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Sex-specific difference in migration schedule as a precursor of protandry in a long-distance migratory bird

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Abstract

Protandry, the earlier arrival of males at the breeding grounds relative to females, is common in migratory birds. However, due to difficulties in following individual birds on migration, we still lack knowledge about the spatiotemporal origin of protandry during the annual cycle, impeding our understanding of the proximate drivers of this phenomenon. Here, we use full annual cycle tracking data of red-backed shrikes *Lanius collurio* to investigate the occurrence of sex-related differences in migratory pattern, which could be viewed as precursors (proximate causes) to protandry. We find protandry with males arriving an estimated 8.3 days (SE = 4.1) earlier at the breeding area than females. Furthermore, we find that, averaged across all departure and arrival events throughout the annual cycle, males migrate an estimated 5.3 days earlier than females during spring compared to 0.01 days in autumn. Event-wise estimates suggest that a divergence between male and female migratory schedules is initiated at departure from the main non-breeding area, thousands of kilometres from-, and several months prior to arrival at the breeding area. Duration of migration, flight speed during migration and spatial locations of stationary sites were similar between sexes. Our results reveal that protandry might arise from sex-differential migratory schedules emerging at the departure from the main non-breeding area in southern Africa and retained throughout spring migration, supporting the view that sex-differential selection pressure operates during spring migration rather than autumn migration.

Keywords Protandry · Songbird migration · Geolocator · Red-backed shrike

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Introduction

To ensure optimal use of local resources, migratory birds need to time their annual migration schedule (McNamara et al. 1998; Thorup et al. 2017). At the breeding grounds, timing of arrival may be particularly important, as it is linked to reproductive output, and thus represents direct fitness consequences (Kokko 1999; Smith and Moore 2005; Gienapp and Bregnballe 2012). Likewise, the year-round migratory schedule of departure and arrival events may undergo selection, if performance at any stage is linked to success at subsequent life-history stages (Harrison et al. 2011; Woodworth et al. 2017). However, in general, the optimization selection process is expected to act on the sexes independently (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982; Bulmer 1983; Kokko et al. 2006).

Protandry, the phenomenon of males preceding females in arrival at reproductive sites, is observed across a variety of taxa and is common in migratory birds (Morbey and

Ydenberg 2001; Coppack and Pulido 2009). Our knowledge on sex-differential timing of migration in birds originates mainly from long-term ringing data series at bird observatories and spring migration stopover sites (e.g., Francis and Cooke 1986; Stewart et al. 2002; Rubolini et al. 2004). Although several mutually non-exclusive hypotheses have been proposed to explain this pattern, protandry in birds is thought to be ultimately driven by males benefitting from gaining priority access to higher quality territories (i.e., rank-advantage hypothesis) and/or mates (i.e., mate-opportunity hypothesis) (Morbey and Ydenberg 2001; Kokko et al. 2006; Morbey et al. 2012). Most studies on protandry have focused on the ultimate drivers with the aim of explaining selection for early arrival in males (Morbey and Ydenberg 2001). The proximate causes remain far less understood, mainly due to the difficulty in following birds on migration (Coppack et al. 2006; Coppack and Pulido 2009). However, recent advances in tracking technology, in terms of geolocators, have enabled us to follow even small songbirds on migration throughout their annual cycle, opening up opportunities for addressing previously unanswered questions regarding the phenology of bird migration (Bridge et al. 2011).

Protandry can result from a general difference in timing, geographical location or migration speed between sexes (Coppack and Pulido 2009). In terms of timing, it is unclear whether a difference in migratory schedule (timing of departure and arrival events) between males and females occurs throughout the annual cycle or is restricted to the last part of spring migration before reaching the breeding grounds. Alternatively, males could achieve early arrival by spending the non-breeding season closer to the breeding grounds, or by migrating faster than females. The latter could be realized if males have more pointed wings (Hedenström and Pettersson 1986) or can carry more fuel (Chandler and Mulvihill 1992) than females, thus allowing them to fly at higher ground speeds or prolong daily migration periods. In addition, males may have higher fuel deposition rates, resulting in less time spent at intermediate stopover sites (Lindström and Alerstam 1992; Seewagen et al. 2013). Recent studies using direct tracking techniques show various proximate causes of protandry in songbirds suggesting that drivers may differ between species. For instance, protandry seems to occur as a result of a difference in migratory schedule between males and females in northern wheatears and pied flycatchers (Schmaljohann et al. 2016; Ouwehand and Both 2017), while non-breeding area latitude may serve as a proximate cause of protandry in savannah sparrows (Woodworth et al. 2016). In contrast, no sign of protandry was found in collared flycatchers or barn swallows (Liechti et al. 2015; Briedis et al. 2016). Clearly, studies are still needed to clarify the extent to which protandry occurs in migratory birds and its proximate causes.

