



Full-year tracking suggests endogenous control of migration timing in a long-distance migratory songbird

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Abstract

Following ongoing technological advances, an increasing amount of full-year tracking data on individual migratory movements is becoming available. This opens up the opportunity to study how migration develops within individuals in consecutive years and the extent to which the migratory program is constrained. Such knowledge is essential for understanding the degree of individual flexibility during the annual cycle, which may help identifying potential bottlenecks, where the range of individual decisions is restricted. In this study, we investigate repeatability in time of a long-distance migratory songbird, the red-backed shrike *Lanius collurio*, tracked across consecutive years ($n = 7$). Furthermore, we explore the population variability and dependencies between consecutive events of departure and arrival throughout the annual cycle in this species ($n = 15$). We find that individuals show high repeatability in timing of departure from their two main non-breeding areas in sub-Saharan Africa. In contrast, low repeatability is found in timing of arrivals to stationary sites throughout the annual cycle. Population variation in timing of departure and arrival was similar across all events, ranging from 30 to 41 days, and was highly dependent on timing of preceding events. We conclude that timing of departures is the key event potentially controlled by the individual innate migration program, while arrivals are more flexible, likely dependent on the environmental conditions experienced en route in red-backed shrikes. Still, apparent flexibility in the individual schedule may be hampered by overall constraints of the annual cycle.

Significance statement

The annual migration schedule of migratory animals is controlled by a combination of endogenous and exogenous factors. Understanding the temporal dynamics within and between individuals across the annual cycle is important to assess to which extent the migratory schedule is constrained in time. By using full-annual cycle tracking data of individual red-backed shrikes tracked across consecutive years, we find that individuals are highly consistent in their decision to depart from their main non-breeding areas in sub-Saharan Africa, whereas arrivals are less consistent throughout the annual cycle. Overall, the migration schedule is highly constrained across the annual cycle, with each arrival and departure event being dependent on the previous event. Our results suggest that departure decision is underlying endogenous control and that little flexibility is available throughout this complex migration system.

Keywords Repeatability · Migration · Endogenous control · Timing · Geolocator · *Lanius collurio*

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Introduction

The extraordinary movements of migratory animals have inspired behavioral ecologists for centuries. The twenty-first century opened up new opportunities for studying these movements, as it became possible to track individuals throughout their annual migration cycle. As technology continues to advance, an increasing amount of tracking data is becoming available, today, even for the smallest migratory passerines (Stutchbury et al. 2009; Tøttrup et al. 2012a). With this data, we can begin to understand the influence of endogenous control mechanisms allowing for optimal scheduling and navigation throughout the annual cycle, thus unraveling the processes that drive migratory movements (Robinson et al. 2010; McKinnon et al. 2013).

Migration in songbirds is thought to be mainly driven by an innate migration program in combination with environmental conditions experienced en route. However, to disentangle the environmental component from the genetic component, we need to understand how migration develops within the individual (van Noordwijk et al. 2006). This has been extensively studied in larger birds such as raptors and seabirds (Alerstam et al. 2006; Guilford et al. 2011; Vardanis et al. 2011, 2016; Yamamoto et al. 2014). Still, little is known about how migration develops within individuals for migratory songbirds, due to the difficulty in obtaining continuous tracking data for these species. Likewise, the temporal dynamics within the annual cycle of migratory songbirds remain poorly studied. However, this knowledge is crucial for understanding the flexibility and constraints faced by migratory birds, and thus their ability to adapt to global changes (Both 2010; Knudsen et al. 2011).

The timing of events across the annual cycle is ultimately constrained, as migratory birds need to match their migration strategy and scheduling of activities such as breeding or molt to local availability of resources (McNamara et al. 1998; Briedis et al. 2016). Time is considered one of the main factors on which selection can occur (Alerstam and Lindström 1990), and spring migration is often found to be more constrained in time as compared to autumn migration, due to the direct fitness cost of a late arrival to the breeding grounds (Kokko 1999). Given stable environmental conditions, selection for time can act at the population level by reducing the range of alternative migration strategies within the population, and at the individual level by increasing the precision of the individual migration schedule between years (Conklin et al. 2013).

In addition to optimizing the migration schedule, individuals need to choose appropriate sites for refueling throughout the annual cycle. Site fidelity may be advantageous due to familiarity with local foraging conditions, predators and acquisition of territories (Greenwood 1980), although, flexibility in site use can be an advantage if conditions are variable (Nichols et al. 1983; Warkentin and Hernández 1996).

Several migratory bird species have been shown to be site faithful to their non-breeding grounds (Newton 2008; Cresswell 2014; Blackburn and Cresswell 2016), while the choice of staging areas used for re-fueling during migration may be more flexible, at least in songbirds (Catry et al. 2004).

