The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration

Anders P. Tøttrup[1,*], Raymond H. G. Klaassen[3], Roine Strandberg[3],
Kasper Thorup[2], Mikkel Willemoes Kristensen[2],
Peter Søgaard Jørgensen[1], James Fox[4,5], Vsevolod Afanasyev[4],
Carsten Rahbek[1] and Thomas Alerstam[3]

[1]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark*
[2]*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark*
[3]*Department of Biology, Lund University, Ecology Building, 22362 Lund, Sweden*
[4]*British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[5]*Migrate Technology Ltd, PO Box 749, Coton, Cambridge CB1 0QY, UK*

The small size of the billions of migrating songbirds commuting between temperate breeding sites and the tropics has long prevented the study of the largest part of their annual cycle outside the breeding grounds. Using light-level loggers (geolocators), we recorded the entire annual migratory cycle of the red-backed shrike *Lanius collurio*, a trans-equatorial Eurasian-African passerine migrant. We tested differences between autumn and spring migration for nine individuals. Duration of migration between breeding and winter sites was significantly longer in autumn (average 96 days) when compared with spring (63 days). This difference was explained by much longer staging periods during autumn (71 days) than spring (9 days). Between staging periods, the birds travelled faster during autumn (356 km d^{-1}) than during spring (233 km d^{-1}). All birds made a protracted stop (53 days) in Sahelian sub-Sahara on southbound migration. The birds performed a distinct loop migration (22 000 km) where spring distance, including a detour across the Arabian Peninsula, exceeded the autumn distance by 22 per cent. Geographical scatter between routes was particularly narrow in spring, with navigational convergence towards the crossing point from Africa to the Arabian Peninsula. Temporal variation between individuals was relatively constant, while different individuals tended to be consistently early or late at different departure/arrival occasions during the annual cycle. These results demonstrate the existence of fundamentally different spatio-temporal migration strategies used by the birds during autumn and spring migration, and that songbirds may rely on distinct staging areas for completion of their annual cycle, suggesting more sophisticated endogenous control mechanisms than merely clock-and-compass guidance among terrestrial solitary migrants. After a century with metal-ringing, year-round tracking of long-distance migratory songbirds promises further insights into bird migration.

Keywords: avian migration; geolocator; passerine; migration speed; phenology; migration routes

1. INTRODUCTION

Billions of songbirds commute thousands of kilometres between temperate breeding sites and the tropics as a natural part of their annual cycle [1,2]. Their small size has long prevented the study of the largest part of their lives, outside the breeding grounds [3,4]. Traditional ring-recovery data, stable isotope analyses and the use of genetic markers have generated much progress in recent years [5,6]. Yet our current knowledge of migration routes and wintering areas, as well as important staging sites of individuals and populations of the vast majority of migrants (particularly songbirds), remains poor [7].

Migratory songbirds fly alone during the night [6,8] (but see [9]). Our present understanding of songbird migration is based on the assumption that an endogenous clock controls birds' movement between breeding and non-breeding areas [10,11]. These movements are believed to include regular stops for refuelling as suitable habitat is available along large parts of the migration routes [1,12], except when birds cross barriers such as the Mediterranean Sea and desert regions, where they move faster with fewer and shorter stops [8,13].

Optimal spring arrival at their temperate breeding sites is believed to be of high importance for individual fitness [14,15], and migrants probably follow their endogenous clock for timing of departure from the wintering area

[11], with some plasticity [13] and adjustment of speed in relation to actual conditions en route [16,17]. Also, males and females seem to follow different strategies for their optimal spring arrival as selection pressures may act differently on males and females [18].

The red-backed shrike *Lanius collurio*, a 30 g, long-distance trans-equatorial Eurasian–African passerine bird, has declined in western Europe and has recently gone extinct from the British Isles [19]. As for other migrants, the requirements and whereabouts of this species during the non-breeding season are poorly known, although there is some information about migration speeds [20], body mass fluctuations [21] and stopover habitats [22]. Here, we use data from miniaturized light-level loggers (geolocators) [23,24] to present a full description in space and time of an entire migratory cycle. Specifically, we analyse and test differences in the temporal (duration, speed and staging) and spatial course of autumn and spring migration for the nine individuals that were tracked.

Ring-recovery analyses have indicated divergent migration routes during autumn and spring in this species, constituting a loop migration [25,26], which is of particular interest for understanding the spatio-temporal control of migration, and to what degree autumn and spring migration habits may evolve independently. For solitary nocturnal passerine migrants, it has traditionally been assumed that control of migration is primarily based on an endogenous clock-and-compass programme during the first outward (autumn) journey. During this first journey, the migrants are assumed to learn cues and acquire skills that are used as complementary mechanisms for the control of the spring return journey and further journeys in the adult life of the birds [5,11]. Analysing differences between autumn and spring migration will help in indicating to what degree such a simple control mechanism, comprising only a sense of time and a predetermined course (or a succession of different predetermined courses) to follow, is sufficient to explain the birds' routes and habits, or if a more elaborate endogenous control system is required to regulate autumn and spring migration in clearly different ways, also including more sophisticated cues of, for example, map/position information and guidance [27,28]. In light of previous studies [11,12,20], we expect that spring migration will be faster when compared with autumn migration, because selection on timing of arrival is believed to act more strongly during spring migration towards the breeding areas [29]. Furthermore, sexual differences in timing are likewise expected because of different selection pressures on males and females [18,30], as well as sex-differentiated migration strategies [31,32]. Our primary objectives are (i) to record and analyse the entire annual migratory cycle for individual long-distance passerine migrants, (ii) to compare and evaluate differences in spatio-temporal behavioural patterns and strategies between autumn and spring migration, and (iii) to investigate possible differences between sexes, as well as timing relationships between individuals in a migratory cohort (tracked during the same annual cycle).

2. METHODS
(a) *Geolocator deployment*
We used archival light-level loggers (geolocators) to reconstruct the migration routes, wintering areas, staging areas, speed and timing of migration of individual red-backed shrikes. This inexpensive system measures and stores light levels that can then be used to calculate latitude and longitude from the sunrise and sunset times, converted to day length and local apparent noon and midnight, respectively [33]. In June and July 2009, 74 adult red-backed shrikes (35 females and 39 males) were trapped, ringed (with a metal ring and a colour ring easing relocation) and fitted with Mk10-S geolocators (1.1 g; developed by the British Antarctic Survey, BAS [33]). In this model, the light sensor is placed on a 0.8 cm stalk in order to raise the sensor above the plumage. Loggers were attached using a leg-loop backpack harness [34].