The red-backed shrike *Lanius collurio* is a long-distance migratory songbird, which breeds across the Palearctic and winters in the south-eastern parts of Africa (Snow and Perrins 1998; Tøttrup et al. 2012a). The migration route is complex, involving a series of longer stationary periods and a loop migration pattern going through central-eastern Africa in autumn and crossing the Arabian Peninsula in spring (Tøttrup et al. 2012a, 2017). Previous studies using standardised ringing data at two spring migration stopover sites located close to the breeding sites have suggested the occurrence of protandry in this species (Coppack et al. 2006; Tøttrup and Thorup 2008).

Here, we use full annual cycle tracking data to investigate the occurrence of protandry as well as behaviour that could be viewed as precursory to protandry in red-backed shrikes. Specifically, we explore whether significant sex differences are detectable in (1) the migration schedule in terms of timing of departure and arrival events at stationary sites, (2) migration speed at any segment of migration between stationary sites and (3) location of stationary sites throughout the annual cycle. Furthermore, we investigate whether average sex differences in migration schedule and speed within autumn and spring are significant, and whether they differ significantly between the two seasons. Finally, we examine whether duration of migration differs between the sexes in autumn and spring, respectively.

Methods

Geolocator deployment and retrieval

We used light-level geolocators (Mk10s, Mk10 and Mk12 developed by the British Antarctic Survey, BAS, weight: 1.1 g and Intigeo P65 from Migrate Technology, weight: 0.75 g) to determine geographical locations of sites where birds were stationary (staging sites during migration and main non-breeding site) and timing of departure and arrival events of individual red-backed shrikes at these sites throughout the annual cycle. During 6 years, a total of 247 individual red-backed shrikes (sex-ratio around 50:50) were caught at three breeding sites across southern Scandinavia: Gribskov in Denmark (55.98° N, 12.33° E, 2009–2014; 164 individuals), Vittskövle (55.85° N, 14.18° E, 2009, 2011–2012; 69 individuals) and Ottenby (56.5° N, 16.5° E, 2009; 14 individuals) in southern Sweden, using spring-traps or mist-nets in close proximity to the nesting sites. At logger deployment, the birds weighed 24.8–39.1 g. Thus, the logger represented a maximum of 4.4% of the body mass. Loggers were attached using a leg-loop backpack harness (Naef-Daenzer 2007). In the following years, 40 birds returned to the Danish breeding site Gribskov (return rate 24%). The return rate is similar to that of a control group of red-backed shrikes with colour rings at

the same site in 2016–2017 (27%, $n = 15$) and to return rates reported in a previous study on this species (18%) (Tøttrup et al. 2017). Return rates could not be assessed for the Swedish breeding sites due to inconsistent search efforts across years. In total, for all three sites, 39 birds were recaptured. At the Swedish breeding sites, the sex-ratio of recaptured birds was 50:50. However, at the Danish breeding site, fewer females (11) were recaptured than males (20). The latter is a common pattern in geolocator studies (McKinnon and Love 2018) and, in this case, likely caused by the more secretive behaviour of females during the breeding season. As some individuals had lost their geolocator and other loggers had failed, this resulted in a total of 31 tracks of red-backed shrikes from the three breeding sites (Gribskov, 16 males and 7 females, 2010–2016; Vittskövle, 5 males and 1 female, 2010–2014 and Ottenby, 1 male and 1 female, 2010). Seven of these were repeated tracks (Gribskov 5 males, Vittskövle 2 males). Tracking data from 20 individuals (27 tracks) have been analysed before and published with a different purpose (Tøttrup et al. 2012a, b; Pedersen et al. 2016, 2018). Data used in the current study are available from the Movebank Data Repository: https://doi.org/10.5441/001.1.j71640kh (Pedersen et al. 2019).

