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Combining direct and indirect tracking techniques to assess the impact of sub-Saharan conditions on cross-continental songbird migration

Lykke Pedersen[1] · Kevin C. Fraser[2] · T. Kurt Kyser[3] · Anders P. Tøttrup[1]

Abstract Understanding how events throughout the annual cycle interact to influence individual fitness and hence population dynamics is crucial to optimize conservation strategies for migratory birds. Despite major advancements in technology, direct tracking devices for passerine songbirds are still limited by the need for recapturing tagged individuals. Stable-isotope analysis of bird tissue has the opportunity to supply information on a larger number of individuals, although it is limited by the indirect knowledge of the geographical position of the birds. In this study, we provide a first attempt to combine annual spatio-temporal data achieved from direct tracking with information on local environmental conditions by using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). We use this approach to investigate if environmental conditions at the wintering area in southern Africa influence timing of spring migration and carry-over to affect breeding performance in a long-distance migratory passerine bird, the Red-backed Shrike (*Lanius collurio*). We found that individuals wintering in relatively moist conditions (depleted in $\delta^{13}C$) and at lower latitudes (closer to the breeding grounds) departed later on spring migration than individuals in more xeric habitats. However, the effect of non-breeding area conditions and latitude were not found at subsequent migration stages and late departing individuals spent fewer days on migration towards the breeding grounds. Although conditions in the non-breeding range have previously been suggested to influence population fluctuations in Red-backed Shrikes, we found no evidence of a carry-over effect on breeding performance. This study highlights the potential of combining different approaches when investigating seasonal interactions in migratory animals.

Keywords Carry-over effects · Non-breeding ecology · Migration · Stable isotopes · Geolocators

✉ Lykke Pedersen
lypedersen@snm.ku.dk

[1] Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

[2] Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, MB, Canada

[3] Department of Geological Sciences and Geological Engineering, Miller Hall, Queen's University, Kingston, ON, Canada

Zusammenfassung

Kombination von direkten und indirekten Ortungsmethoden zur Bewertung des Einflusses der Bedingungen in der Subsahara auf den interkontinentalen Zug von Singvögeln

Das Verständnis dafür, wie die diversen Ereignisse im Verlauf eines ganzen Jahres miteinander zusammenhängen und die individuelle Fitness und damit die gesamte Populationsdynamik beeinflussen, ist ausschlaggebend für die Optimierung von Strategien zum Schutz von Zugvögeln. Trotz erheblicher technischer Fortschritte besteht die Einschränkung, dass Geräte zur direkten Ortung davon abhängig sind, damit ausgestattete Vögel wiederfangen zu müssen. Die Analyse stabiler Isotope aus Vogelgeweben bietet die Möglichkeit, Informationen von einer großen Anzahl Individuen zu sammeln, ist aber dadurch

eingeschränkt, dass sie keine direkten Informationen über die geographische Position der Vögel liefert. In dieser Untersuchung stellen wir einen ersten Versuch vor, räumlich-zeitliche Daten aus direkten Ortungen mit Informationen über lokale Umgebungsbedingungen, gewonnen aus Bestimmungen stabiler Isotopen (δ^{13}C and δ^{15}N), zu kombinieren. Dieser Ansatz wurde gewählt, um herauszufinden, ob die Umgebungsbedingungen an den Überwinterunsgplätzen im südlichen Afrika den Beginn des Frühjahrszugs beeinflussen und beim Langstreckenzieher, dem Neuntöter (*Lanius collurio*), eventuell noch auf den Bruterfolg durchwirken. Wir stellten fest, dass Vögel, die in einer relativ feuchten Umgebung (wenig δ^{13}C) und in geringeren geographischen Breiten (näher an den Brutgebieten) überwintert hatten, den Frühjahrszug später begannen als Vögel aus trockeneren Gebieten. Eine Auswirkung von Umgebungsbedingungen außerhalb der Brutgebiete und/oder von der geographischen Breite auf spätere Stadien des Zugs konnte jedoch nicht festgestellt werden; später startende Individuen verbrachten weniger Tage auf dem Zug in die Brutgebiete. Obwohl schon früher vermutet wurde, dass sich beim Neuntöter die Bedingungen außerhalb der Brutgebiete eventuell auf Populationsfluktuationen auswirkten, konnten wir keinen Beweis für derartige „carry-over"-Effekte auf den Bruterfolg feststellen. Diese Studie unterstreicht das Potential, das bei der Untersuchung saisonaler Interaktionen bei Tieren mit Zugverhalten in der Kombination unterschiedlicher Ansätze liegt.

Introduction

Organisms living in seasonal environments are exposed to regular fluctuations in resource quality and abundance, which influences population dynamics (Fretwell 1972). Events throughout the year are thus inextricably linked, and conditions experienced at one stage may carry over to affect subsequent life-cycle stages (Harrison et al. 2011). This becomes even more complex when considering migratory species that spend the year in widely different geographical locations with great variation in habitat and climatic zones (Greenberg and Marra 2005; Kays et al. 2015).

Migratory bird populations have experienced steep global declines over the past century (Kirby et al. 2008; Robbins et al. 1989; Sanderson et al. 2006); a decline primarily affecting long-distance migrants (Heldbjerg and Fox 2008; Sanderson et al. 2006; Vickery et al. 2014). To optimize conservation efforts for migratory bird species, we need to understand how events and processes interact during different stages of the annual cycle to determine

individual fitness, and hence overall population dynamics (Harrison et al. 2011; Norris and Marra 2007).

Timing of migration in long-distance migrants is assumed to be regulated mainly by endogenous control and photoperiod (Berthold 1996; Gwinner 1996). However, there is growing evidence that environmental factors at the non-breeding grounds (Gordo et al. 2005; Marra et al. 1998; Saino et al. 2007) and en route (Marra et al. 2005, Tøttrup et al. 2008, 2010) can shape the patterns of spring migration. Where determination of migration schedules has hitherto relied on field observation (e.g. sighting records and day of first capture), technological advances have now enabled us to study individual migration, providing detailed information on staging area location, timing, duration, and speed of migration of small songbirds by means of light-level geolocators (McKinnon et al. 2013; Stutchbury et al. 2009; Tøttrup et al. 2012a, b). The majority of work using geolocator technology has so far been focused on describing migration patterns in songbirds. However, the accumulation of sufficient data has sparked an interest in studies considering the ecological context of movement patterns (Bridge et al. 2015; Emmenegger et al. 2014; Fraser et al. 2012, 2013; Streby et al. 2014; Tøttrup et al. 2012b). Despite this progress, tracking devices are still limited by the need for recapturing individuals to retrieve the data (Bridge et al. 2011). Stable-isotope analysis of bird tissue has been a valuable tool in assessing local habitat condition of the moulting site in relation to seasonal interactions and can supply information on a larger number of individuals compared to direct tracking (Marra et al. 1998; Smith et al. 2010; Studds and Marra 2005; but see: Graves et al. 2002). However, it is hampered by the indirect knowledge it provides of the geographical position of the bird. Overall, these limitations stress the importance of combining different methodologies in order to increase our understanding of movement ecology (Korner-Nievergelt et al. 2012; Macdonald et al. 2012; see e.g. Norris et al. 2006; Woodworth et al. 2016).