Individual consistency is usually studied by the repeatability index, r , which in ecological terms describes the proportion of phenotypic variation caused by differences between individuals (Lessells and Boag 1987; Bell et al. 2009; Nakagawa and Schielzeth 2010). Repeatability is a relative measure of both within- and between-individual variations. Thus, a high repeatability value can reflect either low variation within individuals or high variation between individuals. As the variation of both may change across departure and arrival events in the annual cycle, and may differ between studies, comparing the overall population variation is important to make inferences about the potential causes of repeatability (Conklin et al. 2013).

The red-backed shrike *Lanius collurio* undertakes a complex loop migration pattern with multiple stationary sites, from its Palearctic breeding grounds (Snow and Perrins 1998; Tøttrup et al. 2012, 2017). In autumn, migration is interrupted by a 2-week staging period in southern Europe. The main part of the non-breeding season is subsequently spent in the Sahel region and in southern Africa, the latter where red-backed shrikes undergo a complete molt of their feathers (Bruderer 2007). In spring, red-backed shrikes migrate via eastern Africa and the Arabian Peninsula to return to their breeding grounds. A previous study on the activity of red-backed shrikes in captivity, has suggested that the migration program of red-backed shrikes may be strongly influenced by an endogenous temporal program (Gwinner and Biebach 1977). Furthermore, recent activity studies on free-flying red-backed shrikes have opened up the opportunity for measuring activity, and thus, timing of migration, at high temporal resolution throughout the annual cycle (Bäckman et al. 2017a, b). However, to fully understand the endogenous component acting on the individual decision to migrate, tracking individuals across multiple years is necessary.

Here, we use geolocator data on repeatedly tracked red-backed shrikes in two consecutive years, to test if timing is repeated across the annual cycle. If migration is mainly driven by an innate schedule, we hypothesize that timing of departures will be highly repeatable among years, whereas timing of arrivals may be more variable depending on the environmental conditions encountered along the migration route. Furthermore, we investigate the overall constraints in the migratory cycle of all individuals tracked from the population, by comparing variation and dependence in timing across all migratory events throughout the annual cycle. Finally, we analyze the spatial location of the repeatedly tracked individuals by estimating repeatability of longitude at each stationary site along the annual cycle.

Methods

Geolocator deployment and retrieval

We deployed light-level geolocators (Mk 10s, Mk 10, and Mk 12 by the British Antarctic Survey, BAS, weight 1.1 g, and Intigeo P65 from Migrate Technology, weight 0.75 g) on 119 individual male red-backed shrikes over seven consecutive breeding seasons from 2009 to 2015, at three sites in southern Scandinavia: Gribbskov, Denmark (55.98° N, 12.33° E, 80 males), Vittskövle, Sweden (55.85° N, 14.18° E, 32 males), and Ottenby, Sweden (56.5° N, 16.5° E, 7 males). Spring-traps (34 × 34 cm square flaptrap, double spring operated, 4 mm galvanized wire and covered with bird netting) and mist-nets placed near nesting sites were used to capture birds. The birds were then fitted with geolocators attached using a leg-loop backpack harness (Naef-Daenzer 2007). At deployment, the geolocator represented maximum 4.4% of the individuals' body mass. All males tracked were a minimum of two calendar years old during logger deployment. In the following years, 31 males returned to the Danish breeding site (return rate = 39%). The return rate exceeded that of a control group at the same site of red-backed shrikes with color rings 2016–2017 (27%, $n = 15$) as well as previous reports on return rates on the species (18%) (Tøttrup et al. 2017). However, this is due to the fact that only males, which are generally more conspicuous than females were considered in this study. Return rates could not be assessed for the Swedish breeding sites due to inconsistent search efforts across years. However, seven and two males were recaptured from Vittskövle and Ottenby, respectively. In total, we recaptured 33 males and retrieved 22 tracks with viable data, seven of which were repeated tracks, five males from Gribbskov and two males from Vittskövle. Repeated tracks were obtained in consecutive years within the study period (2009–2011, 3 individuals; 2011–2013, 1 individual; 2012–2014, 2 individuals; 2014–2016, 1 individual). Due to battery failure, spatiotemporal data for two repeatedly tracked individuals was not available from September and March in the second year of tracking, respectively. Only two repeatedly tracked individuals had information on breeding area arrival in both years of tracking. As our study involved focal animals in the field, it was not possible to record data blind.

Analysis of geolocator data

We adjusted data for clock drift and used a threshold of 0.3 for log-transformed data from the Intigeo geolocators and 2 for data from BAS geolocators to define twilight occurrences. False twilights, caused by, e.g., shading events during daytime or artificial light sources during nighttime were identified by visual inspection of a plot comparing the specific twilight with the twilight on the previous and following day using the R-

package *BAStag* (Wotherspoon et al. 2016). Thus, twilights that differed substantially from both the previous and following days (between 0 and 50 twilights) were removed from the dataset for each track (Online Resource Table S1).