Light data analyses

Data were adjusted for clock drift, and false twilight events caused by shading were removed by visual inspection of a plot comparing the specific twilight with the twilight on the previous and following day using the R-package *BAStag* version 0.1-3 (Wotherspoon et al. 2016). We chose a threshold value of 2 for BAS geolocators and 0.3 for log-transformed data for the Intigeo geolocators to define twilight occurrences. Between 0 and 50 false twilight events were removed from the data for each track (Online Resource 1 Table S1). The occurrence of false twilights seemed to be roughly evenly distributed across the year. We used on-bird breeding site calibration to estimate individual sun elevation angles ranging from − 4.78 to − 1.4 (Online Resource 1 Table S1). Two daily positions were estimated from day length and local noon and midnight, respectively, using the R-package *GeoLight* version 2.0 (Lisovski and Hahn 2012). During equinox, where day length is approximately the same, estimation of latitude becomes unreliable. Thus, we excluded latitudinal data for up to 26 days around equinox periods for each individual based on visual inspection of a plot of latitude against time (tol: 0.10–0.17, Online Resource 1 Table S1). The statistical software R 3.4.1 (R Core Team 2017) was used for the pre-processing of the data described in this and the following section.

Migration phenology

Stationary sites were defined as areas where migration was interrupted for more than five consecutive days (minimum

number of days required to conservatively identify a stationary period by visual inspection), except for one individual for whom the spring migration stationary period seemed to last only 4 days. Migratory schedules in terms of date of departure and arrival at each stationary site throughout the annual cycle were determined by visual inspection of simultaneous changes in longitude and latitude 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 (Online Resource 1 Fig. S1). Thus, individuals may have had shorter stopovers in between the stationary periods and could have moved shorter distances within each stationary period. During equinox, we based the migration schedule on longitudinal data only (Fudickar et al. 2012; Lisovski et al. 2012). In the following, departure and arrival events are collectively referred to as events (10 events). Locations of the stationary sites were determined as empirically estimated mean longitude and latitude (excluding equinox) within the given stationary period for each individual, and are presented with standard deviations in Fig. 2. For two individuals, stationary sites and migration schedule for most sites could not be determined due to battery failure and poor data quality. Likewise, determination of the timing of arrival at the breeding area was not possible for seven individuals (eight tracks) due to battery failure and poor data quality during spring migration. Segments of migration were defined as the movement between two consecutive stationary sites (5 segments). We calculated great circle distances of migratory segments for each track containing geographical information on stationary sites using the *distVincentyEllipsoid* function in the geosphere R-package version 1.5-5 (Hijmans 2016). To take into account the loop migration pattern of red-backed shrikes in spring, we calculated the final spring migration segment as the sum of distances between the stationary site in eastern Africa to the point on the Arabian Peninsula where the birds change direction (defined as the north-eastern most point while the individual was at the Arabian Peninsula) and from this point to the breeding area. Speed of individual migratory segments was calculated as distance covered per day (km day^{-1}). For details on migration phenology for males and females, see Online Resource 1 Table S2.

Statistical analyses

The annual migratory schedule of each individual was described in terms of days since 1 July (day 1), with each observation indicating a time of departure or arrival at a stationary site (5 sites, 10 events). Potential sex differences in migratory schedule were investigated using a linear mixed effects model with migratory schedule as the response variable. We included fixed effects of sex, event, and their interaction, as well as random intercepts of bird identity and year to account for data