The Red-backed Shrike (*Lanius collurio*) is a long-distance Palearctic-Afrotropical migratory songbird, breeding in most of Europe and western Asia and wintering in southern Africa (Snow and Perrins 1998; Tøttrup et al. 2012a). Like many other long-distance migrants this species has been declining, mainly in the western part of its breeding range (BirdLife International 2004). Recent studies have shown that environmental factors operating outside the breeding area are likely to influence population size as well as reproductive performance at the breeding grounds (Pasinelli et al. 2011; Schaub et al. 2011). Furthermore, habitat segregation between males and females at the non-breeding grounds in Red-backed Shrikes has been reported, with males occupying more arid habitat (Herremans 1997). It is well known that the environment in sub-Saharan Africa is subject to changes due to human

pressure and climate change (Brink and Eva 2009; Müller 2009), which could potentially cause sex-biased effects on individual fitness. Considering that Red-backed Shrikes spend most of the year in southern Africa (Tøttrup et al. 2012a), it is important to investigate to which degree environmental conditions operating at this stage will affect individuals during spring migration and in the subsequent breeding season. As the Red-backed Shrike undergoes a complete moult at the non-breeding area in sub-Saharan Africa (Bruderer 2007), the stable isotope values in the feathers can be used as a measure of the conditions at this stage.

In this study, we combine spatio-temporal tracking data of individuals tracked with light-level geolocators from a northwestern European breeding site with stable-isotope analyses of feathers belonging to the same individuals. The aim is to investigate if habitat conditions experienced by individuals at the wintering grounds in southern Africa may influence timing of spring migration. Furthermore, we include data on reproductive performance from the same breeding population to assess if conditions at the wintering grounds may carry over to affect breeding performance in the Red-backed Shrike. We hypothesize that variation in habitat conditions during the non-breeding season may affect individual timing of migration, leading to a difference in arrival schedules that may have consequences for individual fitness. If habitat conditions experienced during the non-breeding season are indeed an important determinant of individual fitness, we expect to find a relationship between stable isotopic values and reproductive performance in the subsequent breeding season. In addition, we test for a relationship between geographical location derived from geolocator data and stable isotopic values, and whether habitat conditions in the non-breeding season differs between males and females.

Methods

Migration phenology

Geographical locations of individual staging areas were determined from annual tracking of birds from their breeding sites in northwestern Europe (Gribskov in Denmark: 55.98°N, 12.33°E) using light-level geolocators (Mk10 and Mk12, developed by the British Antarctic Survey, BAS). Red-backed Shrike territories were mapped throughout the study site, and individuals were captured using either spring-traps or mist-nets in proximity to the nest site. During four consecutive years (2009–2012), 111 Red-backed Shrikes were colour-ringed and fitted with geolocators using a leg-loop harness. In the following years 31 of these individuals were resighted within the study area (return rate: 28 %), of which 24 were recaptured. Because

some individuals had lost their geolocator this resulted in 16 geolocators recovered with useful data. Of the 16 individuals, we obtained feather samples from 12 and were, thus, able to compare stable isotope and geolocator data (having collected feathers from the year of the retrieval of the geolocator) from 12 individuals (13 tracks, one individual being repeated) breeding in Denmark. Tracking data from 11 of these individuals have been analysed before and published with a different purpose (Tøttrup et al. 2012a, b). Additional data were thus analysed following the same procedure to ensure comparability among tracks. Geolocator positions were estimated from light-level recordings using the software BASTrack (Fox 2010). To define sunrise and sunset times we used a light-level threshold value of two, corresponding to the sun being below the horizon. Latitude and longitude positions were inferred from day length and local noon and midnight, respectively. We established the most suitable sun-azimuth angle for estimating latitude positions for each individual using the Ekstrom-Hill calibration procedure (Ekstrom 2004; Hill and Braun 2001). Departure and arrival dates were determined from two daily estimates of longitude and latitude positions. During periods around equinox where day length is the same, departure and arrival dates were based solely on longitude positions. Individuals were defined as stationary when interrupting migration for more than 5 days. This resulted in the birds having one spring stopover between the wintering area and the breeding site. Location of the wintering site and spring migration stopover sites was estimated as the mean latitude (excluding periods around equinox) and longitude position within the stationary period and presented with standard deviations (Fig. 1). For one individual it was not possible to determine wintering area position and timing of the stopover in eastern Africa due to coincidence with equinox period and poor data quality of longitude positions during this period. Likewise, for two individuals, arrival at the breeding site was not possible to estimate due to poor data quality and battery failure during spring migration. Migration phenology, in terms of (1) non-breeding area departure, (2) departure from the stopover site on the Horn of Africa, and (3) arrival at the breeding grounds were derived from latitude and longitude estimates. However, during equinox periods, where day length is approximately the same, departure and arrival were estimated solely from longitudinal data (Fudickar et al. 2012; Lisovski et al. 2012). For further information on geolocator tracking and light-level geolocator analyses see Tøttrup et al. (2012a).

Stable-isotope analysis

Feathers were collected for individuals where we had obtained information on migration phenology or breeding