Daily positions were calculated from light data using the *coord* function in the R-package, *GeoLight* version 2.0 (Lisovski and Hahn 2012). We used on-bird breeding site calibration to estimate individual sun elevation levels (−4.78 to −1.4). During equinoxes, estimates of latitude become unreliable as day length is approximately the same around the globe. Thus, we excluded latitudinal data from 14 to 26 days around this period in both autumn and spring, based on visual inspection of a plot depicting latitude over time for each individual (tol argument in *coord* function determining number of days to be excluded: 0.1–0.17, Online Resource Table S1).

Stationary sites, in terms of shorter staging areas and longer non-breeding areas, were determined as areas where migration was interrupted for more than five consecutive days, except for one individual where staging in spring seemed to last only 4 days. However, birds could have moved shorter distances within each stationary site. Migratory schedule, in terms of date of arrival and date of departure at each stationary site was determined based on visual inspection of plots of latitude and longitude over time. Events were characterized by simultaneous changes in both latitude and longitude over the course of the annual cycle. Thus, departure was estimated as the date when a clear directed movement away from a stationary site was identified, and arrival as the date when stabilization of longitude and latitude indicated a stationary period. During equinox, we based the migration schedule on longitudinal data only (Fudickar et al. 2012; Lisovski et al. 2012). Locations of stationary sites was determined as empirically estimated mean of latitudinal (excluding equinox) and longitudinal positions and are presented with standard deviations in Fig. 4.

Statistical analysis

For each stationary site throughout the annual cycle, we analyzed the repeatability of departure and arrival events and duration of migratory and stationary segments within the first and second year of repeatedly tracked individuals compared to the variability between the repeatedly tracked individuals. However, a low sample size ($n = 2$) prevented a test of repeatability at arrival to the breeding area. Repeatability was analyzed using the *rpt* function for Gaussian data in the R-package *rptR* version 0.9-2 (Stoffel et al. 2017). In this package, repeatability is estimated using a linear mixed effects model with a random effect of the grouping factor (individual) (Nakagawa and Schielzeth 2010). We ran 9999 bootstraps to obtain confidence intervals and estimated p values using the likelihood ratio test (Stoffel et al. 2017). We note that the sample size in this study is generally low for estimating repeatability ($n = 5–7$ and k (number of samples

per individual) = 2). Thus, confidence intervals are broad and results should be treated with caution (Wolak et al. 2012). To visualize the differences between and within repeated individuals at each departure and arrival event, we estimated the absolute differences in number of days between year 1 and year 2. The between-individual differences were estimated as all possible pairwise combinations of individuals across both years, while the within individual differences were estimated as the difference from year 1 to year 2 for each individual.

To describe the variability in timing of the population, we first calculated the overall population span and standard deviation (SD) for each departure and arrival event for all tracks, excluding repeated journeys ($n = 15$; 2009–2010, 6 individuals; 2010–2011, 1 individual; 2011–2012, 2 individuals; 2012–2013, 3 individuals; 2015–2016, 3 individuals). We then tested if there was a change in standard deviation between all events using Bartlett's test for equal variances. Relationships between consecutive departure and arrival events were tested for all individual tracks, excluding repeated journeys ($n = 15$), using linear mixed effects models with year as a random factor. Models were fitted by maximum likelihood, and we tested the significance of the correlations using likelihood ratio tests. As each event of departure and arrival may be dependent on previous departure and arrival events, we acknowledge that a model structure taking this temporal correlation aspect into account would be preferable (van Wijk et al. 2016). However, due to the low sample size, we did not include timing of events preceding the focal event in the model. We present a correlation diagram with Pearson correlation coefficients for all consecutive events.

To visualize the spatial variability in site use between the first and second years of repeatedly tracked individuals, we created polar plots showing distance and bearing from the first year to the second year using the R-package *plotrix* version 3.6-4 (Lemon 2006). Distances were calculated as great circle distances using the *distVincentyEllipsoid* function in the *geosphere* R-package version 1.5-5 (Hijmans 2016), and bearings were calculated using the R-package *fossil* version 0.3-7 (Vavrek 2011). The inherent inaccuracy of geolocators makes them unsuitable for estimating site fidelity. However, as variation in longitudinal estimates is relatively small, this may give an indication of the degree to which individuals return to similar areas. Thus, we estimated the repeatability of individual mean longitude for each stationary site using a similar approach as described above. All preprocessing of data and statistical analyses were done in the statistical software R 3.4.1 (R Core Team 2017). Data used in this study are available from the Movebank Data Repository: <<https://doi.org/10.5441/001/1.7mf48770>> (Pedersen et al. 2018).