being sampled repeatedly from each individual, and across different years. Estimates of the fixed and random effects of the model are presented in Table 1. Within the framework of the model, the following comparisons were made using *t* tests. First, pairwise comparisons were made between the migratory schedule of males and females at each of the ten events throughout the annual cycle. Then, it was investigated whether the average differences in migratory schedule between males and females during autumn and spring, respectively, were significant, and the two differences were compared between seasons. Finally, total durations of autumn and spring migration, respectively, were compared between sexes. The R packages *lme4* version 1.1-19 (Bates et al. 2015), *lmerTest* version 3.0-1 (Kuznetsova et al. 2017) and *emmeans* version 1.3.2 (Lenth 2019) were used to fit the model, and to compute estimates, standard errors, and *p* values. Degrees of freedom were estimated by the Satterthwaite method. Due to the likelihood that timings of arrival and departure events in the migratory schedule are dependent on previous departures and arrivals (Lindström et al. 2016; van Wijk et al. 2016), and because there were signs of possible autocorrelation among the residuals of the model, we considered extending the correlation structure of the model to permit temporal correlation of the residuals. However, with the data available, no correlation structure remedying the issue was identified.

To investigate differences in migration speed, a second linear mixed model was fitted to the data with the natural logarithm of speed as the response variable, fixed effects of sex, segment, and their interaction, and random intercepts of bird identity and year. Speed was modelled on the logarithmic

scale to achieve a better model fit. As the standard deviation of the random intercept of bird identity was estimated to 0, the model was refitted without this random intercept. Estimates of the fixed and random effects of the model are presented in Online Resource 2 Table S3. Using the same approach as in the model for migration schedule, pairwise comparisons of log-speed were made between males and females at each of the five segments of migration. Furthermore, it was investigated whether, on average, there was a difference in log-speed between males and females during autumn and spring, respectively, and the average differences were compared between the two seasons. Based on diagnostics for the statistical models, speed was modelled on the log-scale in order to allow the assumption of variance homogeneity of the residuals.

To assess differences in the spatial distribution of males and females, we used linear models to describe the individuals' expected locations, using a separate model for each site. Each model had a stacked variable consisting of the respective averages of longitude and latitude observations for each individual as the response variable. Sex, component (a grouping variable designed to distinguish between longitudes and latitudes) and the interaction between these two variables were included as fixed effects. This structure of fixed effects enabled the model to describe expected locations in terms of a (longitude, latitude) pair, with both coordinates allowed to depend on sex. As geolocator data show marked differences in the accuracy of longitudinal and latitudinal estimates (Fudickar et al. 2012; Lisovski et al. 2012), we presume that the variances of the longitude and latitude components of a single, non-averaged position may differ. We also find it

Table 1 Model-based estimates of expected male and female migration schedules and the event-wise differences between the sexes (female timing subtracted from male timing) with corresponding standard errors (SE). *p* values in the last two columns are for the tests comparing the expected timing of males and females at each event throughout the annual cycle. *p* values in the second column have been Holm-Bonferroni adjusted for the ten event-wise tests

Event	Male		Female		Difference (male-female)		*p*	*p*.adj
	Estimate	SE	Estimate	SE	Estimate	SE		
Autumn migration								
Breeding area departure	38.38	3.18	38.13	3.95	0.25	3.90	0.950	1.000
Southern Europe arrival	46.78	3.18	47.57	3.95	− 0.79	3.90	0.841	1.000
Southern Europe departure	63.56	3.21	64.13	3.95	− 0.57	3.93	0.885	1.000
Sahel arrival	72.51	3.21	71.80	3.95	0.71	3.93	0.858	1.000
Sahel departure	125.16	3.20	127.13	3.95	− 1.97	3.92	0.618	1.000
Southern Africa arrival	143.64	3.20	141.35	3.95	2.29	3.92	0.562	1.000
Spring migration								
Southern Africa departure	265.19	3.22	270.46	3.95	− 5.28	3.93	0.186	1.000
Eastern Africa arrival	284.76	3.24	288.80	3.95	− 4.04	3.94	0.312	1.000
Eastern Africa departure	295.97	3.24	299.69	3.95	− 3.72	3.94	0.351	1.000
Breeding area arrival	324.25	3.31	332.50	4.01	− 8.25	4.07	0.048	0.483

Data consisted of 22 male tracks (*n* = 15 individuals) and 9 female tracks (*n* = 9 individuals). For more information on tracks, see "Methods" section

