with winter locations of individuals with the most distant estimated longitudinal positions located about 2000 km apart. This pattern, with individuals from one breeding population spreading out over a large wintering area has now been found in several passerine species (e.g. [31,33]; see also [63]). Thus, migratory

connectivity (spatial connectedness of populations between seasons of the annual cycle [64]) is weak for those populations of wheatears, with individuals from one breeding population spreading out over separate winter 'populations' and wintering areas of different breeding populations overlapping. This conclusion may appear in contrast to the classification of wheatears as having strong connectivity by McKinnon et al. [5]. However, defining migratory connectivity is partly a matter of scale and McKinnon et al. [5] referred to much larger spatial scales with European and Alaskan populations wintering separated from each other in Western and Eastern Africa.

Our Swedish wheatears seemed to make distinct winter movements which were directed towards more southerly locations. Those movements may follow the change in foraging conditions (see also e.g. [35,65]) during the winter stay as more northern locations receive less rain and rains retreat back south earlier during the rainy season during June-August, which means that those northern locations become drier sooner, leading to deteriorating foraging conditions [48]. Wheatears are known to be territorial during winter [66], but they could relocate territories. Latitudinal movements should be interpreted with caution as they may be artefacts resulting from seasonal changes in habitat or weather, or from behavioural changes. Observed shifts in latitudinal positions (and underlying sunrise and sunset) were, however, abrupt rather than changing gradually as would be expected from seasonal habitat or weather changes. We can neither think of a behavioural change leading to such an abrupt shift and remaining constant after the change. Furthermore, clear shifts in latitude were associated with shifts in longitude (Appendix 4 Table A4), and for the three birds equipped with Integeogeo locators positional shifts were associated with temporary drops in temperature (see above) Similar results of change in winter location presumably following changes in seasonal resource availability have been found in other geolocator studies; suggesting that multiple winter sites may be fairly common (e.g. veery *Catharus fuscescens* wintering in the Amazon Basin [65]; great reed warblers *Acrocephalus arundinaceus* in western Africa [31], nightingales in eastern Africa [35], see review [5]).

4.6 Geolocator effects

With respect to migration rate, travel speed and number and duration of stopovers it should be remembered that geolocators can infer costs in terms of energy expenditure that can affect behaviour and performance during migration and, e.g., result in later arrival and/or delayed breeding time [17,67,68]. Thus, individuals fitted with

geolocators may not always correctly reflect behaviour and strategies of uninfluenced individuals; they may need more or longer stopovers that can lead to longer migration duration. Unfortunately, we do not know the size of such geolocator effects during migration [67]. However, comparisons between populations should be valid given a relatively similar size and weight of the geolocators.

5 Conclusion

Our data on wheatears from a Swedish breeding population provide new information on migration duration and stopover behaviour for a long-distance migrant, and population comparison as a first step to relate migration schedules to migration constraints. Our data show that wheatears, like several other species, make relatively long stopovers. Currently, it is unclear what determines long stopovers and overall migration duration. Future studies on more species should be completed in order to relate stopover and migration durations to variation in ecological conditions to identify the ecological factors that select for fast or slow migration. Published geolocator studies show that there is strong individual consistency in migration schedules (timings) in some species, suggesting little individual flexibility, while other species seem flexible adjusting timings in response to, e.g., weather conditions [5,30]. Our results show that despite time constraints, particularly during spring migration, the migration schedule of Swedish wheatears is partly flexible and may allow adjustments to changing conditions. Further studies are needed to identify the factors that determine flexibility and duration of migration schedules; to allow identification of species and populations most at risk by changing environmental conditions.