Results

We found high and significant repeatability in the timing of departure of red-backed shrikes at their two main non-

breeding areas in sub-Saharan Africa ($r = 0.69$ – 0.85 , Table 1, Fig. 1). Likewise, the repeatability estimate of departure from the first staging area in southern Europe was moderate ($r = 0.62$), although non-significant, while repeatability in departure and arrival events at all other sites throughout the annual cycle was generally lower and non-significant ($r = 0$ – 0.44) (Table 1, Fig. 1). All individuals arrived earlier to the second staging area in eastern Africa on spring migration in the second year of tracking (Fig. 2). Likewise, there was a trend of an earlier migration from the breeding area until departure from the first staging area in southern Europe in the second year, but no clear trend between years was seen at any other arrival or departure event of migration (Fig. 2). Repeatability of duration at any migratory or stationary segment during the annual cycle was low and non-significant ($r = 0$ – 0.54 , $p = 0.11$ – 1 , Online Resource Table S2).

The total population span in timing of departure and arrival events of individuals tracked in 1 year ranged from 30 to 41 days, and we found no difference in variation between all departure and arrival events ($K = 2.55$, $df = 9$, $p = 0.98$). In repeated individuals, the between-individual differences of repeatedly tracked individuals was likewise similar across stages, ranging from 20 to 37 days during migratory events ($n = 5$ – 7). At arrival to the breeding area, this difference was 12 days likely due to the small sample size at this event $n = 2$ (Fig. 1). The lowest within-individual difference was found at departure from the second non-breeding area in southern Africa (mean \pm SD, 3.2 ± 2.95 days, $n = 5$) while the highest within-individual difference was found at arrival to that same site (11.8 ± 7.03 days, $n = 6$). At the breeding area, the within-individual differences were 1 and 4 days for the two individuals, respectively.

Timing of migration events was highly dependent on the timing of the preceding event (all $p < 0.01$, $n = 11$ – 15). Likewise, timing of events further back in the annual cycle

Table 1 Repeatability value (r), sample size (n), standard error (SE), confidence interval (CI), and p value of departure and arrival at each migration event throughout the annual cycle of red-backed shrikes. Significant results are highlighted in italics

Migration event	<i>n</i>	<i>r</i>	SE	CI	<i>p</i>
Breeding area departure	7	0.38	0.26	0–0.84	0.197
Southern Europe arrival	7	0.41	0.27	0–0.85	0.175
Southern Europe departure	6	0.62	0.27	0–0.92	0.065
Sahel arrival	6	0.44	0.28	0–0.88	0.181
<i>Sahel departure</i>	6	<i>0.69</i>	<i>0.25</i>	<i>< 0.001–0.94</i>	<i>0.039</i>
Southern Africa arrival	6	0.00	0.22	0–0.71	0.500
<i>Southern Africa departure</i>	5	<i>0.85</i>	<i>0.21</i>	<i>0.12–0.98</i>	<i>0.011</i>
Horn of Africa arrival	5	0.17	0.27	0–0.83	0.450
Horn of Africa departure	5	0.23	0.28	0–0.84	0.393
Breeding area arrival	2	–	–	–	–