Estimated standard deviations of the random intercepts in the model were 7.29 for bird identity and 5.73 for year, while residual standard deviation was 5.90. The *p* value for the interaction between sex and event was *p* = 0.095

reasonable to expect a non-zero correlation between the two components. Furthermore, the number of positions used to calculate the average position for each individual varied. On the basis of these considerations, we included the following dependence structure in each model, assuming independence between individuals. The covariance structure of the average location of each individual was modelled using the covariance matrix for a single, non-averaged position as assumed above (same parameters for all individuals), weighted with the number of observations for the individual in question. Only complete pairs of latitude-longitude observations were included in the analysis, and repeated tracks were excluded, so as to only include observations from the first year each individual was tracked. The models were fitted using the R package *nlme* version 3.1-137 (Pinheiro et al. 2018). Estimates of fixed effects from the models are presented in Online Resource 2 Table S4. For each site, a likelihood ratio (LR) test was used to investigate whether the expected average locations of males and females differ.

The analyses described in this section were run in the statistical software R 3.5.2 (R Core Team 2018). All reported estimates, standard errors, and p values for tests related to the models for migratory schedule, speed, and location are based on restricted maximum likelihood (REML), with the exception that the location models were refitted by maximum likelihood (ML) for the LR tests. p values reported in the text have not been corrected for multiple tests. However, corresponding Holm-Bonferroni adjusted p values can be found in tables for comparison.

Results

All individuals performed a loop migration pattern, leaving the breeding area in August (males, empirical mean = 10 August, SD = 10.0 days; females, 09 August, 10.4 days). In the following year, individuals returned to the breeding area in May (males, 23 May, 9.9 days; females, 30 May, 5.7 days). The annual cycle included two main stationary sites during autumn migration (southern Europe and the Sahel region), the main non-breeding area in southern Africa, and a stationary site in eastern Africa during spring migration.

Based on our model framework, we found protandry in red-backed shrikes with males arriving at the breeding grounds 8.3 days (SE = 4.1) prior to females ($p = 0.048$). None of the other event-wise comparisons between sexes revealed significant differences in migratory schedule. However, model estimates suggest that males initiate spring migration from the main non-breeding area in southern Africa prior to females, and retain an earlier schedule than females throughout their migration towards the breeding grounds (Fig. 1, Table 1). On average, we found no difference in migration schedule between sexes within seasons

(Online Resource 2 Table S5). However, the average difference in migratory schedule between males and females differed significantly between autumn and spring ($p < 0.001$), with males migrating, on average, 5.3 days earlier than females at each event during spring migration compared to 0.01 days earlier during autumn migration (difference between estimates, 5.3 days, SE = 1.6). While the estimated sex differences at each event have varying signs and are not of a substantial size during autumn, they all have the same sign and are of a comparatively larger magnitude during spring. Thus, the data display a consistent difference between male and female migratory behaviour within each of the two seasons, and the comparison of average sex differences in migration schedule between seasons takes into account this consistency. These considerations possibly explain how a significant difference between seasons could be established, even though no significant sex difference was found within seasons. Excluding the two Swedish breeding sites with fewer individuals from the model for migratory schedule revealed similar results, although the difference in time of arrival at the breeding grounds was no longer significant ($p = 0.056$).

We detected no difference in duration of migration between sexes in autumn or spring (Online Resource 2 Table S5) and likewise, no significant differences were found when comparing migration speed between sexes (Online Resource 2 Table S3 and S5). Furthermore, there was no indication of a difference in the location of males and females at any of the stationary sites (southern Europe, $p = 0.13$; Sahel, $p = 0.62$; southern Africa, $p = 0.85$; eastern Africa, $p = 0.08$) (Fig. 2, Online Resource 2 Table S4).

Discussion

Using direct tracking data, we confirm previous indications of protandry in red-backed shrikes with males preceding females in arrival at the breeding grounds. Comparing autumn and spring migration, we find that behaviour likely linked to protandry in this species occurs during spring rather than autumn migration. Estimates suggest that a divergence in migratory schedule between males and females is initiated at the onset of spring migration from the non-breeding grounds in southern Africa.

