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Article

Remarkably similar migration patterns between different red-backed shrike populations suggest that migration rather than breeding area phenology determines the annual cycle

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The regular fluctuation of resources across the Globe guides movements of migratory animals. To ensure sufficient reproductive output and maintain viable population sizes, migratory animals should match arrival at breeding areas with local peaks in resource availability. It is generally assumed that breeding phenology dictates the timing of the annual cycle, but this is poorly studied. Here, we use light-level geolocator tracking data to compare the annual spatiotemporal migration patterns of a long-distance migratory songbird, the red-backed shrike, *Lanius collurio*, breeding at widely different latitudes within Europe. We find that populations use remarkably similar migration routes and are highly synchronized in time. Additional tracks from populations breeding at the edges of the European range support these similar migration patterns. When comparing timing of breeding and vegetation phenology, as a measure of resource availability across populations, we find that arrival and timing of breeding corresponds to the peak in vegetation greenness at northern latitudes. At lower latitudes birds arrive simultaneously with the more northerly breeding populations, but after the local greenness peak, suggesting that breeding area phenology does not determine the migratory schedule. Rather, timing of migration in red-backed shrikes may be constrained by events in other parts of the annual cycle.

Keywords: geolocator, migration, population, resources, songbird, timing



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Introduction

In seasonal environments, migration has evolved as an intriguing mechanism allowing animals to take advantage of excess resources during peak seasons while avoiding unsuitable conditions when resources become scarce (Holdo et al. 2009, Block et al. 2011, Avgar et al. 2014, Bohrer et al. 2014). The journeys of migratory birds, especially those of long-distance migrants, often include multiple staging periods of varying length in time across the annual cycle allowing birds to rest, refuel and moult. This complex spatiotemporal migration program may result in migratory birds being particularly vulnerable to global rates of changes in climate and land use which may alter the timing and extent of resource availability at any given stage of the annual cycle (Newton 2004).

Birds need to arrive at the breeding grounds at the optimal time for breeding (McNamara et al. 1998, Kokko 1999). Strong selection against arriving too early or too late in relation to the local peaks in food availability through direct fitness consequences (Both and Visser 2001), is believed to determine the timing of the rest of the annual cycle. For instance, breeding latitude in temperate regions has been shown to predict migratory schedules across populations in a variety of bird species (Conklin et al. 2010, Briedis et al. 2016, 2020, Van Loon et al. 2017, Gow et al. 2019). However, a recent study suggest that migratory birds, especially long-distance migrants with complex spatiotemporal migration patterns track ephemeral resources throughout the annual cycle (Thorup et al. 2017). Thus, to maximize overall fitness (Barta et al. 2008, Harrison et al. 2011), being on time may be important, not only during the breeding season but throughout the annual cycle. The temporal constraints of migration may vary between populations (Flack et al. 2016, van Wijk et al. 2018). However, the extent to which the annual cycle constrains migratory schedules across populations remains unexplored.

The red-backed shrike *Lanius collurio* is a long-distance migratory songbird breeding across the Palearctic region and spending the non-breeding season in southern Africa. This species performs a loop migration with multiple longer staging periods in between the breeding area and its main non-breeding grounds (Tøttrup et al. 2012a, 2017, Pedersen et al. 2019a). An early study found a discrepancy in the migration timing of red-backed shrikes in relation to the onset of spring across Europe, due to the contrasting direction of spring isoclines (southwest–northeast) and the migratory direction (southeast–northwest) (Southern 1941, Dorst 1962). This finding, suggests that the migration schedule in this species is not related to breeding area phenology, but may rather reflect tracking of resources in other parts of the annual cycle (Thorup et al. 2017).

In this cross-distributional study, we compare the spatiotemporal migration patterns of two migratory populations of red-backed shrikes with breeding areas clearly separated in latitude, in Scandinavia (56°N) and in Spain (43°N), respectively. Our objective is to investigate differences in 1)

migration schedule in terms of departure and arrival events, 2) speed of migration and 3) spatial distribution at each of the staging sites throughout the annual cycle. Furthermore, 4) we present individual annual tracks of red-backed shrikes from six populations breeding at different edges of the European breeding range, unravelling the spatiotemporal migration system and discuss our findings in relation to ancestral migration routes. Finally, 5) to test if the migratory schedule is optimally timed for the birds to profit from assumed peaks in available resources during breeding, we analyse potential differences in timing of breeding and vegetation phenology across three breeding populations in southern Scandinavia, the Netherlands and Spain.