At logger attachment the birds weighed 25–36.5 g. Thus, the logger represented a maximum of 4 per cent of the body mass. The shrikes were trapped during breeding at three different study sites in southern Scandinavia: Gribskov (55.98° N, 12.33° E) in northern Zealand, Denmark; Vittskövle (55.85° N, 14.18° E) in eastern Skåne, Sweden; and Ottenby (56.23° N, 16.46° E) in southern Öland, Sweden. In May–June 2010, geolocators were retrieved from five males and four females. One additional male bird was re-trapped with a damaged geolocator, one female returned without geolocator and we observed but could not capture at least two other returning birds with geolocators attached (one male and one female). The return rate for geolocator birds was 20 per cent for males (7 of 35) and 15 per cent for females (6 of 39). In three individuals (one male and two females), the geolocator battery got drained during spring migration, resulting in incomplete tracks (electronic supplementary material, figure S1 for individual details).

The weights of the birds when captured in 2009 (prior to the attachment of the loggers) did not differ from their weights in 2010 ($t_{paired} = -0.192$, d.f. $= 9$, $p = 0.852$), and weights of the returning logger birds in 2010 did not differ from other individuals trapped in 2010 ($t = -1.50$, d.f. $= 32$, $p = 0.143$). In birds returning with geolocators, we found earlier timing of breeding in 2010 compared with 2009 ($t_{paired} = 4.09$, d.f. $= 4$, $p = 0.015$) and no difference in breeding performance between years ($t_{paired} = 0.431$, d.f. $= 4$, $p = 0.689$). Furthermore, the mean date for crossing of the Middle East during spring migration was 12 May (range: 20 April–25 May), which falls earlier than the main migration wave (17–27 May) reported from Israel [35]. Overall, we found no evidence that the geolocator attachment affected the migration patterns of the returning individuals.

(b) *Light data analyses*
BAS geolocators such as the Mk10-S record light intensity on an arbitrary scale, ranging from 0 to 64. In order to derive positional data from a light-level registration, the link between a certain light intensity value and the corresponding sun azimuth angle must be established. Throughout this study, we use a single fixed light-level threshold value of 2 to define 'sunrises' and 'sunsets', and this value corresponds to the sun well below the horizon. Unlike most other studies to date, we do not use calibration data (with a known location of the logger) to establish the sun azimuth angle corresponding to the threshold value, but followed the Ekstrom–Hill calibration procedure (see below).

The imprecise clock inside any logger may lose or gain a small amount of time over the deployment period. Assuming such clock drift to be linear between the start and end of

Table 1. Comparison of means in the spatio-temporal course of autumn and spring migration of the red-backed shrike *Lanius collurio*. Means (and s.e.) are given for nine individuals on autumn migration and six individuals on spring migration. *p*-values for comparisons of means and scatter are based on paired *t*-tests ($n = 6$) and an *F*-test ($n = 9$), respectively.

comparison of means	autumn		spring		
	mean	s.e.	mean	s.e.	*p*
total duration (no. days)	95.9	2.6	62.8	2.5	0.0001
total staging time (no. days)	70.7	2.6	9.1	1.4	>0
longest staging period (no. days)	53.0	3.4	7.8	1.0	>0
travel time (no. days)	27.3	2.5	51.8	3.4	0.0009
total distance (km)	9719	202	11 862	152	0.0004
total migration speed (km d^{-1})	101	3	190	7	0.0001
travel speed excl. staging (km d^{-1})	356	31	233	13	0.0221
comparison of scatter	s.d.		s.d.		
longitude at 20° N latitude	4.34		0.86		0.0001

logging, timestamps were accordingly adjusted using the program BASTRAK [36]. Threshold crossing times ('sunrises' and 'sunsets') were identified using the graphical data editor and viewer TRANSEDIT [36]. We visually checked for and removed false twilights caused by shading events. Positions were calculated with BIRDTRACKER software [36], in which threshold crossing times (and the corresponding sun azimuth angle; see below) are assumed to correspond to a specific sun azimuth and used to calculate locations using astronomical algorithms [36]. Latitude is inferred from the length of the solar day/night and longitude from the time of local solar noon/midnight. Through an iterative process, we established the most suitable corresponding sun azimuth value by using that which minimized the difference in latitude either side of the equinox during periods when the birds were stationary (stationary assumed from longitude). This procedure is based on the observation that latitude error increases with increasing mismatch between light threshold value and inferred sun angle. This latitude error is of opposing magnitude either side of an equinox [37,38], and we refer to this as the Ekstrom−Hill calibration procedure. In addition, the sun angle corresponding to our chosen light threshold value was also inferred, in the more traditional manner, from 'calibration' data gathered on the bird at the known breeding location during the breeding period. However, we believe that the Ekstrom−Hill calibration procedure is favourable in this study, as the habitat conditions and behaviour (factors that affect shading) of the shrikes around stationary equinox periods are closer to the average conditions during migration and stopover rather than those during the breeding season. Although different calibration methods can have important effects on the resulting tracks, the overall patterns in space and (especially) time remain very similar (electronic supplementary material, figure S2). The practical accuracy of latitude and longitude obtained from similar geolocators has been reported to be 143 ± 62 and 50 ± 34 km ($\pm 95\%$ CI), respectively [39]. Although the theoretical ideal for light-level geolocation offers accuracy of just a few tens of kilometres; unknown shading factors that are encountered in any practical study (e.g. weather) reduce accuracy. Because it is affected by shading, accuracy will vary between species, habitats, habits and, potentially, with differences in light sensor position on the bird. Both midnight and noon locations were used in our analyses whenever ambient light data showed no obvious shading interference. Data on

latitude were excluded for 21 days before and after vernal and autumnal equinox [40].

(c) *Location data analyses*

We used the terms 'staging periods' and 'staging sites' when birds interrupted migration for more than 5 days, though birds could have moved short distances within a given area. During presumed staging periods and while sedentary during the northern winter, locations were determined by calculating average latitude and longitude for the period. The arrival and departure dates for the staging sites and wintering areas were determined from the two daily estimates for latitude and longitude data. Close to equinoxes, departure and arrival dates were estimated only from longitude data [39]. We defined the minimum duration of migration as the time between the last position at the breeding area and the first position at the wintering site. The course of the migration routes between staging sites and wintering areas was derived directly from 3-day mean positions (shown in electronic supplementary material, figure S1). Overall migration distance was defined as the minimum distance between breeding, staging and wintering sites. We calculated direct (loxodrome) distances between sites, rather than cumulative track distance, as the positioning data were too inaccurate for such detailed analysis, and to avoid effects of missing latitude data close to equinoxes. For the spring migration over the Arabian Peninsula, we fitted the shortest two-leg migration route to the 3-day mean positions (electronic supplementary material, figure S1). Travel speed was calculated as migration distance divided by duration of the migration period. Total speed includes the staging periods. It should be noted that our estimates for distances and speeds are rather conservative (and possibly somewhat underestimated) as we relied on direct distances between sites.