Fig. 1 Mean individual positions ±SD during stationary periods on spring migration based on geolocator data. *Triangles* represent the wintering area in southern Africa, *circles* the stopover site in eastern Africa and square the breeding area in Denmark. *Dark grey symbols* represent the early migrating individual while *light grey symbols* correspond to the individual with repeated tracks. *Dashed arrows* show direction of spring migration (Tøttrup et al. 2012a)
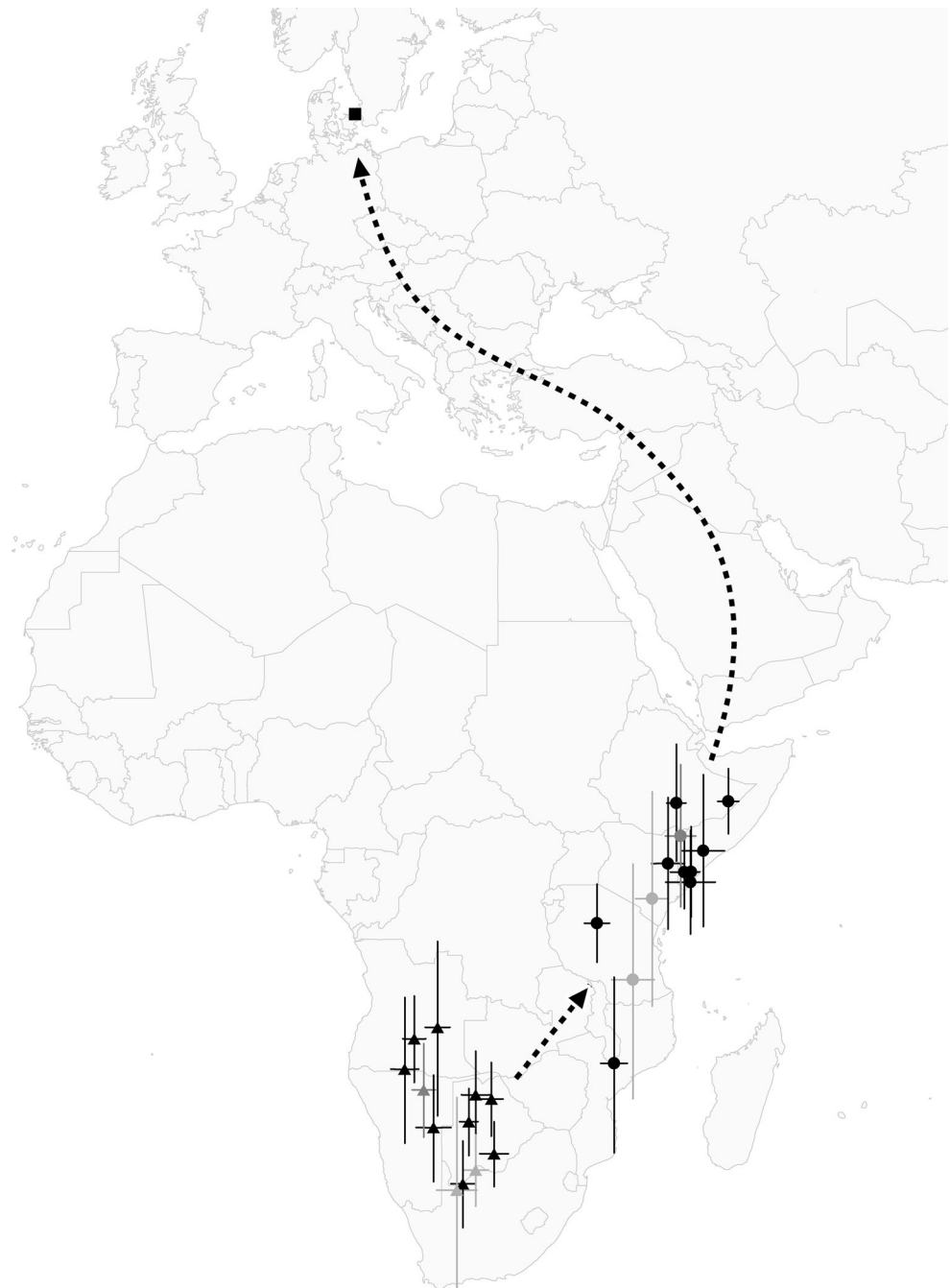
performance. For each individual, the innermost tail feather (T1) was plucked, and feathers were kept dry in paper envelopes until analysis. A total of 57 feathers (belonging to 50 individuals, some individuals were trapped multiple years) were collected.

We analysed feathers for δ^{13}C and δ^{15}N. Feathers are metabolically inert after growth, and hence carry a signature of the conditions of the habitat where the feather was grown (Hobson and Clark 1992). Variation in biochemical

processes in plants using C3 and C4 photosynthetic pathways generate quantifiable differences in δ^{13}C values; C3 plant species being ^{12}C-depleted relative to C4 plant species (Smith and Epstein 1971). Habitats dominated by C3 plants are typically associated with cooler and more mesic habitat conditions, whereas C4 plant dominated habitats are often found in warmer and drier environments (from here on referred to as mesic and arid habitat conditions, respectively) (Hobson 2005; Smith and Epstein 1971).

Likewise, high values of $\delta^{15}N$ may indicate warm xeric habitat conditions (Amundson et al. 2003; Craine et al. 2009).

All feathers ($n = 57$) were cleaned and washed in a 2:1 chloroform:methanol solution for 24–35 h to remove surface oil. The feathers were then stored in open containers in a fume hood to dry for at least 72 h prior to analysis. Samples were analysed at the stable isotope lab at Queens Facility for Isotope Research (QFIR), Canada. Samples were weighed (0.21–0.48 mg, mean ± SD: 0.35 ± 0.07 mg) in tin capsules and subsequently analysed. During analysis, international and in-house standards were used for each isotope and were repeatable to within SDs better than 0.3 ‰ for both $\delta^{15}N$ and $\delta^{13}C$: graphite (UC1, $\delta^{13}C = -25.4\,‰$, $n = 3$; NIST21, $\delta^{13}C = -28.1\,‰$, $n = 1$), cormorant feather ($\delta^{13}C = -16.4\,‰$, $n = 3$; $\delta^{15}N = 14.0\,‰$, $n = 3$), NIST 8551 ammonium sulfate ($\delta^{15}N = 53.2\,‰$, $n = 1$), QKNO3 potassium nitrate ($\delta^{15}N = 4.5\,‰$, $n = 2$). Standard deviation of duplicates (10 % of samples) of feathers averaged 0.3 ‰ ($n = 7$) for $\delta^{15}N$ and $\delta^{13}C$.

Isotope ratios (R) are expressed in δ units where

$$\delta_{\text{sample}} = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000$$

and reported as the R_{sample} relative to the Vienna PeeDee Belemnite for carbon and air for nitrogen. Values of $\delta^{13}C$ ranged from -22 to -13 ‰ (mean ± SD: -18 ± 2.1 ‰, $n = 57$) and $\delta^{15}N$ from 6 to 14 ‰ (10 ± 1.8 ‰, $n = 57$). Information about migration phenology and the respective isotopic values for all tracked individuals can be found in the Online Resource 1.

Breeding performance

Nests were observed at the breeding site at least one time during the breeding season (2010–2013). Breeding performance was measured as the number of eggs or chicks in the nest at the most advanced day of observation and as day of hatching (the day when the first egg in the clutch hatches estimated from nestling age at the time of visitation). Since Red-backed Shrikes tend to replace lost clutches, we only included individuals in our analyses with the first egg in the clutch hatching before 01-Jul, as later breeding attempts could not be separated from possible replacement clutches. For further details regarding nest site preferences and breeding performance in the study population see (Pedersen et al. 2011).

Data analyses

All models were constructed as either linear mixed effect models (LMMs) or generalized linear mixed models (GLMMs) with a log-link function fit by maximum likelihood using the R package "lme4" 1.1–10 (Bates et al. 2015). However, when the variance of the random effect of year was equal to zero in GLMMs we used GLMs to avoid problems with models not converging. To analyse the effect of conditions experienced at the non-breeding area on timing of migration we fitted separate LMMs for each migration step: (1) day of departure from the wintering area in southern Africa, (2) day of departure from the spring migration stopover area in eastern Africa, and (3) day of arrival at the breeding grounds to conditions experienced by the individual birds at the wintering grounds. To investigate further the influence of migration timing on duration of migration, we fitted separate GLMMs or GLMs for each stage of migration: (4) duration (no. of days) between the wintering area and the spring migration stopover site, (5) duration of the spring migration stopover site and (6) duration between the stopover site and breeding area.