Methods

Migration phenology

We used archival light-level geolocators (Mk10s, Mk10 and Mk12 developed by the British Antarctic Survey, BAS, weight: 1.1 g and P65 from Migrate Technology, weight: 0.75 g) to estimate the spatiotemporal pattern of individual red-backed shrikes (n=39, tracks=48) throughout the annual cycle following current recommendations (Lisovski et al. 2019). Birds (n=402) were caught at six breeding populations across a wide latitudinal and longitudinal span of the breeding range of red-backed shrikes covering southern and mid-Scandinavia, Spain, Greece, the Netherlands and Russia during 2009–2016 (Table 1). The loggers measure and store light intensity in relation to time of day which can be converted into geographical positions, where latitude is inferred from solar day/night length and longitude from the time of local noon/midnight (Hill and Braun 2001, Ekstrom 2004). At logger deployment the birds weighed 24.4–39.1 g. Thus, the logger represented a maximum of 4.5% of the body mass. Loggers were attached using a leg-loop backpack harness (Naef-Daenzer 2007). The harness consisted of 1mm braided nylon string. Detailed information on tag deployment, return rates and the processing of light data can be found in the Supplementary information.

From the positional data, stationary periods can be distinguished from periods of migration. We defined stationary periods as intervals where migration was interrupted for more than five consecutive days (except in one case where a stationary period lasted only four days). However, birds could have moved shorter distances within each stationary period. Staging sites were then estimated as mean longitude and latitude (excluding equinox periods) within the given stationary period for each track. Migratory schedule, in terms of day of departure and arrival at each staging site throughout the annual cycle was determined by visual inspection of simultaneous changes in longitude and latitude over the course of the annual cycle. In the following, these departure and arrival events are collectively referred to as events. During equinoxes, we based the migration schedule on longitudinal data only (Fudickar et al. 2012, Lisovski et al. 2012). Determination

Table 1. Overview of capture locations, number of deployed loggers and number of tracks from individuals as well as the period where birds were captured and retrieved.

Population	Location	Coordinates	No. of tracks	No. of individuals	Loggers deployed	Deployment	Retrieval
Southern Scandinavia	Gribskov Vittskövle Ottenby	55.96°N, 12.95°E	31	24	267	2009–2015	2010–2017
Spain	Léon	42.65°N, -5.51°E	8	6	60	2011–2013	2012–2014
Greece	Dadia	41.12°N, 26.15°E	3	3	18	2013	2014
the Netherlands	Bargerveen	52.67°N, 7.02°E	3	3	20	2012	2013
Mid Scandinavia	Uppland	60.38°N, 18.12°E	2	2	20	2013	2014
Russia	Smolny	54.77°N, 45.56°E	1	1	17	2016	2017
Total			48	39	402		

of timing of arrival to the breeding site was not possible for nine individuals (10 tracks) due to battery failure during spring migration and for two individuals, most staging sites and events could not be determined due to poor data quality. Segments of migration were defined as the migratory movement between two consecutive staging sites. We calculated great circle distances of segments for each track using the *distVincentyEllipsoid* function in the *geosphere* R-package ver. 1.5-5 (Hijmans 2016). To take into account the loop migration pattern of red-backed shrikes in spring (Tøttrup et al. 2012a), we calculated the final spring migration segment as the sum of distances between the staging site in eastern Africa to the point on the Arabian Peninsula where birds change direction (defined as the north-eastern most position in the Arabian Peninsula) and from this point to the breeding area. To estimate speed of migration, it can be argued that one should include both the time of flight and the time of fuel deposition (Alerstam and Lindström 1990). However, as no data were available on preparatory refuelling, migration speed was estimated as travel speed for individual migratory segments and calculated as distance covered per day (km d^{-1}).

Tracking data from the southern Scandinavian and Spanish population (30 individuals, 45 tracks) have been analysed before and published with a different purpose (Tøttrup et al. 2012a, b, 2017, Pedersen et al. 2018, 2019b). Data used in the current study are available from the Movebank Data Repository: (<https://doi.org/10.5441/001/1.4bt7365c>) (Pedersen et al. 2020).