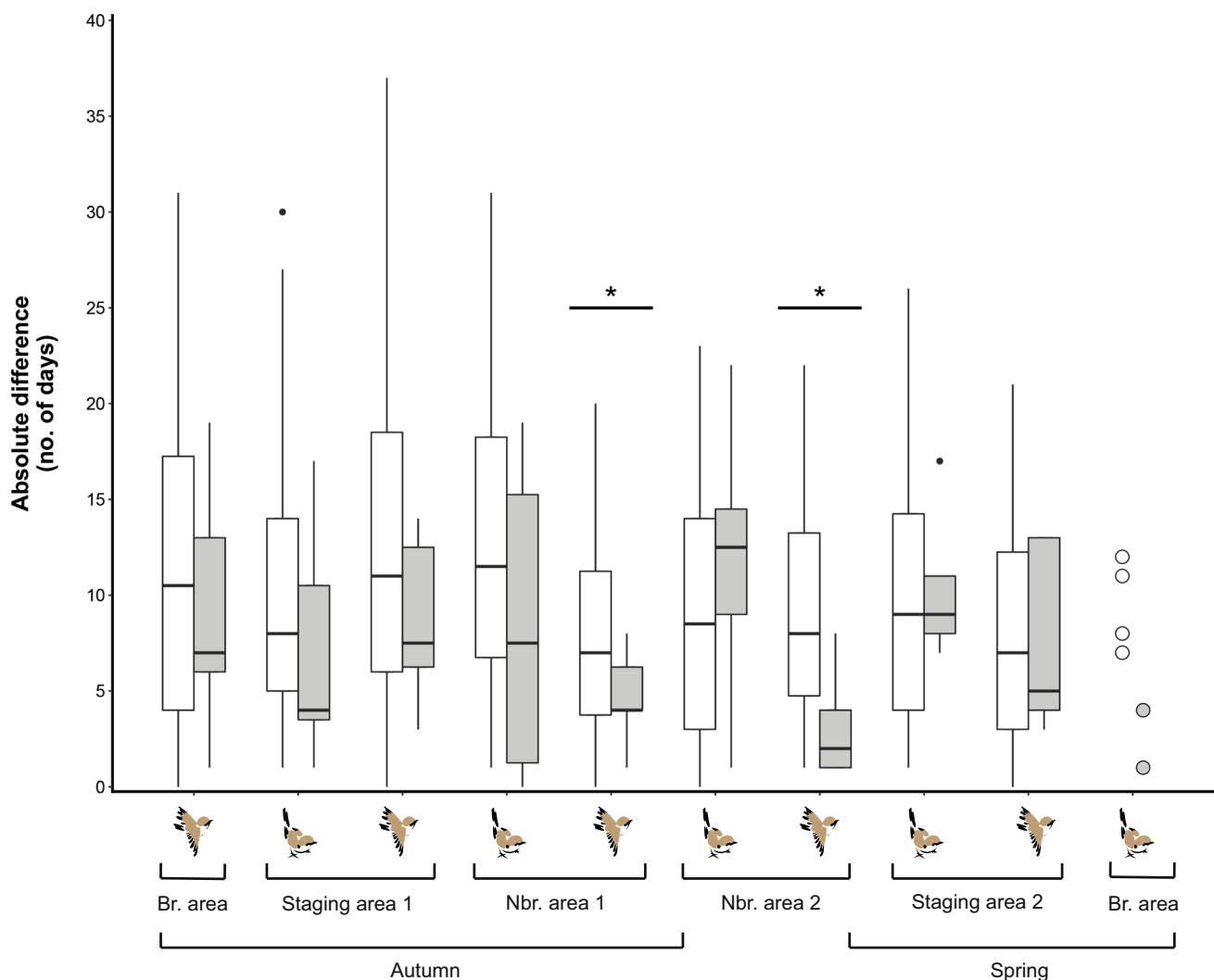


Fig. 1 Pairwise comparisons of absolute differences in number of days from year 1 to year 2 between repeated individuals (white boxes and circles) and within repeated individuals (gray boxes and circles) across migratory departure and arrival events at all stationary sites throughout the annual cycle (see “Methods”). Events are shown in chronological

order from departure at the breeding area to arrival at the same breeding area in the following year. Boxes indicate median values with 25 and 75 percentile. Whiskers represent 5 and 95 percentiles while dots indicate extreme values. Significant events, where the variation within individuals is lower than that between individuals, are marked by asterisk (* $p < 0.05$)

was positively related to the focal event, although dependencies weakened slightly over time (Fig. 3). Individuals leaving the breeding area early seemed to retain an early migration throughout the annual cycle, while late departing individuals retained a later timing throughout the annual cycle, although this was more variable (Online Resource Fig. S1).

The repeated individuals used the same overall stationary sites as the population as a whole (Fig. 4). Mean longitudinal estimates were highly repeatable for the two non-breeding areas in sub-Saharan Africa (Sahel: $r = 0.82$, $p = 0.006$; southern Africa: $r = 0.97$, $p < 0.001$), but not for the first staging area in southern Europe ($r = 0.52$, $p = 0.1$) or the second staging area in eastern Africa ($r = 0$, $p = 1$). The first staging area in southern Europe showed variation in both longitude and latitude, whereas all other sites differed mainly in latitude from the first to the second year of tracking (Fig. 4).

Discussion

Our results show that timing of departure in red-backed shrikes is more repeatable than timing of arrival across multiple stationary sites throughout their annual migration. Furthermore, we find a similar variation in the population timing across all migratory events as well as an extraordinary dependency in time, suggesting an overall rigid migratory schedule in this species.

The repeatability of departures as opposed to arrivals from the two non-breeding areas suggests a strong innate component related to timing of departure in this species (Berthold 1996) whereas timing of arrival is more likely to be caused by inter-annual variation in conditions such as weather experienced en route (Richardson 1978, 1990). However, we note that results should be interpreted with caution given the low sample size in this study. The suggestion of endogenous