3. RESULTS

We found clear spatio-temporal differences in staging periods, migration distance, and speed between autumn and spring migration strategies in the red-backed shrikes (table 1 and figure 1).

Autumn and spring migration tracks revealed three long-term staging areas: southeastern Europe (autumn; mean duration: 15 days, s.e. = 2.03, range 8−24), Sahelian northeast Africa (autumn; mean: 53 days, s.e. = 3.41, range 34−62) and eastern Africa (spring; mean: 8 days, s.e. = 1.02, range 4−13). While four individuals had an
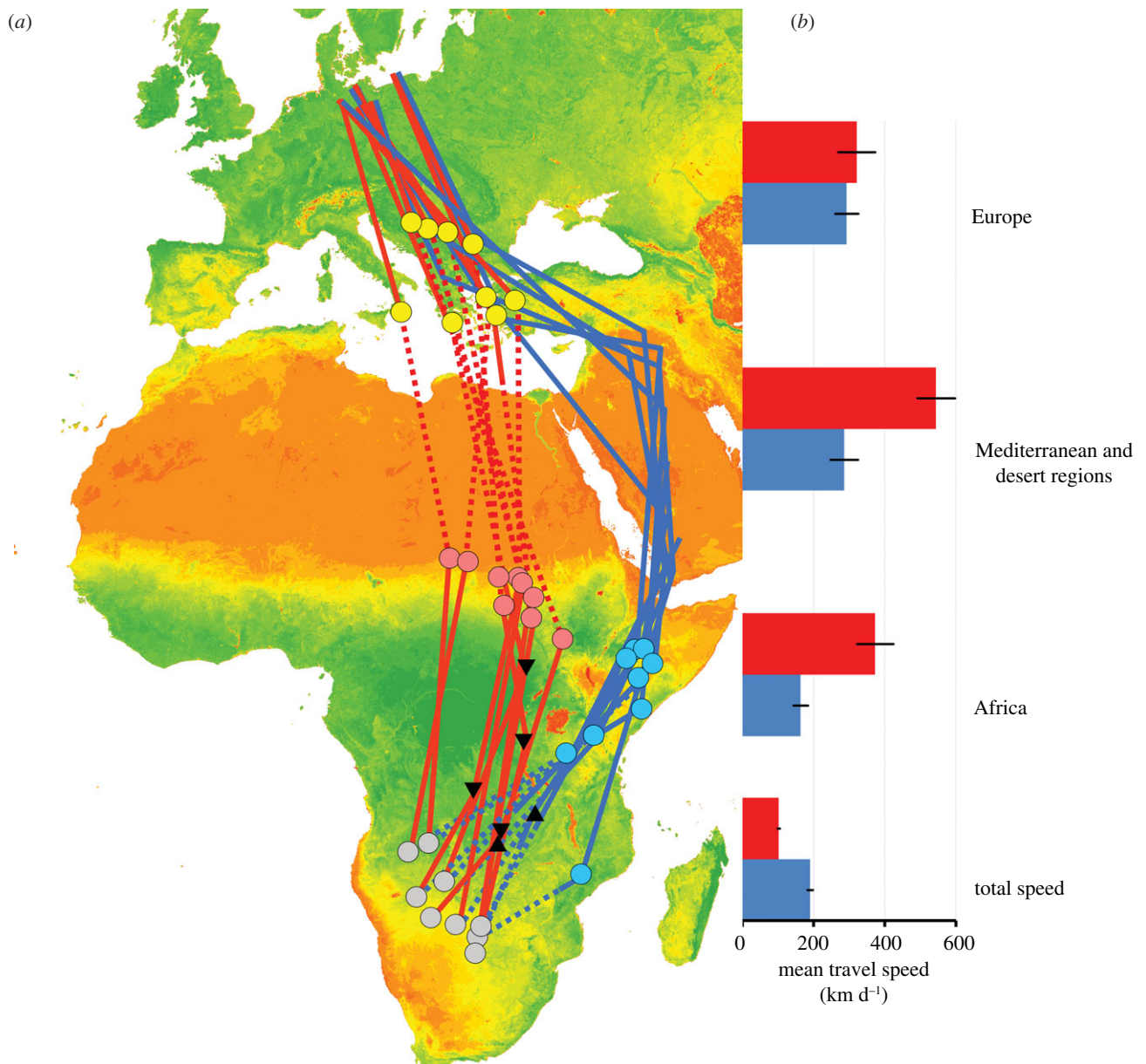
Figure 1. (*a*) The main stopover sites in southeast Europe (autumn: yellow), northeastern Africa (autumn: light red), non–breeding areas in southern Africa (grey) and eastern Africa (spring: light blue) of nine red-backed shrikes *Lanius collurio*. Red and blue tracks indicate autumn and spring migration routes, respectively. Also, four central African stopover sites during autumn (black triangle pointing downwards) and two during spring migration (black triangle pointing upwards) are included. Individual migration tracks with stopover sites are presented in detail in the electronic supplementary material, figure S1. The dashed parts of the lines indicate equinox periods where only longitudinal data were analysed. (*b*) Travel speed (km d^{-1}) averaged for multiple-day travels between main stopover sites excluding staging time (see text and electronic supplementary material, table S1 for details): crossing Europe (top), crossing Mediterranean and desert areas (upper middle) and crossing central Africa (lower middle), as well as total speed including staging time (bottom). Red: autumn migration; blue: spring migration. Standard error to the mean indicated. Background consists of the annual mean for 2009 (January–December) of MODIS/terra Normalized Differential Vegetation Index (NDVI) data in a 0.05° resolution available from Land Processes Distributed Active Archive Center (LP DAAC) at the US Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov).

additional shorter staging area in central Africa, we found no evidence of other staging areas. All individuals were found to be sedentary during the northern winter, with similarly located non-breeding areas in southern Africa (mean: 129 days, s.e. = 3.61, range 114–142; figure 1*a*; electronic supplementary material, table S1). The geographical positions of these wintering areas are consistent with ring recoveries from southern Africa [41].