Breeding phenology

Data on timing of breeding were collected from the southern Scandinavian (Gribskov, Denmark, period: 2008–2017), the Dutch (Bargerveen, 2008–2014) and Spanish populations (Léon, 2011–2014). Nests were visited multiple times over the season from mid-May to mid-July and minimum age of young at the first visit following hatching was estimated based on appearance (Danish and Spanish population) and wing length (Dutch population) (van den Burg et al. 2011). We calculated date of hatching for each clutch as the day when the first egg in the clutch hatches, estimated from nestling age and in some cases, in which an incomplete clutch was found from the date of the beginning of incubation, assuming 14 days of incubation time. Analyses were restricted to clutches hatching before 1 July, as later clutches could be

interpreted as replacement clutches. We recognize the potential bias of standardizing this cut-off date across populations, as the ratio of first to replacement clutches may differ over the season between populations. However, we found this to be the most conservative approach given the data at hand. Thus, we ended up with the following sample size for each population: southern Scandinavia ($n = 54$), the Netherlands ($n = 136$) and Spain ($n = 47$).

Vegetation phenology

We used remote sensing data, in terms of the normalized difference vegetation index (NDVI) as an indicator of vegetation phenology at the local breeding sites, relying on the well-established assumption that insect abundance, and thus resource availability, is ultimately linked to plant productivity (Pettorelli et al. 2011). The NDVI product MOD13C1 was downloaded through NASA (<https://lpdaac.usgs.gov>). This product is a 16-day composite dataset (23 periods per year) with a spatial resolution of 0.05° latitude \times 0.05° longitude. We extracted values for each period over 15 years (2001–2015) for all breeding sites. This was done by averaging across the cell including the midpoint of each breeding site and all neighbouring cells, to account for local variation in NDVI values.

Statistical analyses

We used linear mixed effects models, implemented within the R-package *lme4* ver. 1.1-14 (Bates et al. 2015) to analyse differences between the southern Scandinavian and Spanish breeding population in migratory schedule (10 events), location (4 sites) and travel speed (5 segments). Sample sizes for additional populations were too small to warrant a formal analyses ($n = 1-3$) but are presented as individual estimates. Thus, four models were specified with 1) migratory schedule, 2) longitude, 3) latitude and 4) travel speed as response variables. Each of the models included fixed effects of population and the variable of interest (event, site or segment) their interaction as well as a random intercept of individual and year to account for data being sampled repeatedly from each individual across different years (for model specifications and sample sizes see Supplementary information). Based on diagnostics from the statistical model, travel speed was modelled on the log-scale to allow the assumption of variance

homogeneity of the residuals. Within the framework of the four models, we used approximate t-tests from the R package *lsmeans* version 2.27-2 (Lenth 2016) for comparing the migratory schedule, location (longitude or latitude) and logarithmic travel speed of the two populations at each event, site and segment, respectively. Estimates, standard errors and p-values are based on restricted maximum likelihood (REML) and p-values were Holm–Bonferroni adjusted to account for multiple tests being conducted within the model. To assess differences in timing of breeding between the southern Scandinavian, Spanish and Dutch populations, we fitted a linear mixed effects model for day of hatching (ordinal dates, 1 = 1 January) with a fixed effect of population and a random effect of year. The model was evaluated against a model without the effect of population, using a likelihood ratio test and a pairwise comparison between populations were constructed like described above. All analyses were run in the statistical software R 3.4.2 (<www.r-project.org>).

Results

All populations made use of a similar loop migration route via the east-central Mediterranean in autumn and crossing the Arabian Peninsula in spring (Fig. 1). Despite the latitudinal breadth in breeding locations, we did not find significant differences in timing between the southern Scandinavian and Spanish breeding population at any of the different events throughout the annual cycle (Fig. 2, Supplementary information). Likewise, the migration schedule of individuals from other populations were similar to that of the southern Scandinavian and Spanish populations (Fig. 2). Individuals left their breeding areas in August (overall non-weighted mean: 2 August, range: 26 July–30 August, $n=44$) and arrived at their main non-breeding site in southern Africa in November (20 November, 4 November–12 December, $n=41$), while spring migration was initiated at the end of March (28 March, 7 March–13 April, $n=40$) and birds arrived back at the breeding grounds in May (24 May, 29 April–8 June, $n=35$) (Fig. 2).