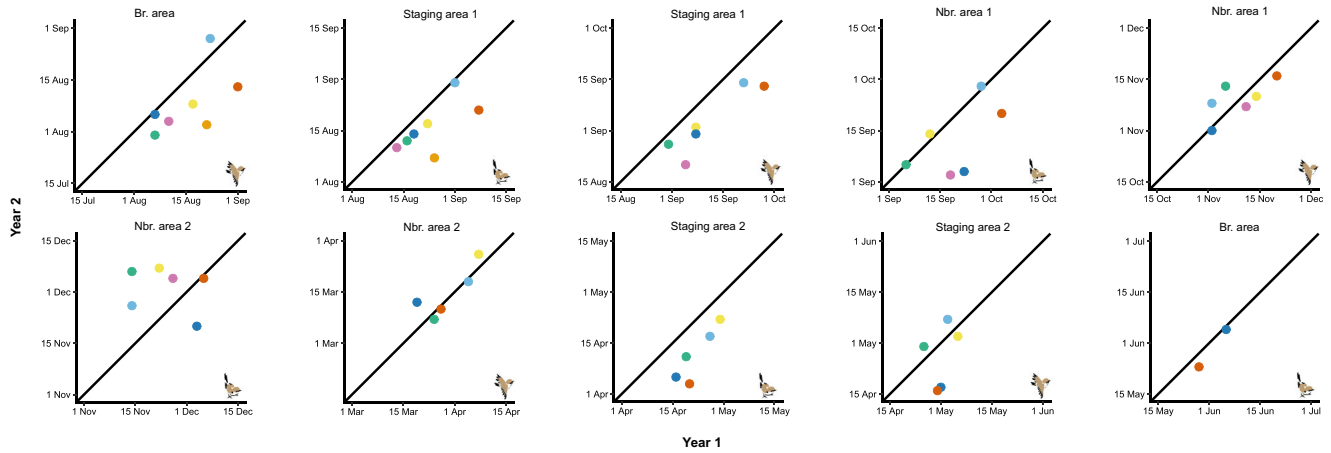


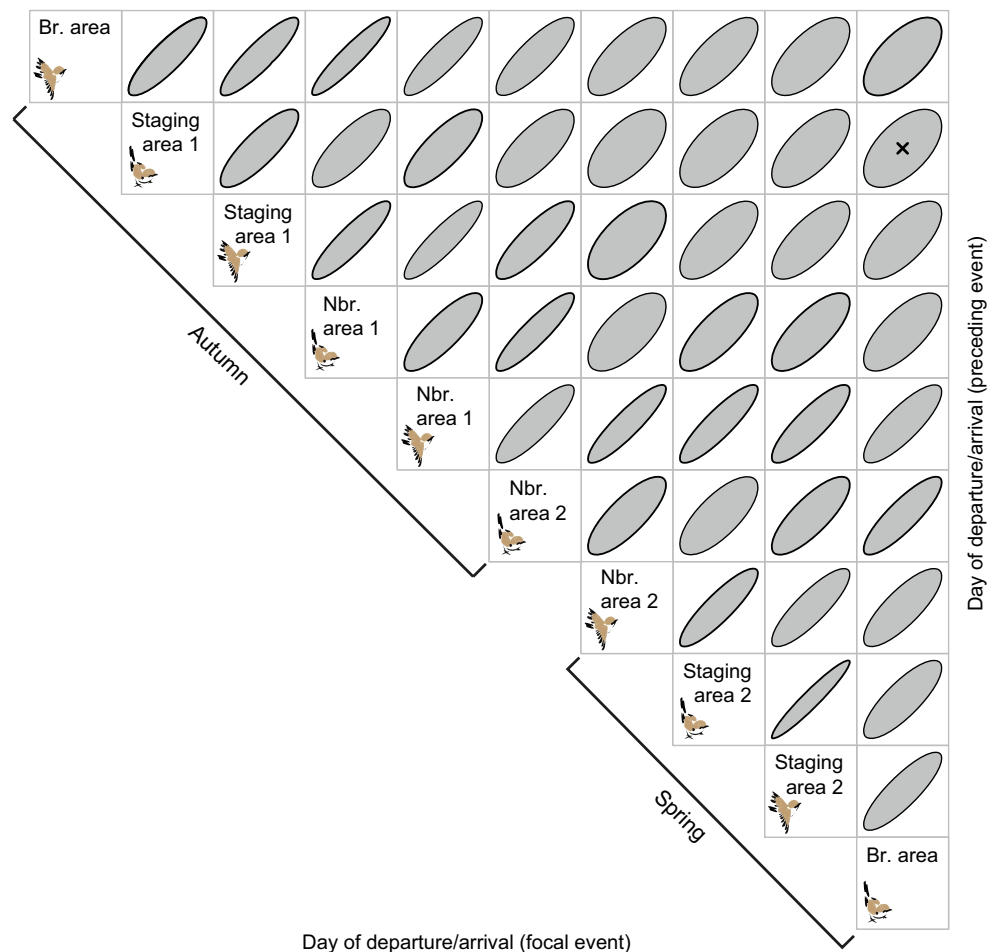
Fig. 2 Timing of migration of repeatedly tracked individuals at consecutive departure and arrival events throughout the annual cycle in year 1 (x-axis) and year 2 (y-axis), respectively. Colors represent different individuals, consistent with colors in Fig. 4. Solid line represents the scenario when individuals depart or arrive at the exact same date in both years. Points beneath and above the line represent an earlier and

later timing, respectively, in the second year of tracking. There is a trend of individuals being earlier in the second year until departure from staging area 1 in southern Europe and again at arrival at staging area 2 in spring, but no clear trend between years is seen at any other arrival or departure event

control on departure decisions corresponds to a previous study on the activity of red-backed shrikes in captivity, which found a low variation between individuals (and between

populations) in the expression of zugunruhe (migratory restlessness), roughly corresponding to the migratory schedule of free-flying red-backed shrikes throughout the annual cycle