Red-backed shrikes travelled a mean total distance of approximately 22 000 km ($\pm$s.e. = 120), with a loop migration pattern including a spring detour of approximately 1200 km ($\pm$s.e. = 226) crossing the Arabian Peninsula. Autumn migration was more broad-fronted (s.d.$_{longitude}$ = 4.34) compared with spring migration (s.d.$_{longitude}$ = 0.86; *F*-test: $p < 0.0001$), where the birds strongly converged at Bab-el-Mandeb, the Red Sea crossing point from continental Africa to the Arabian Peninsula (table 1; figure 1*a*).

Total migration speed (including staging periods) was higher for spring when compared with autumn migration ($t_{paired} = -12.4$, d.f. = 5, $p < 0.0001$), while mean travel
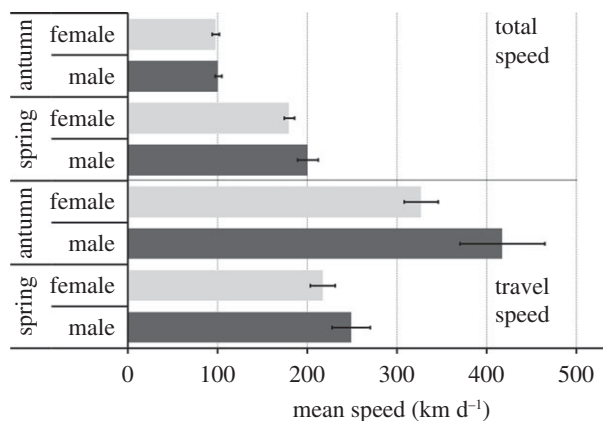
Figure 2. Mean total speed (km d^{-1}) including staging time (upper four bars) and mean travel speed (km d^{-1}) where staging time is excluded (lower four bars) are presented by season and sex. Error bars indicate standard error of the mean for nine individual red-backed shrikes *Lanius collurio* on autumn migration and six individuals on spring migration. See electronic supplementary material, table S1 for details.

speed between staging sites was generally higher during autumn when compared with spring ($t_{paired} = 3.27$, d.f. $= 5$, $p = 0.022$; table 1; figure 1b). As expected, the fastest travel speeds were found when birds crossed presumed barriers such as the Mediterranean Sea and the desert regions. However, contrary to the traditional assumptions of songbird migration strategies, the autumn crossing of central Africa was performed as fast as, for example, the desert regions. An analysis of mean latitudinal travel speed, dissolving the travel speed in further detail, confirmed this pattern (electronic supplementary material, figure S3).

Furthermore, travel speed was found to be significantly higher in males when compared with females ($t = 3.11$, d.f. $= 7$, $p = 0.017$). However, no differences in total migration speed ($t = -0.19$, d.f. $= 7$, $p = 0.85$) or duration of the staging periods ($t = 0.801$, d.f. $= 7$, $p = 0.48$) were recorded (figure 2). The male shrikes tracked in this study had slightly longer wings than the females, although this difference was not significant (males$_{average}$=96.6 mm, s.d. $= 2.24$; females$_{average}$ = 94.8 mm, s.d. $= 2.5$; $t = 1.11$, d.f. $= 7$, $p = 0.304$). Weight is not a good measure of size as the female weight varies throughout the breeding season [42].

Southbound migration was initiated in August (mean date: 14 August, range of dates: 26 July–25 August). Non-breeding areas south of the equator were reached in November (mean date: 20 November, range of dates: 4 November–9 December) and spring migration started in March/April (mean date: 29 March, range of dates: 17 March–13 April). The loop was completed in southeastern Europe, from where birds moved northwest (along the same overall migratory route as used during the autumn migration) towards the breeding areas, which they reached in May (mean date; 26 May, range of dates: 29 April–8 June; figure 1a; see also electronic supplementary material, figure S1 and table S1 for individual details). We found a higher degree of scatter between individuals in non-breeding area departure date (s.d. $= 11.4$ days) compared with autumn breeding area departure date (s.d. $= 9.0$ days; F-test: $p < 0.05$, $n = 9$), while no difference in temporal variation was found

between arrival date in non-breeding areas (s.d. $= 10.9$ days) and arrival in breeding areas (s.d. $= 14.5$ days; F-test: $p = 0.72$, $n = 6$).

Overall, the temporal patterns presented in figure 3 indicate that individuals followed rather strict migration schedules: breeding area departure time was correlated with spring arrival time in the next year ($r^2_{Spearman} = 0.81$, $n = 6$, $p < 0.05$), autumn migration initiation and termination correlated more weakly ($r^2_{Spearman} = 0.62$, $n = 9$, $p = 0.07$), and spring migration start and stop dates were also positively correlated ($r^2_{Spearman} = 0.84$, $n = 6$, $p = 0.04$). Finally, arrival at the non-breeding grounds after autumn migration was positively correlated with time of departure on spring migration ($r^2_{Spearman} = 0.68$, $n = 9$, $p = 0.04$).

4. DISCUSSION
The tracking results revealed that the red-backed shrikes completed autumn and spring migration between their breeding sites in southern Scandinavia (56° N) and their non-breeding areas in Botswana/Angola (about 20° S) in profoundly different ways, both geographically and temporally (table 1; electronic supplementary material, table S1). This pattern suggests that the evolution of spatio-temporal migration strategies has occurred independently for autumn and spring migration to a large degree.

The total duration of autumn migration was much longer, covering about three months (82–107 days), than spring migration, which was completed in about two months (53–71 days). The birds spent much longer staging time during autumn than spring, and all individuals stopped for a very long period—one to two months (34–62 days) in the Sahel/savannah zone of southern Sudan (10° N) after having crossed the Sahara desert in autumn. This long staging period (on average 53 days; table 1) was not quite as long as the breeding residence in Scandinavia (on average about 2.5 months; electronic supplementary material, table S1) or the winter residence south of the equator (about 4.5 months; electronic supplementary material, table S1), but still qualifies for being considered as a third main residence period in the annual cycle of the red-backed shrike. It is likely that the birds exploit favourable foraging conditions in the northern savannah zone after the summer rains, waiting for the same favourable conditions to develop in the southern savannah zone, where the birds arrived in November–December (at the onset of the rainy season there, and when the northern savannah is getting dry owing to lack of rain). The long stopover in the northern savannah zone cannot be explained by moult as this takes place in the final winter quarters [43,44], so the birds presumably spend the staging period in the northern savannah exploiting the favourable living conditions and storing fuel for a rapid southward movement to their final winter quarters in November. A strategy of tracking seasonal rain and vegetation patterns at a continental scale might be very common for migrants wintering in eastern and southern Africa [20,45].