In terms of timing of breeding, we detected no difference in hatching date between the southern Scandinavian and Spanish breeding population ($p=0.87$, Fig. 2). However, clutches from the Dutch population hatched significantly earlier ($16 \text{ June} \pm 6.9 \text{ days}$, mean \pm SD) than clutches in southern Scandinavia ($20 \text{ June} \pm 6.9 \text{ days}$, $p < 0.001$) and Spain ($19 \text{ June} \pm 6.9 \text{ days}$, $p=0.008$), respectively.

Arrival at the breeding site corresponded with increasing NDVI values for the majority of populations. However, the Spanish and Greek breeding population arrived after the peak in NDVI (Fig. 2). Timing of breeding matched local peaks in NDVI at the southern Scandinavian and Dutch breeding sites, whereas at the Spanish breeding site clutches hatched during a period with decreasing plant productivity (Fig. 2, Supplementary information).

We found a longitudinal segregation between the southern Scandinavian and Spanish breeding population at the

main non-breeding grounds in southern Africa, with the southern Scandinavian population wintering further to the west than the Spanish breeding population ($p_{\text{adj.}} < 0.001$, Fig. 1 and Supplementary information). This segregation was likewise apparent in wintering ground latitude ($p_{\text{adj.}} = 0.01$). Individuals from the mid Scandinavian and Russian population as well as two individuals from the Dutch population seemed to segregate with the southern Scandinavian population, while individuals from the Greek populations and a single Dutch individual wintered in the same area as the Spanish population (Fig. 1). In contrast, we found no difference in either longitude or latitude between the southern Scandinavian and Spanish breeding population at any other staging sites throughout the annual cycle (Supplementary information), and individuals from all European populations seemed to overlap spatially at all staging sites in between the respective breeding grounds (Fig. 1). However, the Russian individual did not join the European populations in the Balkans during autumn migration (Fig. 1). Instead, this individual migrated along a more direct route towards a staging area in Turkey. The Russian individual had more stops during autumn migration and seemed to move gradually in spring, with no prolonged staging periods in between the main non-breeding area in southern Africa and the breeding grounds (Fig. 1). We found an overall correlation between non-breeding area latitude and timing of spring migration departure, with early departing individuals being further south than late departing individuals (LM: $\beta=0.7$, $t_{42}=2.58$, $p=0.01$). However, there was no sign of a correlation between non-breeding area longitude and departure on spring migration (LM: $\beta=-0.05$, $t_{42}=-0.29$, $p=0.78$).

The southern Scandinavian and Spanish populations did not differ in travel speed, except for the segment on autumn migration between Sahel and the main wintering grounds where the Spanish population seemed to migrate at a slower pace than the southern Scandinavian population, spending more days covering a shorter distance (Fig. 3 and Supplementary information). Likewise, the travel speed of individuals from other populations was within the range of the southern Scandinavian and Spanish populations (Fig. 3).

Discussion

Tracking individual red-backed shrikes from six populations across the European breeding range revealed remarkably similar migration patterns in space and especially in time throughout the annual migration cycle. At northern latitudes timing of arrival and breeding coincided with local peaks in vegetation greenness, while at lower latitudes birds arrived simultaneous with the more northerly breeding populations, after the local peak in vegetation greenness. Our study also revealed an intriguing segregation of the breeding populations at the main non-breeding area in southern Africa while speed of migration was similar between populations.

The highly synchronized temporal migration and breeding patterns across different populations, despite the important