Fig. 3 Composite figure showing the 45 bivariate correlation plots between departure and arrival events, arranged in sequence of their occurrence throughout the annual cycle (top left to bottom right). In each of the plots, the x-axis represents timing of the focal event and the y-axis represents timing of a preceding event, respectively. Shape of the ellipses indicates the strength of the correlation from circle (no correlation) to narrow ellipse (strong correlation). Crosses represent non-significant correlations. Note that all correlations are positive



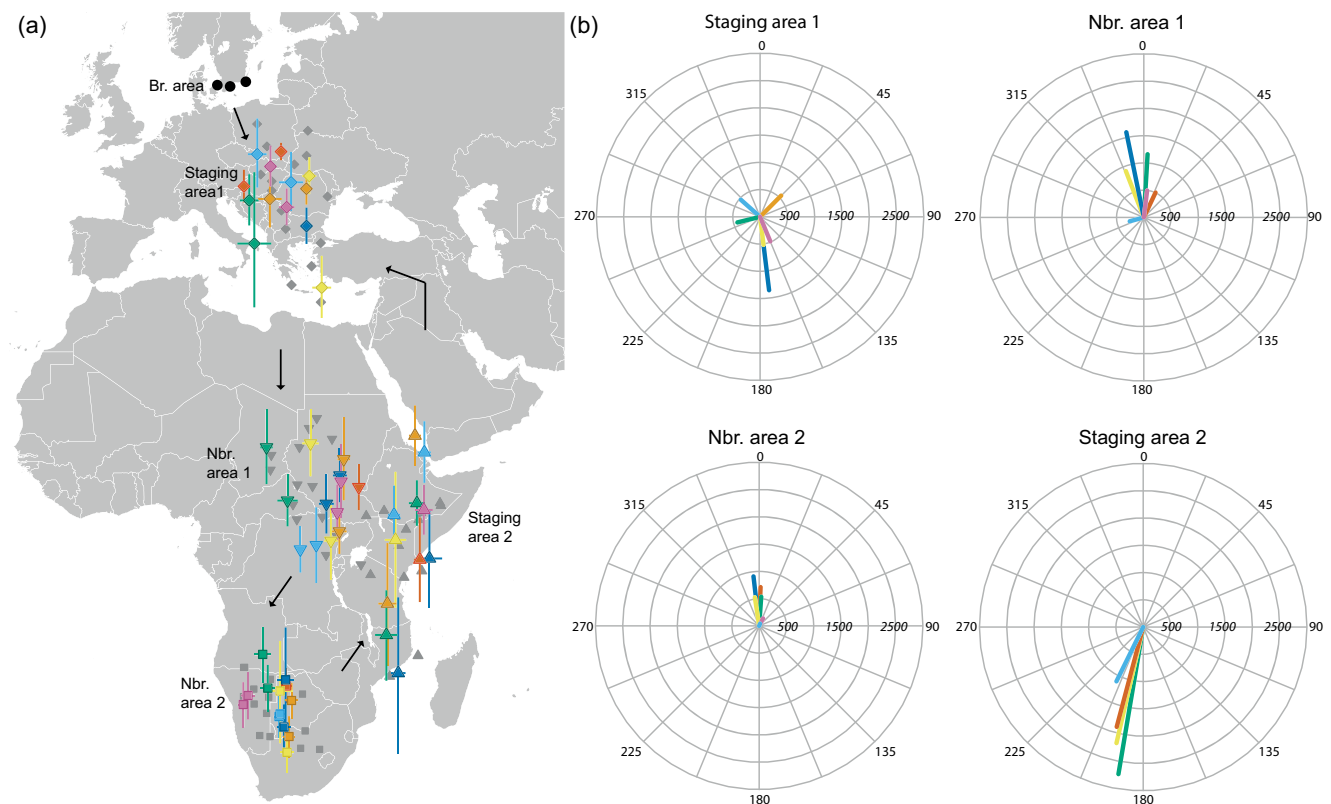


Fig. 4 Map (a) shows repeated individual mean positions \pm SD (colors in pairs) and mean positions of individuals tracked for 1 year (gray). Symbols denote stationary sites (circles, breeding area; diamonds, staging area 1; inverted pyramids, non-breeding area 1; squares, non-

breeding area 2; and pyramids, staging area 2). Arrows give migratory direction. Polar plots (b) show the direction (bearing) and magnitude of change (in km) from year 1 (center of plot) to year 2 for each individual across all staging areas