The full model for day of departure from the wintering area contained fixed effects of local habitat condition ($\delta^{13}C$ and $\delta^{15}N$) and latitude at the wintering area; reasoning that individuals may depart on migration based on their relative geographic position in relation to the breeding ground. For day of departure from the spring migration stopover site in eastern Africa, we included local habitat conditions (only $\delta^{13}C$ to reduce the number of variables due to the small sample size), latitude at the wintering area, as well as day of arrival at the spring migration stopover site as fixed effects. When analysing timing of arrival at the breeding area we included fixed effects of habitat conditions ($\delta^{13}C$) at the wintering area and departure from the spring migration stopover site. All migration models contained a random effect of year.

Time spent at the spring migration stopover area in spring was fitted as a GLMM including a fixed effect of day of arrival at the stopover site and a random effect of year. Duration of migration between wintering area and the stopover area, as well as between the stopover area and the breeding area were fitted as GLMs with an effect of day of departure from the non-breeding area and day of departure at the stopover area, respectively.

Because of the small sample size we were not able to account for potential differences in migration phenology between sexes. The dataset contained a single repeated individual, which we accounted for by running all models without the repeated track (Online Resource 2). Dates of departure and arrival were transformed into ordinal dates ($1 =$ 01-Jan) and presented as median dates with interquartile ranges (IQR).

Breeding success (measured as brood size) was fitted as a GLMM with the model including a fixed effect of local habitat conditions at the wintering area ($\delta^{13}C$ and $\delta^{15}N$) and a random effect of year. Timing of breeding (measured as day of hatching) was modelled as an LMM with the

model likewise including a fixed effect of local habitat conditions at the wintering area ($\delta^{13}C$ and $\delta^{15}N$) and a random effect of year. As we did not obtain information on breeding success from individuals tracked with geolocators, it was not possible to add migration phenology to the model. To explain variation in isotopic signatures we used LMMs with a full model including fixed effects of year and sex and a random effect of individual.

We evaluated the significance of model variables by removing the parameter of interest from the full model and comparing this reduced model to the full model using a likelihood-ratio test (Zuur et al. 2009). Slope estimates ± standard errors (SE) are given for model parameters excluding non-significant fixed effects.

Homoscedasticity and normality of residuals were determined from visual inspection of QQ-plots and residual plots (Zuur et al. 2009). To avoid potential problems associated with collinearity of model parameters, we calculated the variance inflation factor (VIF). All variables had VIF < 3 and could thus be included in the models (Zuur et al. 2010). All analyses were conducted in R 3.2.2 64-bit (R Development Core Team 2015) using the platform R Studio 0.99.486 (RStudio Team 2015).

Results

By combining direct annual tracking with information on local conditions, we show that individuals wintering in mesic areas (more depleted in $\delta^{13}C$) departed later from the wintering grounds than those wintering in more arid areas ($\delta^{13}C$: $\beta = -2.84 \pm SE = 1.1$, $\chi_1^2 = 3.94$, $p = 0.047$, $n = 12$, Fig. 2a). There was no effect of the $\delta^{15}N$ isotope and latitude at the wintering area on departure decisions ($\delta^{15}N$: $\beta = -1.43 \pm 2.51$, $\chi_1^2 = 0.13$, $p = 0.719$; latitude: $\beta = 1.13 \pm 0.52$, $\chi_1^2 = 2.59$, $p = 0.108$, $n = 12$). However, when removing the early migrating outlying individual from the analyses (Fig. 2) it was not possible to disentangle the effect of latitude and local conditions in terms of $\delta^{13}C$ on departure decision from the wintering area ($\delta^{13}C$: $\beta = -1.47 \pm 0.56$, $\chi_1^2 = 4.24$, $p = 0.04$; latitude: $\beta = 1.15 \pm 0.24$, $\chi_1^2 = 11.81$, $p < 0.001$, $n = 11$), whereas $\delta^{15}N$ was still not significant ($\delta^{15}N$: $\beta = 1.54 \pm 1.2$, $\chi_1^2 = 1.53$, $p = 0.216$, $n = 11$). There was no relationship between wintering area latitude and the $\delta^{13}C$ isotope ($r = -0.25$, $p = 0.435$, $n = 12$, Online Resource 3). Departure from the stopover site in eastern Africa was strongly related to individual migration schedules with late arriving individuals also leaving this stage late ($\beta = 0.75 \pm 0.08$, $\chi_1^2 = 17.63$, $p < 0.001$, $n = 12$). However, we found no effect of conditions and latitude at the wintering area on timing of departure from the stopover site ($\delta^{13}C$: $\beta = 0.1 \pm 0.54$, $\chi_1^2 = 0.46$, $p = 0.5$; latitude: $\beta = 0.15 \pm 0.24$, $\chi_1^2 = 0.82$, $p = 0.364$, $n = 12$). This result did not change when removing the early migrating individual (stopover arrival: $\beta = 0.74 \pm 0.12$, $\chi_1^2 = 10.04$, $p = 0.002$; $\delta^{13}C$: $\beta = 0.06 \pm 0.6$, $\chi_1^2 = 0.28$, $p = 0.596$; latitude: $\beta = 0.21 \pm 0.28$, $\chi_1^2 = 0.78$, $p = 0.377$, $n = 11$). Breeding area arrival did not seem to be related to either
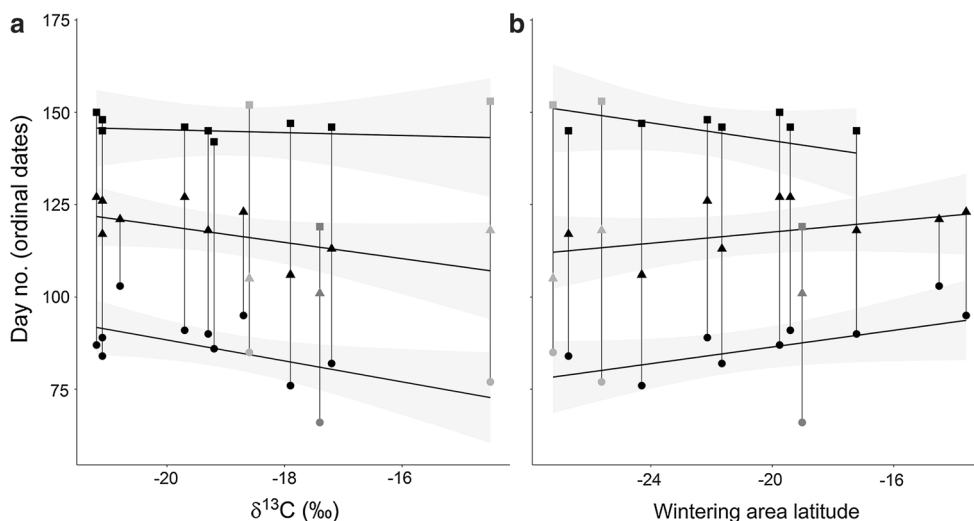
Fig. 2 Relationship between **a** $\delta^{13}C$ from feathers of Red-backed Shrikes grown at the wintering grounds and **b** latitude at the wintering grounds and timing of spring migration. *Circles* correspond to wintering area departure, *triangles* to departure from the spring stopover site in eastern Africa, and *squares* to arrival at the breeding grounds in Denmark. *Black segments* connect the migration schedule for each individual. *Dark grey symbols* represent the early migrating individual, while *light grey symbols* correspond to the individual with repeated tracks. The *top-fitted line* in **b** is driven by the early migrating individual. *Grey panels* represent 95 % confidence intervals