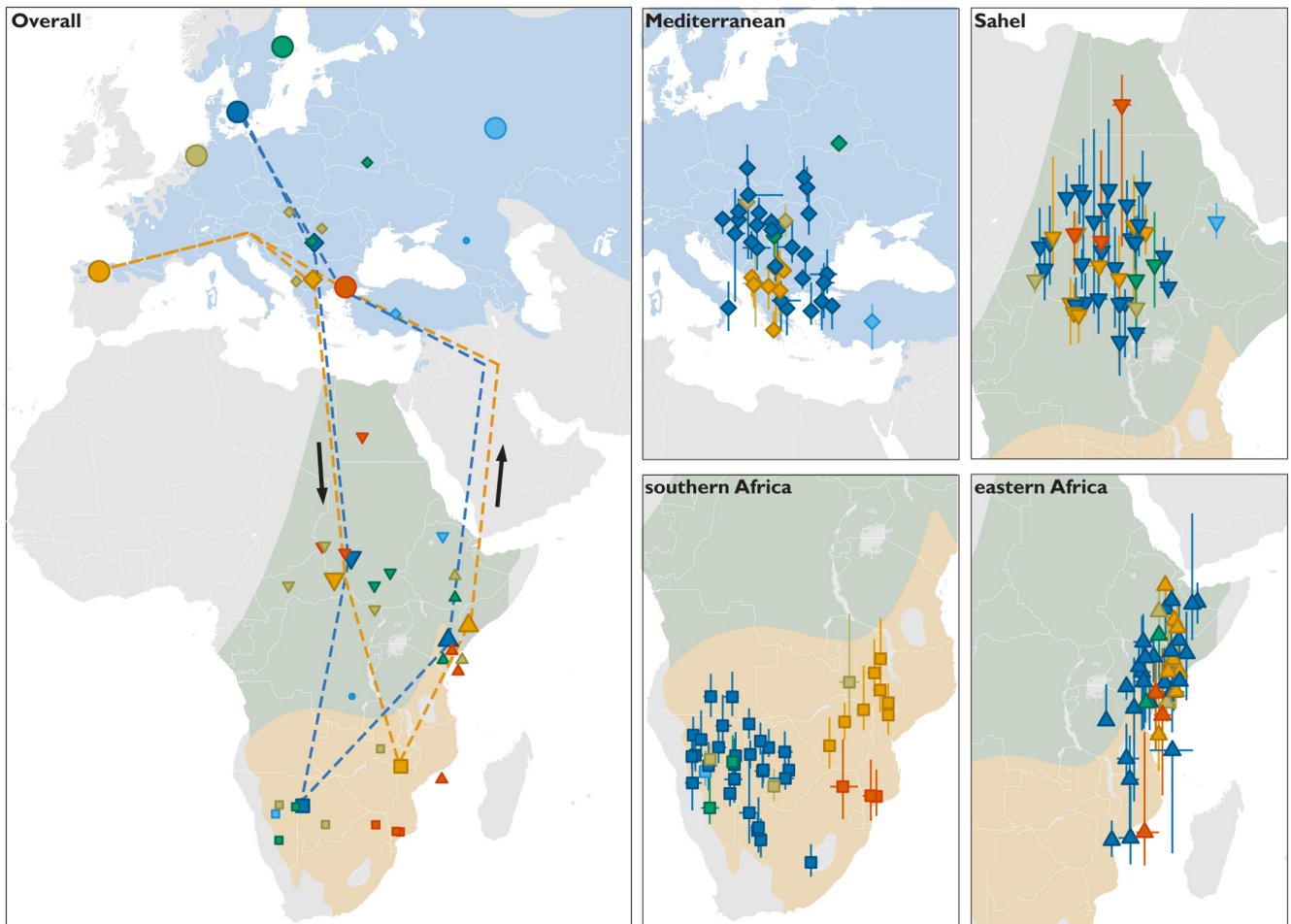


Figure 1. Overall median staging positions for the southern Scandinavian and Spanish breeding population and individual median positions for populations with ≤ 3 individuals (large map left). Dashed lines illustrate overall migration routes for the southern Scandinavian and Spanish breeding population and arrows indicate migratory direction. Small maps (right) show individual median positions \pm interquartile ranges at each staging site separately. Symbols represent staging sites (circles: breeding area, diamonds: Mediterranean, inverted pyramids: Sahel, squares: southern Africa, pyramids: eastern Africa, dots: shorter stopovers during autumn migration identified for the individual breeding in Russia). Colours depict different breeding populations (dark blue: southern Scandinavia, orange: Spain, khaki: the Netherlands, red: Greece, green: mid Scandinavia and light blue: Russia). Background map represents BirdLife International distribution maps (blue: breeding range, orange: wintering range, green: passage) (BirdLife International 2016b). Maps are shown in Mercator projection.