(Gwinner and Biebach 1977; Bäckman et al. 2017a, b). As repeatability is a relative measure comparing both within- and between-individual differences in behavior, the causes of repeatability can be low variation within individuals or high variation between individuals. In red-backed shrikes, the variation within and between individuals was lower during departure from the two non-breeding areas (on average 4.7 and 3.2 days within, as opposed to 20 and 22 days between, respectively) compared to other events, suggesting a strong selection for time at their main non-breeding areas. A similar pattern of repeatability in departure from the non-breeding grounds has been found in the Nearctic-Neotropical migratory songbird, the wood thrush *Hylocichla mustelina* with a similar between-individual variation (27 days) (Stanley et al. 2012). Likewise, repeatability in timing of migration at single sites has been reported for multiple songbird species indicating that the innate migration program may indeed be important in regulating the migratory schedule in songbirds (Thorup et al. 2013; Tarka et al. 2015; Both et al. 2016). However, great reed-warblers *Acrocephalus arundinaceus* show a contrasting pattern of low repeatability in timing of migration despite a similar variability in timing between individuals across migratory events (26–32 days) (Hasselquist et al. 2017). This might be due to the specific habitat requirements of great reed-

warblers, being dependent on wetlands, which may show higher inter-annual variation in the time of suitability, consequently leading to a lower selection for time.

Although repeatability was evident in departure from the main non-breeding areas in sub-Saharan Africa, we did not find repeatability in departure across all events. At the breeding area, departure is likely to be influenced by breeding investment (Sokolov et al. 1999; Phillips et al. 2005; Becker and Zhang 2010). The red-backed shrike lays replacement clutches, and thus, it is likely that differential investments in breeding efforts across years, due to differences in predation rate, local weather conditions, or physiological state, may have caused a low repeatability at departure from the breeding area. The low repeatability in timing of arrival and departure from the second staging area in eastern Africa could be explained by all repeatedly tracked individuals choosing an earlier, and thus more southerly located staging area in this part of the annual cycle in the second year of tracking. This was a surprising finding, which may be related to a more gradual migration strategy during spring than autumn migration in red-backed shrikes (Bäckman et al. 2017a). As the data were collected over multiple seasons, the pattern is unlikely to represent a year effect. However, due to the low sample size, we were unable to formally test this assumption.

The overall population variation in timing of migration was similar across all events of the annual cycle. Thus, we detected no sign of a synchronization effect previously reported for other species (Alerstam et al. 2006; Senner et al. 2014; Lindström et al. 2016; van Wijk et al. 2016). However, we found a clear dependency of migratory events throughout the annual cycle. This finding is similar to what has recently been described in a study on European nightjars *Caprimulgus europaeus* (Norevik et al. 2017). In conjunction with the repeatability results, this suggests that selection for time in red-backed shrikes acts on the individual rather than on the overall population (Conklin et al. 2013). Thus, individuals may be highly precise in their departure decision from the non-breeding grounds from year to year, with selection in different years favoring either early or late individuals across the annual cycle. We suggest that the overall similarity in variation is caused by a highly constrained migration pattern in red-backed shrikes, closely linked to the availability of resources across the annual cycle (Thorup et al. 2017). In addition, constraints related to molt at the main non-breeding area may explain why late individuals are not capable of initiating spring migration at an earlier stage (Buehler and Piersma 2008, but see Conklin and Battley 2012).

We found a high repeatability in longitude at the two non-breeding areas. This indicates that individuals may use a restricted longitudinal range within the overall population non-breeding areas (Tøttrup et al. 2012). The result is in agreement with a study predicting that songbirds are less site-faithful to stopover sites than their breeding and non-breeding areas (Catry et al. 2004). However, positions varied highly in latitude from year to year. This variation could be due to a true change of site but could likewise be an artifact of sun elevation angle calibrated to the habitat experienced at the breeding grounds, or by itinerant movements within the non-breeding season which cannot be detected by geolocators. Indications of this behavior have been suggested for red-backed shrikes using activity loggers (Bäckman et al. 2017a, b).

All individuals in this study were adults and have thus migrated at least one time before they were tracked for this study. This is due to the expected lower survival (Sæther 1989) and generally higher dispersal of juveniles in migratory bird species (Greenwood and Harvey 1982), making it practically impossible to track juveniles with geolocators, where individuals need to be recaptured. With ongoing advances in technology, transmitting tags that do not require the recapture of individuals will soon come within reach (Wikelski et al. 2007; Pennisi 2011). Age and thus experience is likely to improve individual migration strategies (Hake et al. 2003; Thorup et al. 2007). Thus, future research should aim at mapping juvenile migratory movements, as the behavior of juveniles is paramount to understanding the degree to which migration is inherited or can be learned.

Understanding how individual migratory birds are constrained across the annual cycle is crucial in predicting how migrants may respond to environmental changes. Here, we show that departures in red-backed shrikes are the key events underlying endogenous migration control, while arrivals may be more flexible. Still, the annual cycle appears to be overall constrained with high dependency in timing across migratory events, suggesting a rigid migration system potentially hampering the opportunities for red-backed shrikes to adapt to global changes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures in this study complied with the ethical standards of Danish and Swedish authorities. Capture and sampling methods, including spring-traps, were approved by the Copenhagen Bird Ringing Center with permission from the Danish Nature Agency (J.nr. SN 302-009). In Sweden, capture methods were approved by the Swedish Ringing Center with permission from the ethical committees in Malmö/Lund (M112-09).

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