individual migration schedules (stopover site departure: $\beta = 0.5 \pm 0.28$, $\chi_1^2 = 3.11$, $p = 0.078$, $n = 10$; without early individual: $\beta = -0.05 \pm 0.12$, $\chi_1^2 = 0.07$, $p = 0.792$, $n = 9$) or local conditions at the wintering area ($\delta^{13}C$: $\beta = -0.41 \pm 1.41$, $\chi_1^2 = 0.42$, $p = 0.515$, $n = 10$; without early individual: $\beta = 0.6 \pm 0.4$, $\chi_1^2 = 1.89$, $p = 0.169$, $n = 9$). In terms of duration of migration in between stages, we found that individuals arriving late at the stopover site in eastern Africa spent significantly fewer days at this stage than early arriving individuals ($\beta = -0.03 \pm 0.01$, $\chi_1^2 = 5.23$, $p = 0.019$, $n = 12$; without early individual: $\beta = -0.03 \pm 0.01$, $\chi_1^2 = 3.8$, $p = 0.051$, $n = 11$). Likewise, individuals departing late from the stopover site spent fewer days on migration towards the breeding grounds ($\beta = -0.02 \pm 0.01$, $\chi_1^2 = 20.73$, $p = 0.01$, $n = 10$; without early individual: $\beta = -0.03 \pm 0.01$, $\chi_1^2 = -19.9$, $p < 0.001$, $n = 9$). In contrast, we found no influence of a late departure from the wintering area on duration of migration in between the wintering area and the stopover site ($\beta = 0 \pm 0$, $\chi_1^2 = -17.84$, $p = 0.149$, $n = 12$; without early individual: $\beta = -0.01 \pm 0.01$, $\chi_1^2 = -2$, $p = 0.157$, $n = 11$).

There was no indication that local habitat conditions at the wintering area ($\delta^{13}C$ and $\delta^{15}N$) carried over to influence breeding performance in terms of brood size ($\delta^{13}C$: $\beta = -0.03 \pm 0.05$, $\chi_1^2 = 0.34$, $p = 0.562$; $\delta^{15}N$: $\beta = 0 \pm 0.06$, $\chi_1^2 = 0$, $p = 0.991$, $n = 18$) or day of hatching ($\delta^{13}C$: $\beta = 0.56 \pm 0.54$, $\chi_1^2 = 0.66$, $p = 0.418$; $\delta^{15}N$: $\beta = 0.95 \pm 0.69$, $\chi_1^2 = 1.51$, $p = 0.22$, $n = 22$). Removing observations where only eggs had been observed did not change this result (brood size: $\delta^{13}C$: $\beta = -0.03 \pm 0.05$, $\chi_1^2 = 0.27$, $p = 0.603$; $\delta^{15}N$: $\beta = 0 \pm 0.07$, $\chi_1^2 = 0.01$, $p = 0.904$, $n = 13$; day of hatching: $\delta^{13}C$: $\beta = 0.07 \pm 0.54$, $\chi_1^2 = 0.02$, $p = 0.901$; $\delta^{15}N$: $\beta = 0.85 \pm 0.72$, $\chi_1^2 = 1.31$, $p = 0.25$, $n = 16$).

Departure dates from the wintering area ranged from 07-Mar to 13-Apr (median: 27-Mar, IQR: 9 days). At the spring stopover area individuals departed in between 11-Apr and 07-May (median: 28-Apr, IQR: 13 days), while arrival dates at the breeding ground ranged from 29-April to 02-Jun (median: 26-May, IQR: 4 days). Re-running all analyses on migration phenology without the single repeated track revealed similar results as those presented here with only a few exceptions, most likely caused by a small sample size (n = 8-9) (Online Resource 2, 4). Isotopic values of $\delta^{13}C$ and $\delta^{15}N$ were not associated ($r = 1.68$ $t_{55} = 1.26$, $p = 0.212$, $n = 57$) and did not differ between years or sex ($\delta^{13}C$, year: $\chi_1^2 = 7.4$, $p = 0.193$; sex: $\chi_1^2 = 0.02$, $p = 0.879$, $n = 57$), ($\delta^{15}N$, year: $\chi_1^2 = 5.68$, $p = 0.339$; sex: $\chi_1^2 = 0.79$, $p = 0.374$, $n = 57$).

Discussion

We found that individuals wintering in relatively mesic habitats and at lower latitudes departed later from the wintering site than those exposed to more arid habitat conditions. However, the effect of local non-breeding area conditions and latitude were not present at subsequent stages of migration and late departing individuals spent fewer days on spring migration. Furthermore, there was no apparent carry-over effect of habitat conditions at the non-breeding area on breeding performance.

Timing of spring migration

Given competition for optimal arrival at the breeding grounds, individuals departing late from the non-breeding grounds must reduce the amount of time spent on migration in order to catch up with early departing individuals (Kokko 1999; McNamara et al. 1998). This can be achieved by (1) shorter migration distance (by wintering closer to the breeding area), and/or (2) increasing the speed of migration by, e.g., reducing the number of days spent migrating or staging. Here we show that although individuals in more mesic habitat (depleted in $\delta^{13}C$) departed later from the wintering site, the effect of habitat conditions on departure from the spring migration stopover site and on breeding area arrival were absent, suggesting a simultaneous arrival at the breeding site despite variation in departure schedules from the wintering grounds. This was further supported by results of the models indicating that late departing individuals spent relatively fewer days at the stopover area and on the last part of migration towards the breeding area. Furthermore, we found a consistency in individual timing of departure from the spring stopover site in eastern Africa, while there was no apparent difference in timing of arrival at the breeding site. This may be due to individuals using different strategies to ensure arriving at the breeding grounds at a specific time, which could reflect individual capabilities or a difference in migration routes involving stopovers of different habitat quality that may be more important for determining timing of migration in this species (Tøttrup et al. 2012b). A single early migrating individual highly influenced our results, making it difficult to distinguish between the effect of habitat conditions and latitude on departure times from the non-breeding area. However, we found no correlation between habitat conditions and latitude, suggesting that these factors explained different parts of the variation in departure times (Online Resource 3). Because of our small sample size, we acknowledge that other factors not included here may impact the results. Still, we are able to present patterns in the individual variation explained by conditional proxies

and support for individual adjustments in timing of migration indicating individual strategies.