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References

- [1] Dingle H., *Migration. The Biology of Life on the Move*, 2nd ed., Oxford University Press, 2014
- [2] Alerstam T., Bird flight and optimal migration, *Trends Ecol. & Evol.*, 1991, 6, 210–215
- [3] Alerstam T., Optimal bird migration revisited, *J. Ornithol.*, 2011, 152 (Suppl 1), S5–S23
- [4] Kaiser A., Stopover strategies in birds: a review of methods for estimating stopover length, *Bird Study*, 1999, 46(S1), S299–S308
- [5] McKinnon E.A., Fraser K.C., Stutchbury B.J.M., New Discoveries in Landbird Migration using Geolocators, and a Flight Plan for the Future, *Auk*, 2013, 130, 211–222
- [6] Stanley C.Q., MacPherson M., Fraser K.C., McKinnon E.A., Stutchbury B.J.M., Repeat Tracking of Individual Songbirds Reveals Consistent Migration Timing but Flexibility in Route, *PLoS ONE*, 2012, 7(7), e40688, DOI: 10.1371/journal.pone.0040688
- [7] Conklin J.R., Battley P.F., Potter M.A., Absolute Consistency: Individual versus Population Variation in Annual-Cycle Schedules of a Long-Distance Migrant Bird. *PLoS ONE*, 2013, 8(1), e54535. DOI: 10.1371/journal.pone.0054535
- [8] Liechti F., Witvliet W., Weber R. Bächler E., First evidence of a 200-day non-stop flight in a bird, *Nature Communications*, 2013, 4, 2554. DOI: 10.1038/ncomms3554
- [9] Weimerskirch H., Wilson R.P., Guinet C., Koudil M., Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean, *Marine Ecology Progress Series*, 1995, 126, 299–303
- [10] Thiebot J.-B., Pinaud D., Quantitative method to estimate species habitat use from light-based geolocation data, *Endangered Species Research*, 10, 341–353.
- [11] Fransson T., Hall-Karlsson S., *Swedish Bird Ringing Atlas. Volume 3, Passerines*, Swedish Museum of Natural History, 2008
- [12] Schmaljohann H., Buchmann M., Fox J.W., Bairlein F., Tracking migration routes and the annual cycle of a trans-Saharan songbird migrant, *Behav. Ecol. Sociobiol.*, 2012, 66, 915–922
- [13] Schmaljohann H., Fox J.W., Bairlein F., Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world, *Anim. Behav.*, 2012, 84, 623–640
- [14] Pärt T., The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe Oenanthe*, *Anim. Behav.*, 2001, 62, 379–388
- [15] Arlt D., Pärt T., Nonideal breeding habitat selection: A mismatch between preference and breeding success, *Ecology*, 2007, 88, 792–801
- [16] Arlt D., Pärt T., Post-breeding information gathering and breeding territory shifts in northern wheatears, *J. Anim. Ecol.*, 2008, 77, 211–219
- [17] Arlt D., Low M., Pärt T., Effect of geolocators on migration and subsequent breeding performance of a long-distance migrant, *PLoS ONE*, 2013, 8(12), e82316, DOI: 10.1371/journal.pone.0082316
- [18] Rappole J.H., Tipton A.R., New Harness Design for Attachment of Radio Transmitters to Small Passerines, *J. Field Ornithol.*, 1990, 62, 335–337