The birds followed very different routes on autumn and spring migration, making a striking detour across the Arabian Peninsula during spring. The shortest distance along a direct route between breeding and winter sites was on average 8489 km. The autumn routes were only
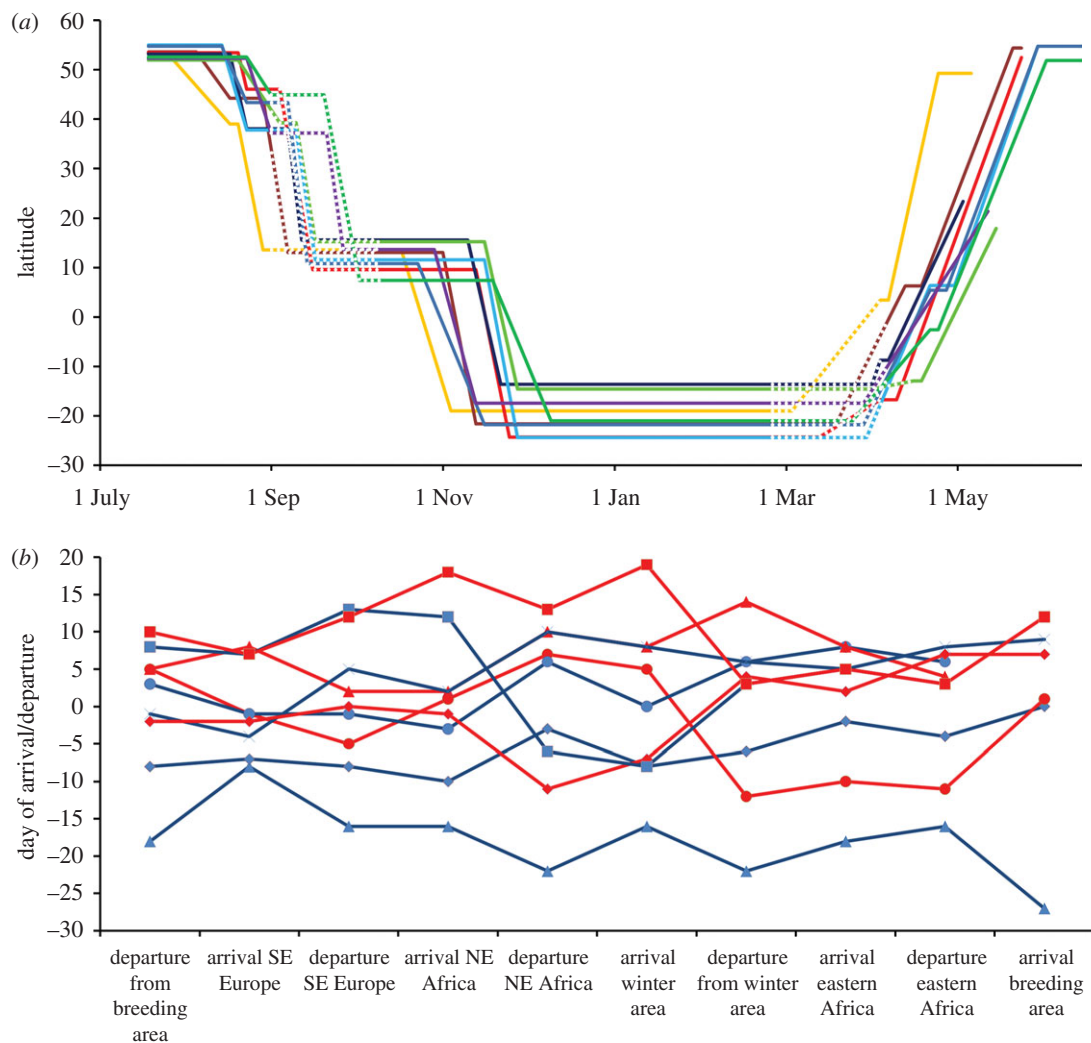
Figure 3. (*a*) Individual tracks of nine red-backed shrikes *Lanius collurio* for latitude versus time, indicating main stopover sites, wintering area and the related phenological patterns. The dashed parts of the lines indicate equinox periods where only longitudinal data was analysed. (*b*) Average days of arrival and departure from breeding, non-breeding and main staging areas relative to the mean for all nine individual birds. Males, blue; females, red. Note that the *y*-axis is the difference from the average for each *x*-axis category and that negative values indicate earlier than average movement. In three individuals, the geolocator battery got drained during spring migration, resulting in incomplete tracks.

14 per cent longer than this (on average 9719 km), while the spring routes were 40 per cent longer (on average 11 862 km; table 1; electronic supplementary material, table S1). This pattern of loop migration with a more easterly spring migration has previously been broadly indicated from ring recoveries [25,26], but the data now obtained using geolocators demonstrate very well-defined geographical patterns and consistency among individual birds. There are two main possible explanations for the distinct loop migration of the red-backed shrikes: that it is determined by regional differences in habitat availability and foraging conditions during the two seasons [17,45], and/or that it is an adaptation to wind conditions along the journey (and especially during the passages across the large deserts of Sahara/Arabia) [46]. In fact, the large body masses recorded for the red-backed shrikes and other migrants during their passage and stopover in northeast Africa in spring [20,45], associated with the spring rains in this region, may suggest that the northeast African stopover and fuel deposition may be of key importance for the evolution of a spring migration route at more easterly longitudes compared with autumn migration. In addition,

winds seem to be more favourable for a passage across the Arabian Desert compared with Sahara in spring, while the reverse holds for the autumn migration (Klaassen, R. H. G., Tøttrup, A. P., Strandberg, R., Kristensen, M. W., Vardanis, Y., Thorup, K. & Alersam, T., analysis of habitat/wind influence in preparation).

Because of the longer distance and shorter total duration of spring migration, the total migration speed (including staging time) was almost twice as fast during spring compared with autumn (table 1), confirming former studies based on ringing data [20]. This may indicate that there is stronger selection for time minimization during spring compared with autumn migration [29,30]. Since there were few staging periods (of more than 5 days) in spring, the birds proceeded with a rather uniform average travel speed of 233 km d^{-1} (excluding staging time; table 1). Assuming that the birds normally fly at ground speeds in the range 35–50 km h^{-1} [46], this corresponds to 4.5–6.5 h of flight per day, suggesting that the birds fly on average at least every second night (assuming a full night's flight of 9–13 h). It seems that in spring the shrikes make frequent but very short stopovers, a strategy

that requires favourable feeding conditions along the whole migratory route. In addition, the birds may have deposited large fuel reserves before spring departure from their southern winter sites and then again during their spring stopover in northeast Africa [20], and these reserves may be gradually used up as a complementary source of energy to that obtained along the spring migration route.