The estimated 8-day earlier arrival of males relative to females exceeds the 1–3 day average reported in previous studies on red-backed shrikes based on standardised ringing data (Coppack et al. 2006; Tøttrup and Thorup 2008). However, we note that our modelled standard errors are relatively large and when applying a Holm-Bonferroni correction for the ten event-wise tests, the difference is no longer significant (Table 1). The finding that sex-specific migration schedules seem to arise at the beginning of spring migration is in accordance with the findings of recent studies using geolocators

Fig. 1 Model estimates of expected difference in migratory schedule (number of days ± SE vertical lines) for departure and arrival events at all stationary sites throughout the annual cycle (female migratory schedule subtracted from male migratory schedule). Symbols correspond to stationary sites shown in Fig. 2. Stationary site abbreviation: Br Breeding area, s.Eur southern Europe, s.Afr southern Africa, e.Afr eastern Africa
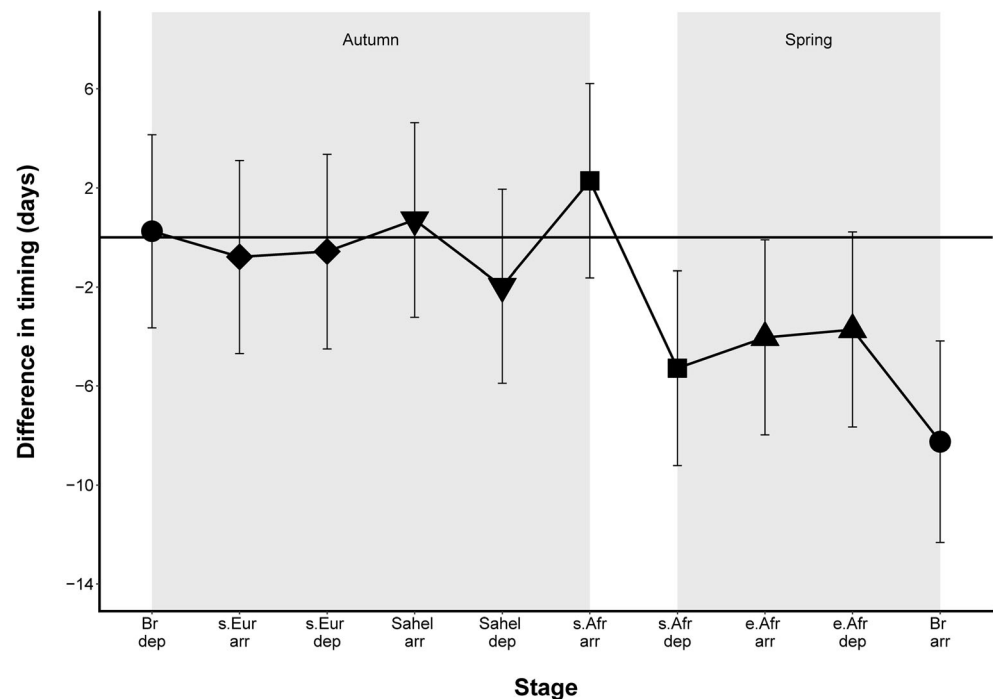
across a range of species (Jahn et al. 2013, McKinnon et al. 2016, Ouwehand and Both 2017, Briedis et al. 2019, but see Liechti et al. 2015, Briedis et al. 2016). In addition, observational studies on American redstarts and Kirtland's warblers have suggested earlier departure of males relative to females from the non-breeding area (Studds and Marra 2011; Wunderle et al. 2014). It is possible that small effect sizes, as well as limited sample sizes, generally presented in geolocator studies are preventing us from seeing a significant effect of sex-specific departure time. However, the proximate causes underlying protandry also vary with species and between continents (Coppack and Pulido 2009).