Previous studies using stable-isotope analysis to investigate environmental conditions at the non-breeding grounds in relation to carry-over effects in the Nearctic-Neotropic system have shown that moist habitat conditions are generally associated with an early departure from the non-breeding grounds (Marra et al. 1998; Studds and Marra 2005), improved body condition (Bearhop et al. 2004; Marra et al. 1998; Smith et al. 2010), and an early arrival at the breeding site (Marra et al. 1998; Norris et al. 2004; Tonra et al. 2011). However, a recent study suggests that this pattern may not hold for all species or even among individuals of the same species wintering in different regions (Gonzalez-Prieto and Hobson 2013). Furthermore, Yohannes et al. (2012) found a late arrival at a spring staging area to be related to moist habitat conditions at the African non-breeding grounds in garden warblers (*Sylvia borin*) and (Tøttrup et al. 2008) found later migration in years with favourable conditions in five long-distance warbler species. These differences may be due to species having different habitat requirements during the non-breeding season (Arizaga et al. 2013; Jenni-Eiermann et al. 2011; Maggini et al. 2015). Furthermore, it should be noted that isotopic values reflect the composition of the diet at the specific time of moult, thus providing a snapshot of the habitat conditions at the particular time when the individual moulted rather than the overall habitat conditions that may vary in isotopic values across the season (Ostrom et al. 1997). However, our results further suggest that the link between the non-breeding area and the breeding grounds may be more complex and not necessarily dependent on conditions experienced at the wintering grounds.

Breeding performance

We found no carry-over effect of local non-breeding area conditions on breeding performance in terms of brood size and day of hatching. This is in correspondence with recent studies finding that non-breeding area habitat in western Africa may not be limiting populations of whinchats (Blackburn and Cresswell 2015, 2016). In contrast, Schaub et al. (2011) found that breeding success of Red-backed Shrikes in southwestern Germany was mainly influenced by factors operating at the autumn migration staging area in the Sahel region. Similarly, previous studies covering a variety of songbird species have found effects of non-breeding area conditions on breeding performance (Both et al. 2006; Drake et al. 2013; McKellar et al. 2013; Norris et al. 2004; Rockwell et al. 2012; Sillett et al. 2000). However, like this study, these did not take into account conditions experienced at the breeding grounds. As breeding performance is likely to be influenced primarily

by timing of arrival and local conditions at the breeding site (Gienapp and Bregnballe 2012; Norris et al. 2004; Ockendon et al. 2013), we recommend taking these factors into account in future studies within this field. In addition, we recognise that the sample size in this study may not have been large enough to detect a difference in breeding performance, thus causing a Type II error.

The range of δ^{13}C values indicated overall dry conditions at the wintering site (Smith and Epstein 1971) confirming the preference for semi-arid environmental conditions (Bruderer and Bruderer 1993, 1994) and in concordance with values of δ^{13}C reported in previous studies of this species (Jakober et al. 2007). We found no association between values of δ^{15}N and δ^{13}C. However, it is well known that δ^{15}N is confounded by other factors such as trophic level of prey items, species composition, land-use and mycorrhizal associations and thus, may provide less credible information on habitat conditions (Kelly 2000; Pardo and Nadelhoffer 2010).

Habitat segregation between males and females at the non-breeding grounds in Red-backed Shrikes have previously been reported, with males occupying more arid habitat (Herremans 1997). We found no indication that sex had an influence on the variation of stable isotopic values, suggesting that male and female shrikes occupy similar habitats during the non-breeding season, which is consistent with the findings of (Jakober et al. 2007). The lack of a difference between sexes could be due to isotopic values reflecting diet rather than being a measure of habitat conditions. We recognize that age-class variation may be important when investigating seasonal interactions as strength of carry-over effects may vary with age (Drake et al. 2013). However, determination of age in Red-backed Shrikes from the second calendar year is unreliable (Svensson 1992), and hence age was not considered in this study.

The return rate of Red-backed Shrikes equipped with geolocators in this study (28 %) is similar to what has previously been found in ringing studies on this species in northern Italy and in the southwestern part of the Czech Republic (Massa et al. 1993; Šimek 2001). However, return rates as high as around 50 % in southwestern Germany and the Netherlands have been reported (Geertsma et al. 2000; Jakober and Stauber 1987) while extremely low return rates were found in Poland (3–4 %), potentially owing to the wider availability of high quality habitats in this region (Tryjanowski et al. 2007).

Assessing how events during the year interact and influences individuals is important to understand the underlying causes of population dynamics. This study challenges the view that long-distance migrant populations may be limited by habitat conditions at the non-breeding

grounds. Furthermore, it highlights the potential value of combining different methodologies in order to benefit from the advantages of each approach. Future research should continue to draw on novel tracking technologies, such as miniaturized geolocators, providing enhanced opportunities to collect information on year-round movements of individuals to address still unresolved questions regarding seasonal interactions.

References

Amundson R, Austin AT, Schuur EAG, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D, Baisden WT (2003) Global patterns of the isotopic composition of soil and plant nitrogen. Glob Biogeochem Cycles 17:1031. doi:10.1029/2002GB001903

Arizaga J, Maggini I, Hama F, Crespo A, Gargallo G (2013) Site-and species-specific fuel load of European-Afrotropical passerines on arrival at three oases of southeast Morocco during spring migration. Bird Study 60:11–21. doi:10.1080/00063657.2012.735222

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. doi:10.18637/jss.v067.i01

Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proc R Soc B-Biol Sci 271:S215–S218. doi:10.1098/rsbl.2003.0129

Berthold P (1996) Control of bird migration. Chapman & Hall, London

BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. (BirdLife Conservation Series No. 12). BirdLife International, Cambridge, UK

Blackburn E, Cresswell W (2015) Fine-scale habitat use during the non-breeding season suggests that winter habitat does not limit breeding populations of a declining long-distance Palearctic migrant. J Avian Biol 46:622–633. doi:10.1111/jav.00738

Blackburn E, Cresswell W (2016) High within-winter and annual survival rates in a declining Afro-Palaearctic migratory bird suggest that wintering conditions do not limit populations. Ibis 158:92–105. doi:10.1111/ibi.12319

Both C, Sanz JJ, Artemyev A, Blaauw B, Cowie RJ, Dekhuijzen A, Enemar A, Jarvinen A, Nyholm NEI, Potti J (2006) Pied flycatchers Ficedula hypoleuca travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date. Ardea 94:511–525

Bridge ES, Ross JD, Contina AJ, Kelly JF (2015) Do molt-migrant songbirds optimize migration routes based on primary productivity? Behav Ecol. doi:10.1093/beheco/arv199 **(arv199)**