During autumn, the shrikes attained even faster travel speeds between the staging sites: on average, 355 km d^{-1} (table 1), and up to 550 km d^{-1} during the crossing of the Mediterranean Sea and the Sahara desert (figure 1b). This corresponds with 7–10 h of flight per day, and even 11–16 h of flight per day for the Sahara crossing. These figures suggest that the shrikes in autumn fly almost every night when travelling between the staging sites, and during the crossing of the Mediterranean Sea and Sahara desert they may even extend their nocturnal flights to continue during some of the daytime hours [8,47–49]. Even during the crossing of tropical forested regions, the shrikes travelled relatively fast, indicating that this habitat is perceived as a barrier by the shrikes, as suggested by Strandberg *et al.* [50]. The high travel speeds during autumn are probably explained by the birds' deposition of large fuel reserves at the staging sites, which make it possible for them to travel almost every night without the need for much further refuelling between the flights. In contrast, during spring, when the birds do not make long stopovers for extensive fuel deposition, they have to spend a few refuelling days between the flights and cannot fly every night.

Temporal synchrony has been shown within and between individual migrating raptors when studied both within and between years [51,52]. Our results also indicate individual migration schedules, with early-departing birds in autumn being consistently early during the entire migration cycle. Thus, the timing of migration, to a large extent, seems to be a characteristic of the individual, although repeated journeys are required to be able to distinguish between individual-based and environmental effects. Following the relative order of individuals in our cohort of red-backed shrikes throughout the annual cycle indicated that the wintering period in southern Africa was a period when the temporal order between individuals was more likely to change compared with other phases of the migratory cycle (figure 3). However, more data of this kind are needed to reveal the critical periods for possible temporal transpositions among individuals.

Sex-specific migration patterns in songbirds have already been broadly described in relation to breeding area arrival time [18]. However, most of our knowledge is based on population-level analyses and data from single study sites [53] in a year-long possibly connected time schedule [54]. For the red-backed shrikes, we found no significant difference in total migration speed between males and females either in autumn or in spring. This suggests that the earlier spring arrival found in male red-backed shrikes compared with females [53] may primarily be owing to the males being on average earlier in timing of their annual cycle (figure 3b). However, we found a sex difference in travel speed between staging sites (males travelling faster than females) and further tracking data are needed to clarify the possible differences in migratory performance between the sexes.

The restricted spatial extent of staging areas and winter grounds indicates that the shrikes are dependent on relatively specific areas, both temporally and spatially, as also indicated by the non-random distribution of ring recoveries in the eastern Mediterranean reported by Fransson *et al.* [22]. We expect that the migrants would need to navigate to reach these areas. Such goal-area navigation en route is presumably possible in experienced migrants [55,56], similar to the homing performance shown on the breeding grounds [6]. The similarity of routes, with occasional strong route convergence (for example, near Bab-el-Mandeb), and the similarity in timing among individuals is surprising given that the young of this species presumably migrate alone, without guidance from experienced conspecifics, following a relatively imprecise clock-and-compass strategy [5], and that the migration patterns in first-time migrants are probably repeated in later migrations. This seems to call for a more precise spatio-temporal migration programme than expected from a clock-and-compass programme used by first-time migrants [57]. Perhaps social influences [9] or high mortality for first-time migrants that do not reach the appropriate goal areas [58] cannot be excluded as contributory causes of the remarkably similar migration patterns (not least the spring routes) among the individuals in the observed shrike population.

The need to understand the alarming population declines in long-distance migratory songbirds reported from both sides of the Atlantic Ocean [59,60] requires the study of movement patterns and migration strategies, as well as impacts of global change in land use and climate in all stages of the migratory life cycle [61,62]. By unravelling the migration system of a long-distance migrant, demonstrating the existence of fundamentally different adaptations/strategies between the two seasons, we illustrate the opportunities geolocators provide as a tool for guiding future research focusing on long-distance bird migration. This basic knowledge about the whereabouts and movements of birds in their wintering areas is needed to develop efficient conservation initiatives for Eurasian–African migratory birds such as the red-backed shrike.