differences in breeding latitude, supports the idea of a migration schedule regulated by the annual cycle rather than breeding area phenology. Our results are in sharp contrast to a previous study on collared flycatchers, finding a difference in migration timing throughout the annual cycle corresponding to the breeding phenology of populations across different latitudes (Briedis et al. 2016). Likewise, studies on multiple species have found breeding latitude as a main predictor of timing and duration of migration (Conklin et al. 2010, Van Loon et al. 2017, van Wijk et al. 2018, Gow et al. 2019, Briedis et al. 2020). Our finding, however, is contrasting not only because red-backed shrike populations migrated synchronously throughout the annual cycle, but because they did so, despite spending both the breeding season and non-breeding season in widely different areas. These spatiotemporal patterns are likely a result of the complex migration route

of red-backed shrikes, optimizing seasonal changes in resource availability throughout the annual cycle (Thorup et al. 2017). If this is the case, constraints in timing should likewise be expected in other songbird species with similar complex migration strategies, migrating in response to rainy seasons in eastern and southern Africa such as the thrush nightingale (Morel 1973, Pearson 1990, Jones 1995). We note, that the relatively small sample sizes from the two populations (31 tracks from 24 individuals in southern Scandinavia and 8 tracks 6 individuals from Spain), may have resulted in a type II error, failing to reject the null hypothesis of no difference in timing between the populations.

The mismatch in timing of arrival and breeding with local seasonal vegetation phenology of the southerly populations may indicate that these populations do not breed at the optimal time. However, the actual peak in insect