- [19] Lisovski S., Hewson C.M., Klaassen R.H.G., Korner-Nievergelt F., Kristensen M.W., Hahn S., Geolocation by light: accuracy and precision affected by environmental factors, *Meth. Ecol. Evol.*, 2013, 3, 603–612
- [20] R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, 2013, URL <http://www.R-project.org/>
- [21] Lisovski S., Hahn S., Geolight - processing and analyzing light-based geolocation in R, *Meth. Ecol. Evol.*, 2012, 3, 1055-1059
- [22] Meeus J., *Astronomical Algorithms*, Willman-Bell, Inc., Richmond, 1991
- [23] Ekstrom P., An advance in geolocation by light, *Memoirs of the National Institute of Polar Research*, 2004, Special Issue 58, 210-226
- [24] Schaub M., Jenni L., Body mass of six long-distance migrant passerine species along the autumn migration route, *J. Ornithol.*, 2000, 141, 441–460
- [25] Salewski V., Schmaljohann H., Liechti F., Spring passerine migrants stopping over in the Sahara are not fall-outs, *J. Ornithol.*, 2010, 51, 371-378
- [26] Maggini I., Bairlein F., Body condition and stopover of trans-Saharan spring migrant passerines caught at a site in southern Morocco, *Ringling & Migration*, 2011, 26, 31-37
- [27] Jahn A.E., Cueto V.R., Fox J.W., Husak M.S., Kim D.H., Landoll D.V., et al., Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America, *Auk*, 2013, 130, 247–257
- [28] Stutchbury B.J.M., Gow E.A., Done T., MacPherson M., Fox J.W., Afanasyev V., Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics, *Proc. R. Soc. Lond. B*, 2011, 278, 131–137
- [29] Åkesson S., Klaassen R., Holmgren J., Fox J.W., Hedenström A., Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators, *PLoS ONE*, 2012, 7(7), e41195
- [30] Tøttrup A.P., Klaassen R.H.G., Strandberg R., Thorup K., Willemoes K.M., Søgaard Jørgensen P., et al., The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration, *Proc. R. Soc. Lond. B*, 2012, 279, 1008-1016, DOI: 10.1098/rspb.2011.1323
- [31] Lemke H.W., Tarka M., Klaassen R.H.G., Åkesson M., Bensch S., Hassequist D., et al., Annual Cycle and Migration Strategies of a Trans-Saharan Migratory Songbird: A Geolocator Study in the Great Reed Warbler, *PLoS ONE*, 2013, 8(10), e79209, DOI: 10.1371/journal.pone.0079209
- [32] Willemoes M., Strandberg R., Klaassen R.H.G., Tøttrup A.P., Vardanis Y., Howey P.W., et al., Narrow-Front Loop Migration in a Population of the Common Cuckoo *Cuculus canorus*, as Revealed by Satellite Telemetry, *PLoS ONE*, 2014, 9(1), e83515, DOI: 10.1371/journal.pone.0083515
- [33] Eraud C., Rivière M., Lormée H., Fox J.W., Ducamp J.-J., Boutin J.-M., Migration Routes and Staging Areas of Trans-Saharan Turtle Doves Appraised from Light-Level Geolocators, *PLoS ONE*, 2013, 8(3), e59396, DOI: 10.1371/journal.pone.0059396
- [34] Callo P.A., Morton E.S., Stutchbury B.J.M., Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*), *Auk*, 2013, 130, 240–246
- [35] Stach R., Jakobsson S., Kullberg C., Fransson T., Geolocators reveal three consecutive wintering areas in the thrush nightingale, *Anim. Migr.*, 2012, 1, 1-7, DOI: 10.2478/ami-2012-0001
- [36] Schmaljohann H., Liechti F., Bruderer B., Songbird migration across the Sahara – the non-stop hypothesis rejected!, *Proc. R. Soc. Lond. B*, 2007, 274, 735–739
- [37] Dierschke V., Delingat J., Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances, *Behav. Ecol. Sociobiol.*, 2001, 50, 535-545. DOI: 10.1007/s002650100397
- [38] Dierschke V., Mendel B., Schmaljohann H., Differential timing of spring migration in Northern Wheatears *Oenanthe oenanthe*: hurried males or weak females?, *Behav. Ecol. Sociobiol.*, 2005, 57, 470-480
- [39] Ottosson U., Sandberg R., Pettersson J., Orientation cage and release experiments with migratory wheatears (*Oenanthe oenanthe*) in Scandinavia and Greenland: the importance of visual cues, *Ethology*, 1990, 86, 57–70
- [40] Schmaljohann H., Dierschke V., Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*, *J. Anim. Ecol.*, 2005, 74, 131-138
- [41] Lindström Å., Maximum fat deposition rates in migrating birds, *Ornis Scand.*, 1991, 22, 12-19
- [42] Fransson T., Barboutis C., Mellroth M., Akriotis T., When and where to fuel before crossing the Sahara desert—extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*, *J. Avian Biol.*, 2008, 39, 133–138
- [43] Gannes L.Z., Mass change pattern of blackcaps refueling during spring migration: evidence for physiological limitations to food assimilation, *Condor*, 2002, 104, 231-239
- [44] Bauchinger U., Kolb H., Afik D., Pinshow B., Biebach H., Blackcap Warblers Maintain Digestive Efficiency by Increasing Digesta Retention Time on the First Day of Migratory Stopover, *Physiol. Biochem. Zool.*, 2009, 82, 541-548
- [45] McWilliams S.R., Karasov W.H., Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: defining the limits of animal design, *Proc. R. Soc. Lond. B*, 2014, 281, 20140308, DOI: 10.1098/rspb.2014.0308
- [46] Delingat J., Dierschke V., Schmaljohann H., Mendel B., Bairlein F., Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear *Oenanthe oenanthe*, *Ardea*, 2006, 94, 593–605
- [47] Wojciechowski M.S., Yosef R., Pinshow B., Body composition of north and southbound migratory blackcaps is influenced by the lay-of-the-land ahead, *J. Avian Biol.*, 2014, 45, 264-272
- [48] Zwarts L., Bijlsma R.G., van der Kamp J., Wymenga E., *Living on the edge: wetlands and birds in a changing Sahel*, Zeist: KNNV Publishing, 2009
- [49] Limiñana R., Romero M., Mellone U., Urios V., Mapping the migratory routes and wintering areas of Lesser Kestrels *Falco naumanni*: new insights from satellite telemetry, *Ibis*, 2012, 154, 389–399
- [50] Newton I., *The Migration Ecology of Birds*, Academic Press, London, 2008
- [51] Shariatinajabadi M., Wang T., Skidmore A.K., Toxopeus AG, Köllsch A., Nolet B.A., et al., Migratory Herbivorous Waterfowl Track Satellite-Derived Green Wave Index, *PLoS ONE*, 2014, 9(9), e108331, DOI: 10.1371/journal.pone.0108331