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Figure S1. Individual tracks of nine red-backed shrikes *Lanius collurio* showing three-day mean positions (small black dots) and the identified main stop-over areas: south-east Europe (yellow), north-eastern Africa (autumn: pink, spring: light blue) and central Africa (autumn: triangle pointing up, spring: triangle pointing down) as well as the non-breeding areas (grey) in southern Africa with red and blue tracks indicating autumn and spring migration routes, respectively. In three individuals, the geolocator battery got drained during spring migration, resulting in incomplete tracks See table S1 for further individual details.
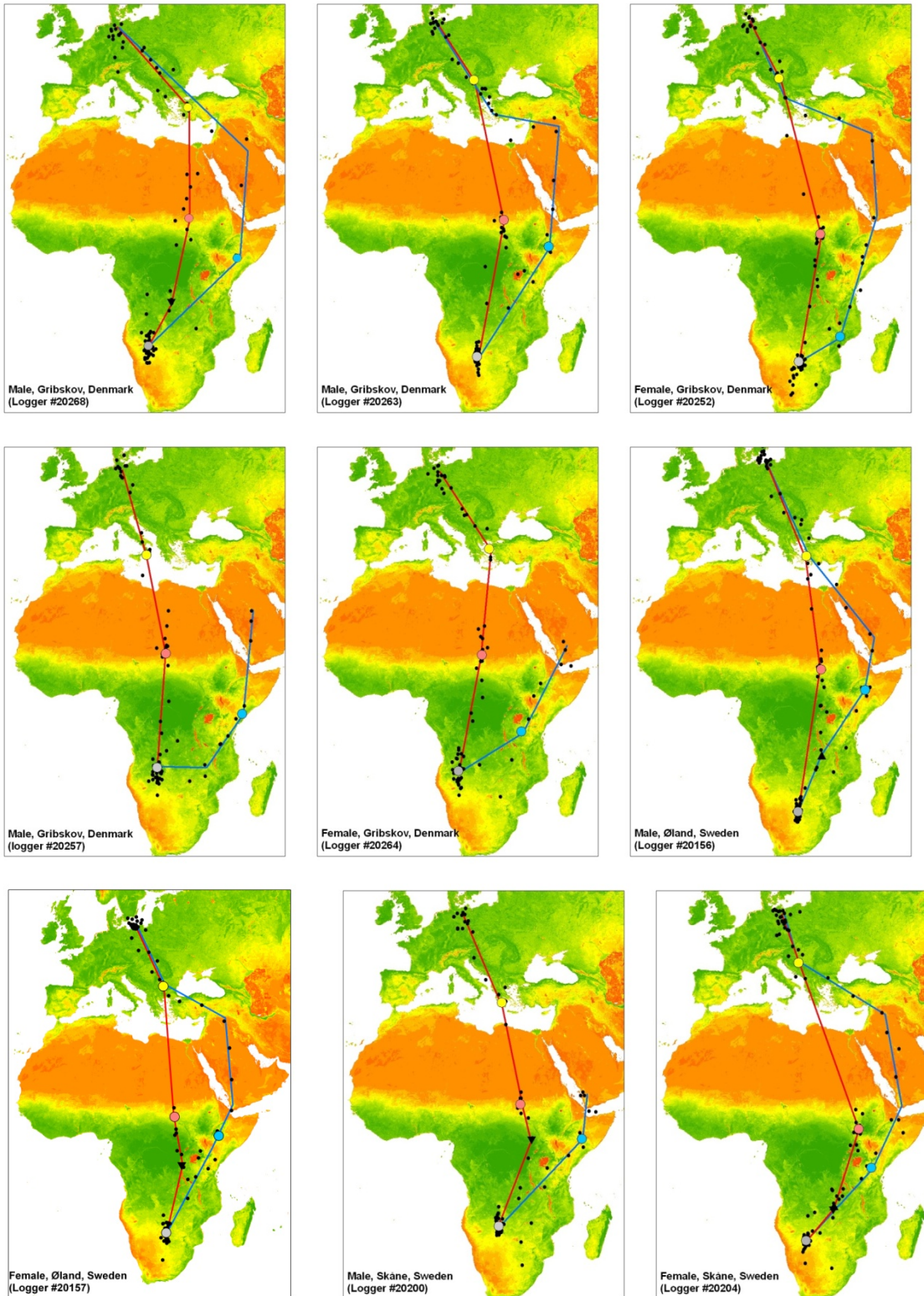
Figure S2. Individual tracks of nine red-backed shrikes *Lanius collurio* by use of 3-day mean positions according to different sun angle inference for the light threshold used: breeding area calibrated sun angles in red and green lines for 2009 and 2010, respectively (when the same sun angle is applied a red line is used); blue for individually calibrated Ekstrom-Hill Sun angle (ranging from 4.0 to 5.5 degrees below horizon); black line for the mean of the nine Ekstrom-Hill Sun angles (5.0 degrees below horizon). In all figures, 21 days has been deleted before and after equinoxes. In three individuals, the geolocator battery got drained during spring migration, resulting in incomplete tracks (see Methods section for details).
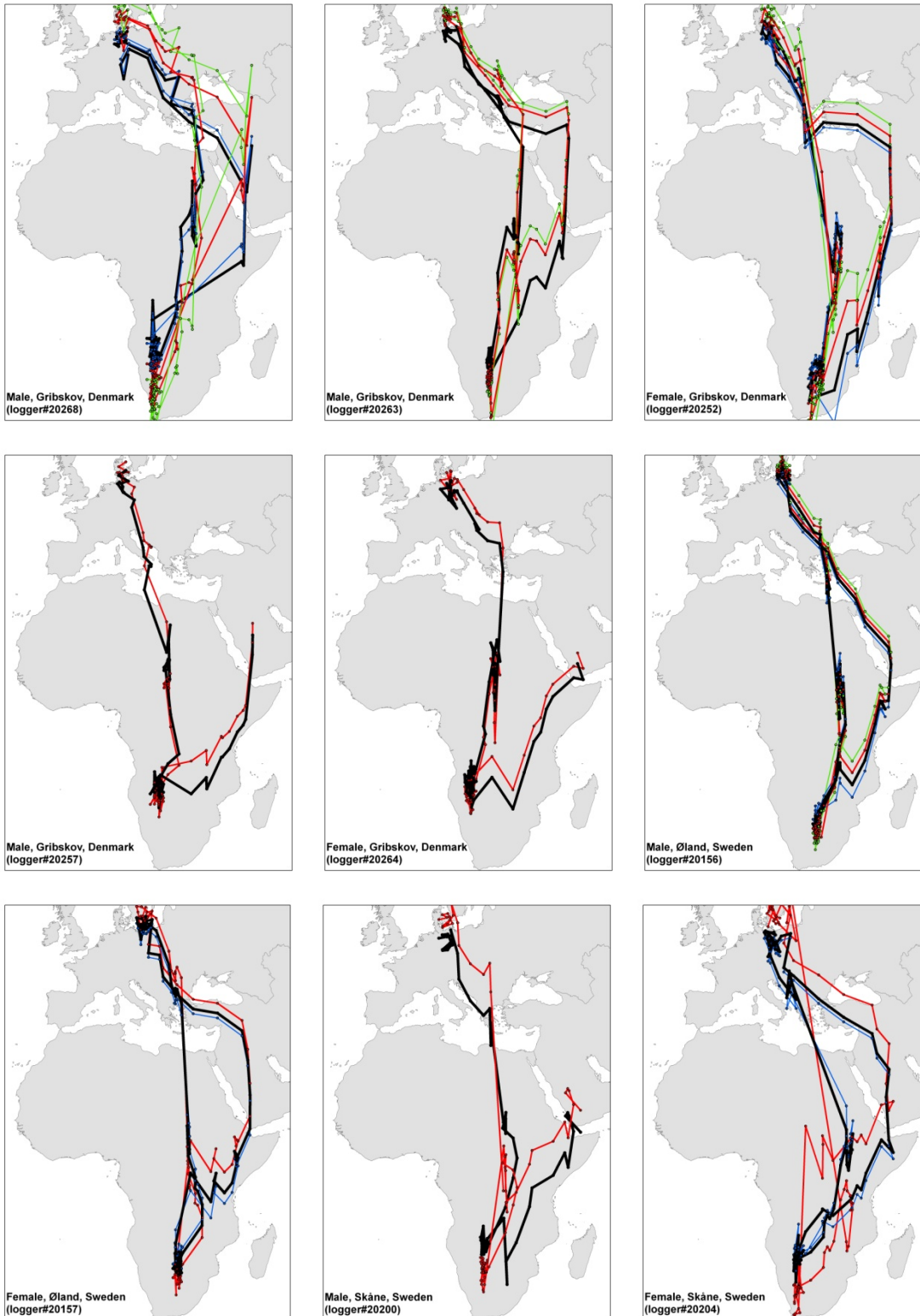
Figure S3. Mean latitudinal speed (km/day) for all nine individual red-backed shrikes *Lanius collurio* during autumn (red stars) and spring (blue stars) migration with each 3-day mean latitudinal speed measure indicate as black dots.
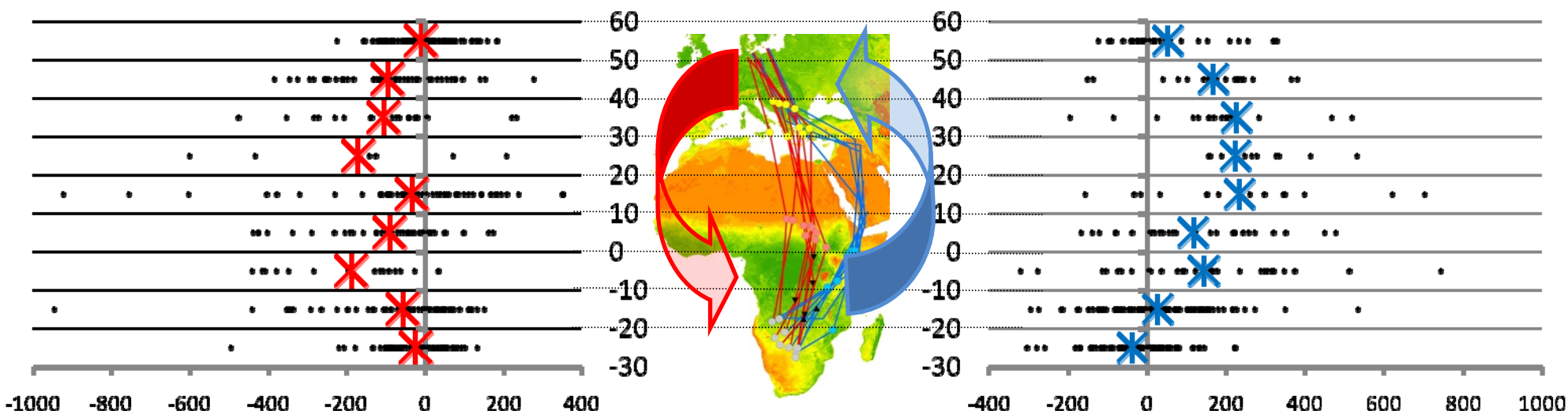
Table S1. Summary information on all nine individual red-backed shrikes *Lanius collurio* tracked through autumn and spring migration, including sex and breeding site information as well as details on staging periods, migration distance and speed. Mean values and SE are also presented.