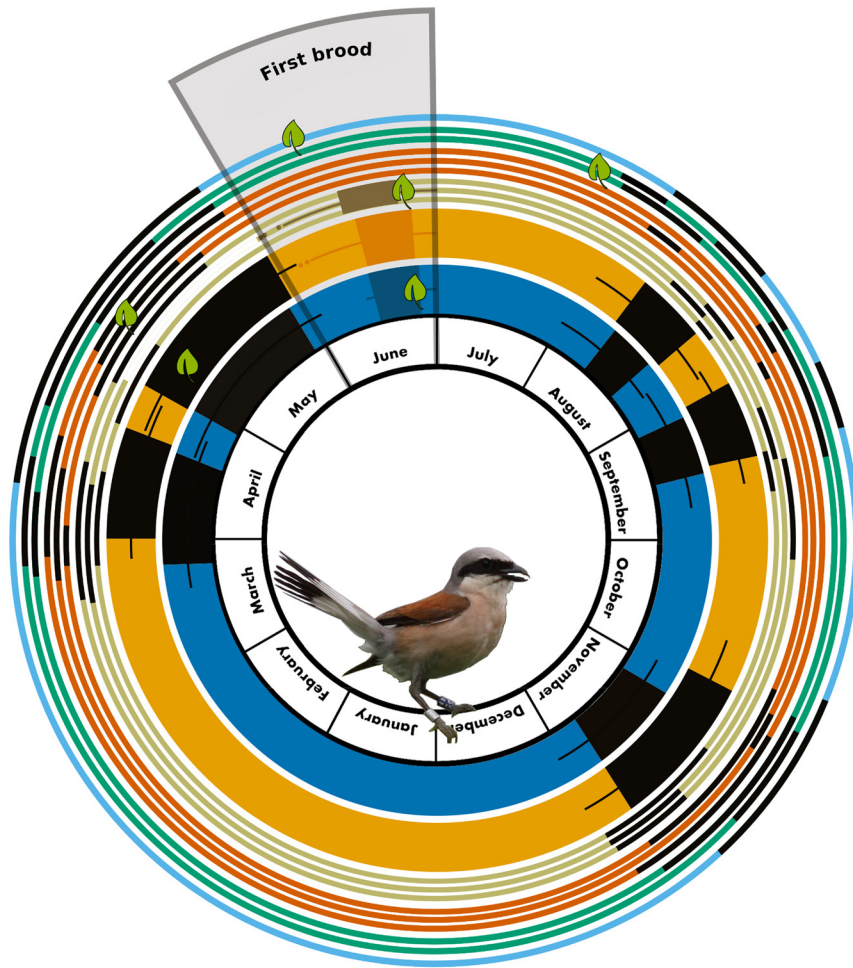


Figure 2. Mean relative timing (\pm SD) of migration of the southern Scandinavian and Spanish breeding population as well as individual timing of populations with ≤ 3 individuals to and from main staging sites throughout the annual cycle. Colours depict different breeding populations corresponding to Fig. 1 (dark blue: southern Scandinavia, orange: Spain, khaki: the Netherlands, red: Greece, green: mid Scandinavia and light blue: Russia) while black areas indicate migration. Dark shading during June, indicate date of hatching of presumed first brood clutches hatched in southern Scandinavia, the Netherlands and Spain, presented as interquartile ranges (IQR) with whiskers ($1.5 \times$ IQR) and outliers as dots. Green leaves represent the peak in mean NDVI of each of the population specific breeding sites over a 15-year period (2001–2015).

abundance is typically delayed compared to the peak in vegetation greenness (Pettorelli et al. 2011), and the extent of this delay may differ across region, depending on e.g. weather, climatic conditions, topography, plant- and insect communities. Thus, a mismatch with vegetation phenology does not necessarily imply a mismatch with actual food abundance. The breeding site in Greece showed an overall higher vegetation greenness than the Spanish site and a more gradual seasonal development of vegetation greenness over the breeding season, suggesting that this population experiences a different extent of resource availability compared to the Spanish breeding population (Supplementary information). Still, both populations are declining (SEO/Birdlife 2013, BirdLife International 2016a, Portolou and Kati 2017, Tellería 2018a) compared to the more northerly populations in Scandinavia and the Netherlands which are recorded as being stable and increasing, respectively

(BirdLife International 2016a). Furthermore, a recent study showed a preference for highland areas with cooler temperatures during the breeding season in northern Spain (Tellería 2018b), which may support a mismatch with local resources at least at lower altitudes. Red-backed shrikes are among the latest arriving migratory bird species in Europe during spring and thus, one could argue that the general late arrival may be responsible for the mismatch with local vegetation greenness. However, a recent study on swifts (another late arriving species in Europe) have shown a clear difference in timing of arrival with southern populations arriving earlier than northern populations (Åkesson et al. 2020). Another possibility is that there is no, or only insignificant penalties on fitness of late breeding attempts across red-backed shrike populations. For instance, no sign of lowered reproductive success was reported from the southern Scandinavian breeding population despite a delay in spring arrival time

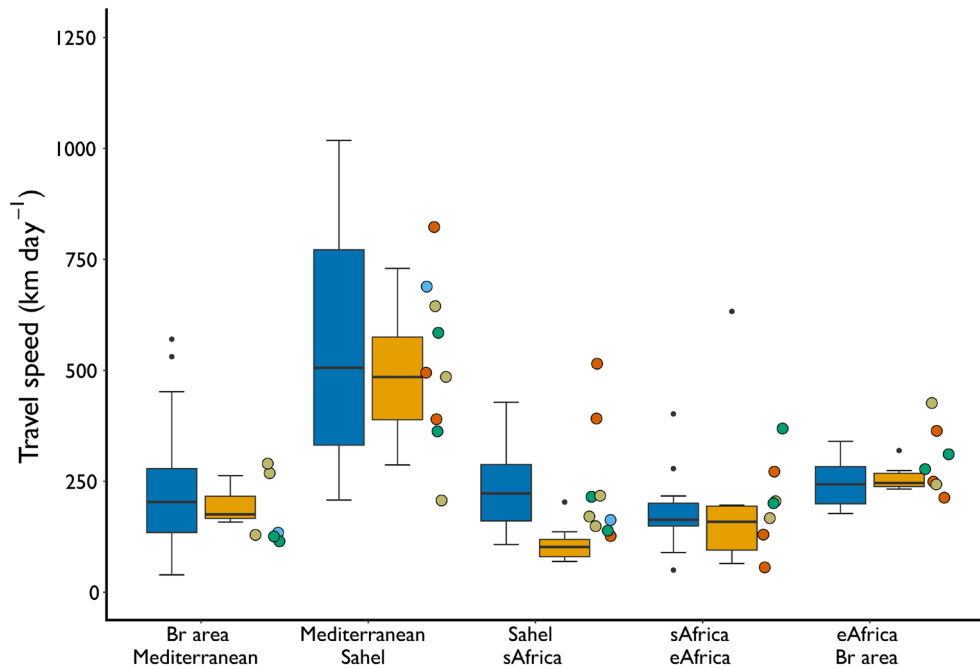


Figure 3. Travel speed of main travel segments throughout the annual cycle. Colours depict different breeding populations corresponding to Fig. 1, 2 (dark blue: southern Scandinavia, orange: Spain, khaki: the Netherlands, red: Greece, green: mid Scandinavia and light blue: Russia). Boxes indicate median values with 25 and 75 percentiles. Whiskers represent 5 and 95 percentiles while dots indicate extreme values.