- [52] Kokko H., Competition for early arrival in migratory birds, *J. Anim. Ecol.*, 1999, 68, 940–950
- [53] Smith R.J., Moore F.R., Arrival timing and seasonal reproductive performance in a long-distance migratory landbird, 2005, *Behav. Ecol. Sociobiol.*, 57, 231–239
- [54] Verhulst S., Nilsson J.-Å., The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding, *Phil. Trans. R. Soc. Lond. B*, 2008, 363, 399–410
- [55] Schaub M., Jenni L., Stopover durations of three warbler species along their autumn migration route, *Oecologia*, 2001, 128, 217–227
- [56] Nilsson C., Klaassen R.H.G., Alerstam T., Differences in speed and duration of bird migration between spring and autumn, *Am. Nat.*, 2013, 181, 837–845
- [57] Arlt D., Pärt T., Sex-biased dispersal: a result of a sex-difference in breeding site availability, *Am. Nat.*, 2008, 171, 844–850
- [58] van Oosten H.H., Versluijs R., van Wijk R., Two Dutch Northern wheatears in the Sahel: unravelling migration routes and wintering areas, *Limosa*, 2014, 87, 168–172
- [59] Fraser K.C., Stutchbury B.J.M., Silverio C., Kramer P.M., Barrow J., et al., Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore, *Proc. R. Soc. B*, 2012, 279, 4901–4906
- [60] Seavy N.E., Humple D.L., Cormier R.L., Gardali T., Establishing the Breeding Provenance of a Temperate-Wintering North American Passerine, the Golden-Crowned Sparrow, Using Light-Level Geolocation, *PLoS ONE*, 2012, 7(4), e34886, DOI: 10.1371/journal.pone.0034886
- [61] Stanley C.Q., McKinnon E.A., Fraser K., Macpherson M.P., Casbourn G., Friesen L., et al., Connectivity of Wood Thrush Breeding, Wintering, and Migration Sites Based on Range-Wide Tracking, *Cons. Biol.*, 2015, 29, 164–174
- [62] Hahn S., Amrhein V., Zehndindijev P., Liechti F., Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird, *Oecologia*, 2013, 173, 1217–1225
- [63] Cresswell W., Migratory connectivity of Palaearctic–African migratory birds and their responses to environmental change: the serial residency hypothesis, *Ibis*, 2014, published online, DOI: 10.1111/ibi.12168
- [64] Norris R.D., Marra P.P., Seasonal interactions, habitat quality, and population dynamics in migratory birds, *Condor*, 2007, 109, 535–547
- [65] Heckscher C.M., Taylor S.M., Fox J.W., Afanasyev V., Veery (Catharus fuscescens) Wintering Locations, Migratory Connectivity, and a Revision of Its Winter Range using Geolocator Technology, *Auk*, 2011, 128, 531–542.
- [66] Cramp S. (Ed.), *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, Volume V: Tyrant flycatchers to thrushes*, Oxford University Press, New York, 1988
- [67] Constantini D, Møller A.P., A meta-analysis of the effects of geolocator application on birds, *Curr. Zool.*, 2013, 59, 697–706
- [68] Scandolara C., Rubolini D., Ambrosini R., Caprioli M., Hahn S., Liechti F., et al., Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits, *J. Avian Biol.*, 2014, DOI: 10.1111/jav.0041

Published data

The data used in this study, including estimated dates and positions for all stationary periods, are available on Movebank (movebank.org, study name: Oenanthe oenanthe Turdidae Uppsala) and published in the Movebank Data Repository (DOI 10.5441/001/1.nn55rh75).

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