Geolocator ID	20268	20263	20252	20257	20264	20156	20157	20200	20204	Mean	SE
Sex	male	male	female	male	female	male	female	male	female		
Locality	Gribskov	Gribskov	Gribskov	Gribskov	Gribskov	Oland	Oland	Skåne	Skåne		
Autumn migration											
Departure from breeding area (date)	26/07/09	06/08/09	19/08/09	17/08/09	19/08/09	13/08/09	12/08/09	22/08/09	24/08/09	14/08/09	3.01
Staging time Europe (no. days)	6	13	11	15	8	24	17	21	20	15.0	2.03
Staging time NE Africa (no. days)	47	60	59	62	61	61	42	34	48	53.0	3.41
Staging time C Africa (no. days)	6						6	8	7	6.8	0.48
Travel time breeding area - stop Europe (no. days)	20	10	3	5	13	6	9	8	6	9.0	1.70
Travel time stop Europe - stop NE Africa (no. days)	7	6	13	5	7	4	6	6	13	7.4	1.09
Travel time stop NE Africa - winter area (no. days)*	15	9	12	8	12	12	13	5	13	11.0	1.03
Distance breeding site - stop Europe (km)	2988	1948	1604	2517	2484	3052	2150	2648	1401	2310.3	192.86
Distance stop Europe - stop NE Africa (km)	3176	4107	4613	2872	3037	3260	4155	2961	5078	3695.5	269.84
Distance stop NE Africa - winter area (km)	3876	3988	3709	3274	3395	4129	3749	3711	3588	3713.3	90.25
Arrival winter area (date)	04/11/09	12/11/09	25/11/09	20/11/09	28/11/09	28/11/09	13/11/09	12/11/09	09/12/09	20/11/09	3.63
Total duration (no. days)	101	98	98	95	101	107	93	82	107	95.9	2.55
Total duration excl main staging periods (no. days)	42	25	28	18	32	22	28	19	32	27.3	2.50
Total distance (km)	10040	10044	9926	8663	8916	10442	10055	9320	10067	9719.1	201.60
Total speed (km/d)	99	102	101	91	88	98	108	114	94	101.4	2.67
Total speed excl main staging periods (km/d)	239	402	354	481	279	475	359	491	315	355.6	30.58
* excluding staging time C Africa											
Total duration in non-breeding area (no. days)	123	131	112	136	136	128	141	141	114	128.5	3.61
Spring migration											
Departure from winter area (date)	07/03/10	23/03/10	17/03/10	05/04/10	13/04/10	05/04/10	03/04/10	02/04/10	02/04/10	29/03/10	3.81
Staging time C Africa (no. days)						5			7	6.0	1.00
Staging time NE Africa (no. days)	11	6	7	6	4	11	13	6	6	7.8	1.02
Travel time winter area - stop NE Africa (no. days)**	24	25	23	22	14	14	18	22	15	19.7	1.48
Travel time stop NE Africa - breeding area (no. days)	18	33	41			31	30		39	32.0	3.33
Distance winter area - stop NE Africa (km)	3572	3762	1388	2884	2133	4001	3490	3453	2800	3053.7	282.17
Distance stop NE Africa - breeding area (km)	8250	8349	11100			7540	8153		8767	8693.2	507.76
Arrival breeding area (date)	29/04/10	26/05/10	27/05/10			05/06/10	03/06/10		08/06/10	26/05/10	5.94
Total duration (no. days)	53	64	71			61	61		67	62.8	2.51
Total duration excl main staging periods (no. days)	42	58	64			45	48		54	51.8	3.41
Total distance (km)	11822	12111	12488			11541	11643		11567	11862.1	152.08
Total speed (km/d)	223	189	176			189	191		173	190.1	7.29
Total speed excl main staging periods (km/d)	281	209	195			256	243		214	233.1	13.37
** excluding staging time C Africa											

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