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fleron RW, Hartl P, Kays R, Kelly JF, Robinson WD, Wikelski M (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. Bioscience 61:689–698. doi:10.1525/bio.2011.61.9.7

Brink AB, Eva HD (2009) Monitoring 25 years of land cover change dynamics in Africa: a sample based remote sensing approach. Appl Geogr 29:501–512. doi:10.1016/j.apgeog.2008.10.004

Bruderer B (2007) Notes on the moult of red-backed shrikes (Lanius collurio) in their non-breeding range. J Ornithol 148:557–561. doi:10.1007/s10336-007-0190-9

Bruderer B, Bruderer H (1993) Distribution and habitat preference of red-backed shrikes Lanius collurio in southern Africa. Ostrich 64:141–147. doi:10.1080/00306525.1993.9632651

Bruderer B, Bruderer H (1994) Numbers of red-backed shrikes Lanius collurio in different habitats of South Africa. Bull Br Ornithol' Club 114:192–202

Craine JM, Elmore AJ, Aidar MPM, Bustamante M, Dawson TE, Hobbie EA, Kahmen A, Mack MC, McLauchlan KK, Michelsen A, Nardoto GB, Pardo LH, Penuelas J, Reich PB, Schuur EAG, Stock WD, Templer PH, Virginia RA, Welker JM, Wright IJ (2009) Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytol 183:980–992. doi:10.1111/j.1469-8137.2009.02917.x

Drake A, Rock C, Quinlan SP, Green DJ (2013) Carry-over effects of winter habitat vary with age and sex in yellow warblers Setophaga petechia. J Avian Biol 44:321–330. doi:10.1111/j.1600-048X.2013.05828.x

Ekstrom PA (2004) An advance in geolocation by light. Mem Natl Inst Polar Res Spec Issue 58:210–226

Emmenegger T, Hahn S, Bauer S (2014) Individual migration timing of common nightingales is tuned with vegetation and prey phenology at breeding sites. BMC ecol 14:9. doi:10.1186/1472-6785-14-9

Fox J (2010) Geolocator manual. Version 8. British Antarctic Survey, Cambridge

Fraser KC, Silverio C, Kramer P, Mickle N, Aeppli R, Stutchbury BJM (2013) A trans-hemispheric migratory songbird does not advance spring schedules or increase migration rate in response to record-setting temperatures at breeding sites. PLos One 8:e64587. doi:10.1371/journal.pone.0064587

Fraser KC, Stutchbury BJM, Silverio C, Kramer PM, Barrow J, Newstead D, Mickle N, Cousens BF, Lee JC, Morrison DM, Shaheen T, Mammenga P, Applegate K, Tautin J (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proc R Soc B-Biol Sci 279:4901–4906. doi:10.1098/rspb.2012.2207

Fretwell SD (1972) Populations in a seasonal environment. Princeton University, New Jersey

Fudickar AM, Wikelski M, Partecke J (2012) Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Methods Ecol Evolut 3:47–52. doi:10.1111/j.2041-210X.2011.00136.x

Geertsma M, van Berkel H, Esselink H (2000) Are high fitness values sufficient to maintain a dutch population of the red-backed shrike (Lanius collurio)? Ring 22:79–88

Gienapp P, Bregnballe T (2012) Fitness consequences of timing of migration and breeding in cormorants. PLoS one 7:e46165. doi:10.1371/journal.pone.0046165

Gonzalez-Prieto AM, Hobson KA (2013) Environmental conditions on wintering grounds and during migration influence spring

nutritional condition and arrival phenology of Neotropical migrants at a northern stopover site. J Ornithol 154:1067–1078. doi:10.1007/s10336-013-0975-y

Gordo O, Brotons L, Ferrer X, Comas P (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Glob Change Biol 11:12–21. doi:10.1111/j.1365-2486.2004.00875.x

Greenberg R, Marra PP (2005) Birds of two worlds: the ecology and evolution of migration. The John Hopkins University, Baltimore

Gwinner E (1996) Circannual clocks in avian reproduction and migration. Ibis 138:47–63. doi:10.1111/j.1474-919X.1996.tb04312.x

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. J Anim Ecol 80:4–18. doi:10.1111/j.1365-2656.2010.01740.x

Heldbjerg H, Fox T (2008) Long-term population declines in Danish trans-Saharan migrant birds. Bird Study 55:267–279. doi:10.1080/00063650809461532

Herremans M (1997) Habitat segregation of male and female red-backed shrikes Lanius collurio and lesser grey shrikes Lanius minor in the Kalahari basin Botswana. J Avian Biol 28:240–248. doi:10.2307/3676975

Hill RD, Braun MJ (2001) Geolocation by light level - the next step: latitude. In: Sibert JR, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Dordrecht, pp 315–330

Hobson KA (2005) Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. Auk 122:1037–1048. doi:10.1642/0004-8038(2005)122[1037:siatdo]2.0.co;2

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of C-13 in tissues. Condor 94:181–188. doi:10.2307/1368807

Jakober H, Stauber W (1987) Zur Populationsdynamik des Neuntöters (Lanius collurio). Beih Veröff Naturschutz Landschspfl Bad-Württ 48:71–78

Jakober H, Stauber W, Bairlein F, Voss M (2007) Analysis of stable isotopes in feathers of Red-backed Shrikes (Lanius collurio): no evidence for different wintering habitats of males and females. J Ornithol 148:129–131. doi:10.1007/s10336-006-0110-4

Jenni-Eiermann S, Almasi B, Maggini I, Salewski V, Bruderer B, Liechti F, Jenni L (2011) Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. J Ornithol 152:113–128. doi:10.1007/s10336-010-0572-2

Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478. doi:10.1126/science.aaa2478

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool-Rev Canadienne Zool 78:1–27. doi:10.1139/cjz-78-1-1

Kirby JS, Stattersfield AJ, Butchart SHM, Evans MI, Grimmett RFA, Jones VR, O'Sullivan J, Tucker GM, Newton I (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conserv Int 18:S49–S73. doi:10.1017/s0959270908000439

Kokko H (1999) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950. doi:10.1046/j.1365-2656.1999.00343.x

Korner-Nievergelt F, Jenni L, Tøttrup AP, Pasinelli G (2012) Departure directions, migratory timing and non-breeding distribution of the Red-backed Shrike Lanius collurio: do ring re-encounters and light-based geolocator data tell the same story? Ring Migr 27:83–93. doi:10.1080/03078698.2012.748508

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy

and precision affected by environmental factors. Methods Ecol Evol 3:603–612. doi:10.1111/j.2041-210X.2012.00185.x

Macdonald CA, Fraser KC, Gilchrist HG, Kyser TK, Fox JW, Love OP (2012) Strong migratory connectivity in a declining arctic passerine. Anim Migr 1:23–30. doi:10.2478/ami-2012-0003

Maggini I, Hama F, Robson D, Rguibi Idrissi H, Bairlein F, Gargallo G (2015) Foraging behavior of three species of songbirds during stopover in southeastern Morocco during spring migration. J Field Ornithol 86:266–276. doi:10.1111/jofo.12115

Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315. doi:10.1007/s00442-004-1725-x

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886. doi:10.1126/science.282.5395.1884

Massa R, Bottoni L, Fornasari L (1993) Site fidelity and population structure of the red-backed shrike Lanius collurio in northern Italy. Ring Migr 14:129–132. doi:10.1080/03078698.1993.9674055

McKellar AE, Marra PP, Hannon SJ, Studds CE, Ratcliffe LM (2013) Winter rainfall predicts phenology in widely separated populations of a migrant songbird. Oecologia 172:595–605. doi:10.1007/s00442-012-2520-8

McKinnon EA, Fraser KC, Stutchbury BJM (2013) New discoveries in landbird migration using geolocators, and a flight plan for the future. Auk 130:211–222. doi:10.1525/auk.2013.12226

McNamara JM, Welham RK, Houston AI (1998) The timing of migration within the context of an annual routine. J Avian Biol 29:416–423

Müller C (2009) Climate change impact on Sub-Saharan Africa: an overview and analysis of scenarios and models. Discussion Paper. German Development Institute/Deutsches Institut für Entwicklungspolitik (DIE), vol 3. ISBN 978-3-88985-451-3

Norris DR, Marra PP (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. Condor 109:535–547. doi:10.1650/8350.1

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc R Soc B-Biol Sci 271:59–64. doi:10.1098/rspb.2003.2569

Norris DR, Wunder MB, Boulet M (2006) Perspectives on migratory connectivity. Ornithol Monogr 61:79–88

Ockendon N, Leech D, Pearce-Higgins JW (2013) Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biol Lett 9. doi:10.1098/rsbl.2013.0669

Ostrom NE, Macko SA, Deibel D, Thompson RJ (1997) Seasonal variation in the stable carbon and nitrogen isotope biogeochemistry of a coastal cold ocean environment. Geochim Cosmochim Acta 61:2929–2942. doi:10.1016/S0016-7037(97)00131-2

Pardo LH, Nadelhoffer KJ (2010) Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: understanding movements, pattern and process on Earth through isotope mapping. Springer, New York, pp 221–250

Pasinelli G, Schaub M, Häfliger G, Frey M, Jakober H, Muller M, Stauber W, Tryjanowski P, Zollinger JL, Jenni L (2011) Impact of density and environmental factors on population fluctuations in a migratory passerine. J Anim Ecol 80:225–234. doi:10.1111/j.1365-2656.2010.01754.x

Pedersen PE, Petersen TL, Jørgensen PS, Tøttrup AP (2011) The breeding population of Red-backed Shrike Lanius collurio in Gribskov. Dan Ornitol Foren Tidsskr 105:179–182

R Development Core Team (2015) R: a language and environment for Statistical Computing https://www.r-project.org/. Accessed 14 Aug 2015

Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North-American birds that migrate to the Neotropics. Proc Natl Acad Sci USA 86:7658–7662. doi:10.1073/pnas.86.19.7658

Rockwell SM, Bocetti CI, Marra PP (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (Setophaga kirtlandii). Auk 129:744–752. doi:10.1525/auk.2012.12003

RStudio Team (2015) R Studio: Integrated development environment for R, 0.99.486 ed., Boston, MA http://www.rstudio.com/. Accessed 7 Oct 2015

Saino N, Rubolini D, Jonzen N, Ergon T, Montemaggiori A, Stenseth NC, Spina F (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. Clim Res 35:123–134. doi:10.3354/cr00719

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol Conserv 131:93–105. doi:10.1016/j.biocon.2006.02.008

Schaub M, Jakober H, Stauber W (2011) Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. Oecologia 167:445–459. doi:10.1007/s00442-011-1999-8

Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042. doi:10.1126/science.288.5473.2040

Šimek J (2001) Patterns of breeding fidelity in the Red-backed Shrike (Lanius collurio). Ornis Fenn 78:61–71

Smith BN, Epstein S (1971) Two categories of ^{13}C/^{12}C ratios for higher plants. Plant Physiol 47:380–384. doi:10.1104/pp.47.3.380

Smith JAM, Reitsma LR, Marra PP (2010) Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91:2874–2882. doi:10.1890/09-2212.1

Snow DW, Perrins CM (1998) The birds of the Western Palearctic, vol 2. Oxford University, New York

Streby HM, Kramer GR, Peterson SM, Lehman JA, Buehler DA, Andersen DE (2014) Tornadic storm avoidance behavior in breeding songbirds. Curr Biol 25:1–5. doi:10.1016/j.cub.2014.10.079

Studds CE, Marra PP (2005) Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385. doi:10.1890/04-1145

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V (2009) Tracking Long-Distance Songbird Migration by Using Geolocators. Science 323:896–896. doi:10.1126/science.1166664

Svensson L (1992) Identification Guide to European Passerines. Märstatryck, Stockholm

Tonra CM, Marra PP, Holberton RL (2011) Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. J Avian Biol 42:397–404. doi:10.1111/j.1600-048X.2011.05333.x

Tøttrup AP, Klaassen RH, Strandberg R, Thorup K, Kristensen MW, Jørgensen PS, Fox J, Afanasyev V, Rahbek C, Alerstam T (2012a) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proc R Soc B: Biol Sci 279:1008–1016. doi:10.1098/rspb.2011.1323

Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R, Vardanis Y, Lindstrom A, Rahbek C, Alerstam T, Thorup K (2012b) Drought in Africa caused delayed arrival of European Songbirds. Science 338:1307–1307. doi:10.1126/science.1227548

Tøttrup AP, Rainio K, Coppack T, Lehikoinen E, Rahbek C, Thorup K (2010) Local temperature fine-tunes the timing of spring migration in birds. Integr Comp Biol 50:293–304. doi:10.1093/icb/icq028

Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E, Rahbek C (2008) Avian migrants adjust migration in response to environmental conditions en route. Biol Lett 4:685–688. doi:10.1098/rsbl.2008.0290

Tryjanowski P, Golawski A, Kuzniak S, Mokwa T, Antczak M (2007) Disperse or stay?exceptionally high breeding-site infidelity in the Red-backed Shrike Lanius collurio. Ardea 95:316–320. doi:10.5253/078.095.0214

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Skorpilová J, Gregory RD (2014) The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156:1–22. doi:10.1111/ibi.12118

Woodworth BK, Newman AE, Turbek SP, Dossman BC, Hobson KA, Wassenaar LI, Mitchell GW, Wheelwright NT, Norris DR (2016) Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia 181:413–422. doi:10.1007/s00442-015-3527-8

Yohannes E, Lee R, Popenko V, Bauchinger U (2012) Bone collagen and muscle delta C-13 in relation to the timing of the migration of Garden Warblers Sylvia borin during return migration from Africa. J Ornithol 153:783–791. doi:10.1007/s10336-011-0794-y

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14. doi:10.1111/j.2041-210X.2009.00001.x

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York