Decision of departure from the non-breeding area in long-distance migrants is generally assumed to be underlying endogenous control (Berthold 2001; Bazzi et al. 2015; Saino et al. 2015; Pedersen et al. 2018) in combination with environmental cues (Thorup et al. 2017), experience (Mitchell et al. 2015) and, on a finer temporal scale, weather conditions and habitat quality (Studds and Marra 2011; Tøttrup et al. 2012b; Cooper et al. 2015). Thus, local conditions experienced at the non-breeding sites could shape the pattern of individual migratory schedules in spring (Reudink et al. 2009; Tøttrup et al. 2012b; Pedersen et al. 2016). It is important to note that, ideally, the decision of when to depart should include the time spent fattening up before migration (Alerstam and Lindström 1990). For instance, if females experience lower habitat quality than males, they may require more time to gain an adequate body condition for migration which may lead to sex differences in departure dates (Cooper et al. 2015) potentially despite similar endogenous programs.

Although no sex-specific difference has been found in isotopic signatures of feathers grown at the non-breeding area (Jakober et al. 2007; Pedersen et al. 2016), male and female red-backed shrikes have been suggested to occupy different habitat structures at non-breeding sites in southern Africa (Bruderer and Bruderer 1994; Herremans 1997). Sex-related differences in migratory behaviour have been shown for northern wheatears and black-throated blue warblers in captivity in the absence of environmental cues, suggesting sex-differential endogenous control of departure decision independent of the surrounding environment in these species (Maggini and Bairlein 2012; Deakin et al. 2019).

Although sex-differential timing of migration can potentially occur throughout the annual cycle, events leading to protandry are assumed to occur mainly during spring migration, due to the direct fitness benefits of early arrival at the breeding grounds (Kokko 1999). In contrast, protogyny, the earlier migration of females compared to males, has been suggested in some species during autumn migration (Mills 2005). Here, we found no indication that females migrated earlier than males during autumn migration.

Time constraints in spring may result in increased migration speed (Stanley et al. 2012; Nilsson et al. 2013; Senner et al. 2014; Sergio et al. 2014) and sex-differential selection pressures (Morbey and Ydenberg 2001) could further act to differentiate speed between the sexes on spring migration. To increase speed, birds must either fly faster than their conspecifics or spend less time at stopover sites, replenishing their body stores at higher rates (Alerstam 2003; Hedenström 2008). There has been some indication of differences in wing

Fig. 2 Emperical mean location (± SD) of male and female red-backed shrikes across all stationary sites (1–5) throughout the annual cycle, black dots, breeding areas; diamonds, southern Europe; inverted pyramids, Sahel; squares, southern Africa; pyramids, eastern Africa. Blue and red colours represent male and female locations, respectively, and arrows give migration direction. Background map is shown in Mercator projection
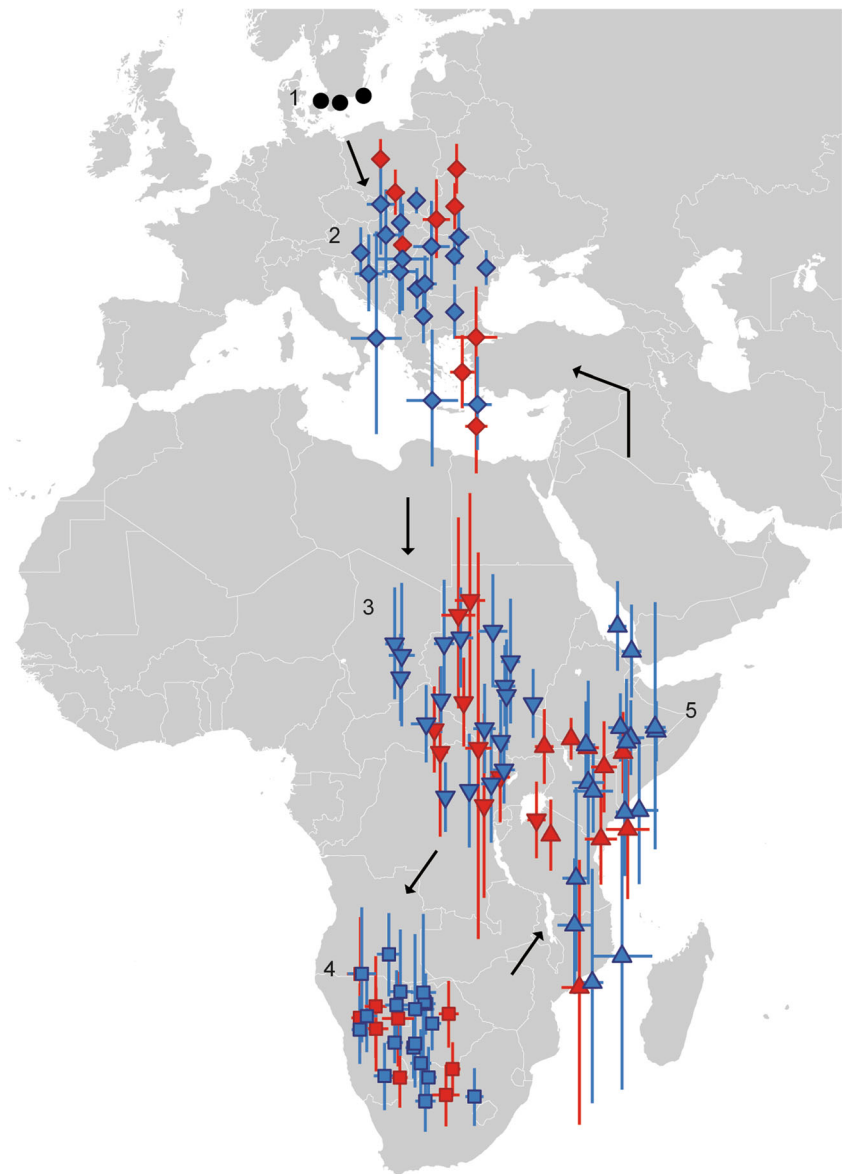
morphology between males and females (Hedenström and Pettersson 1986), as well as increased fuel deposition rates in males at stopover sites from previous studies (Dierschke et al. 2005; Seewagen et al. 2013; Schmaljohann et al. 2016). Our data did not allow for such analysis. However, we found no difference between males and females with respect to speed at any travel segment or total duration of migration (including time spent re-fueling at stopover sites), suggesting similar constraints on migration speed between sexes in this species.