(Tøttrup et al. 2012b). This would support our finding of migration, rather than breeding area phenology determining migratory schedules. However, previous studies on the Dutch breeding population suggest a high cost on recruitment in the following year of late breeding attempts (van den Burg et al. 2011). Thus, future studies exploring the direct link between vegetation greenness, insect abundance, fitness and recruitment will be essential to understand how the temporal fluctuating resources affect population dynamics in migratory bird species.

In southern Africa, we found a clear spatial separation in longitude correlated with breeding area latitude. A similar pattern of longitudinal segregation related to breeding area latitude was also found in pied flycatchers wintering in western Africa and black-throated blue warblers in the Americas (Rubenstein et al. 2002, Ouwehand et al. 2016). In pied flycatchers, this segregation was suspected to be related to differences in spring migratory schedules. Although, we found a general correlation between non-breeding area latitude and timing of spring migration departure, this pattern was not detected in longitude and thus, it cannot explain the differences between breeding populations as these did not differ in the timing of spring departure (cf. above). In addition, we found a correlation between breeding latitude and latitude at the southern African staging site. However, as estimated latitude in geolocator studies is highly dependent on the calibration procedure, this result should be treated with caution. For none of the other staging sites was there a significant segregation between populations, although a partly divergent

spatiotemporal migration pattern may hold for easterly populations of red-backed shrikes. The single individual from Russia included in this study suggested such a possibility, although more data are needed to assess the annual spatiotemporal cycles of shrikes from easterly breeding grounds.

The spatiotemporal patterns by red-backed shrike populations may reflect long-term adaptation to resources in terms of food and habitat availability (Alves et al. 2012, Thorup et al. 2017), wind-assistance (Erni et al. 2005, Tøttrup et al. 2017), predator avoidance (Klaassen et al. 2006, Ydenberg et al. 2007), conserved migration programmes (Pedersen et al. 2018) and historical colonization routes (Dorst 1962, Sutherland 1998, Ruegg and Smith 2002, Alerstam et al. 2003). Perhaps the Balkan region has served as a past refugium in the Pleistocene from where the populations have spread across the breeding range (Taberlet et al. 1998, Hewitt 2000). The segregation in southern Africa may have occurred at a later stage due to competition for resources at the non-breeding grounds leading to a parallel or leapfrog migration pattern at this stage of the annual cycle (Salomonsen 1955, Lundberg and Alerstam 1986). Another possible explanation is that red-backed shrikes from Spain and Greece would benefit from a shorter spring migration distance that would promote earlier arrival at breeding sites, which would be adaptive for birds from Mediterranean populations where spring development (and the peak of breeding resources) is early. However, this is clearly refuted by the results of our analysis, showing the same spring migration schedule for the different populations, in support of a spring

migration that is similarly constrained for all populations. Still, another explanation is that, because of the difference in habitat and climate conditions experienced by the populations in the Mediterranean and north European breeding areas, these populations are preadapted to having their optimal wintering conditions in different regions of southern Africa, depending on the regional habitat/climate conditions. However, this is purely speculative and it remains to be investigated if there exists any correspondence between habitat/climate conditions in breeding and main non-breeding regions. Future research combining direct tracking and genetics will help clarify the population specific migration patterns and their historical component.

Understanding the spatiotemporal patterns of geographically distinct populations of migratory species is important to assess the extent to which the migratory programme is flexible in time and space. Further, this will help us understand how populations may be able to adapt to global changes in land use and climate.

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Transparent Peer Review

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Data accessibility

The data and code used to obtain conclusions in this paper will be made available at the Movebank Data Repository (<https://doi.org/10.5441/001/1.4bt7365c>) (Pedersen et al. 2020).

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Supplementary information (available online as Appendix jav-02475 at <www.avianbiology.org/appendix/jav-02475>).