We found no indication of a spatial segregation of males and females at any site throughout the non-breeding season. This finding contributes to the accumulating number of studies suggesting that sex-specific broad scale spatial segregation is not a common phenomenon in migratory birds within the European-Afrotropical migratory system (Berthold 2001;

Newton 2008; Liechti et al. 2015; Schmaljohann et al. 2016; Ouwehand and Both 2017).

Recent studies suggest that individual migratory schedules may, overall, be more synchronized in spring than in autumn (Conklin et al. 2013, Lindström et al. 2016, van Wijk et al. 2016, but see Pedersen et al. 2018). This finding has implications for protandry, as one could expect event-wise differences in variance depending on sex-differential selection pressures. However, we found no need to take sex differences in variance into consideration in this study (Online Resource 1 Fig. S2).

As age determination in red-backed shrikes is unreliable (Svensson 1992), we were not able to explore a potential age effect. However, the combination of the relatively low sample size of females relative to males and the unknown age distribution may indeed have obscured the differences in migration schedules in this study. An age effect on timing of

departure from the non-breeding grounds has been shown in wood thrushes (McKinnon et al. 2014) and is commonly demonstrated upon arrival at the breeding sites (Hill 1989; Lozano et al. 1995; Potti 1998; Smith and Moore 2005; Both et al. 2016; Schmaljohann et al. 2016).

Understanding the intra-specific spatiotemporal organization throughout the annual cycle in migratory songbirds is important for assessing the link between migration and other life-history stages. The continued advancements in tracking technology offer new research opportunities and may in combination with on ground experiments and observations in Sub-Saharan Africa (Robinson et al. 2010; Underhill and Brooks 2016) improve our understanding of the proximate causes underlying protandry, enabling us to predict how migratory birds are constrained in time and space. Here, we find that inter-sexual selection pressures occurring at the breeding grounds may act throughout spring migration, supporting the view that spring migration is under stronger sex-differential selection pressures than autumn migration.

Compliance with ethical standards

Informed consent   Informed consent was obtained from all individual participants included in the study.

Ethical approval   All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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