

Population-specific assessment of carry-over effects across the range of a migratory songbird

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48 **Consent to participate**

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Authors' contributions

PP and VB conceived the idea of the study. VB, DD, AG, SH, BH, DH, TE, GM, SP, PP and MW participated in retrieving geolocators and collecting feather samples. VB designed the methodology with input from SH, BH, DH, TE, GM, PP and MW. VB and GM analysed the light-level data. EY analysed the stable isotopic composition of feather samples. BH, DH, SH and PP acquired funding. VB gathered the remote sensing data and conducted the final analysis. VB took lead in the manuscript writing. All authors read and commented on the manuscript and approved the final version of the manuscript.

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Abstract

Annual cycle events may be interlinked, influence following annual cycle stages and may alter performance of individuals. Such links, called carry-over effects, can explain individual variation in timing or reproductive success in migratory species. Identifying the key links affecting fitness may reveal mechanisms of species population dynamics but the current evidence for the strongest carry-

over effects is equivocal. Here, we aim at assessing carry-over effects in great reed warblers *Acrocephalus arundinaceus*, a long-distance migratory songbird, using 103 full-annual tracks from three European and two Asian breeding populations. Our results showed strong positive relationships within autumn and spring migration periods and buffering capacity of the non-breeding period preventing events to carry over between these periods. Moreover, we found no profound relation between the non-breeding habitat quality or seasonality (quantified using stable isotopes and remote sensing data) and the timing of spring migration. The strongest carry-over effects occurred in individuals from the southern European breeding population compared to the northern and the central European populations. A moderate relationship between the habitat seasonality during moult and the spring migration timing indicates the importance of the complete moult. The overall weak carry-over effects of non-breeding habitat conditions found in this study contrast with previous results and imply between-species differences in these crucial relationships. Moreover, the population-specific carry-over effects highlight the importance of multi-population approach and advise caution in interpretation of results from single-population studies. Finally, the carry-over effect from the moulting period indicates significance of a so far neglected link in the species.

Significance statement

Environmental conditions vary in space and time. Therefore, migratory species adjust timing of migration in order to maximise their fitness. However, the links between annual cycle events in multiple populations and the consequences of environmental conditions outside the breeding range are scarcely known. In this study, we used tracking data of the great reed warbler, an insectivorous bird species breeding across western Eurasia and wintering in Africa, to study a complex system of links between annual events. We found that the strength of these links differed between geographically distinct populations but not between sexes. Moreover, harsh environmental conditions during moult delayed timing of subsequent events. Our findings could help explain large-scale differences in population size changes observed in some species and highlight the importance

of energetically demanding moult period for the life of migratory species. Finally, our results demonstrate the need for multi-population approach in studies on seasonal interactions.

Keywords

migration, remote sensing, seasonal interactions, stable isotope, tracking

Introduction

Identifying key periods that affect individual fitness is crucial for our ability to understand population changes, especially in declining long-distance migrants (Sanderson et al. 2006; Vickery et al. 2014). Besides impacting individual fitness in a given phase of the annual cycle (Newton 1998; Robinson et al. 2007), regional conditions may also carry over to the subsequent phases and impose additional fitness costs (Harrison et al. 2011; Senner et al. 2015). Therefore, knowing carry-over effects within the annual cycles is essential for a better understanding of links between environmental conditions and population dynamics (Norris and Taylor 2006; Rakhimberdiev et al. 2018).

Previous studies mostly focused on delayed fitness consequences of non-breeding habitat quality in long-distance migratory birds but the evidence for such a relationship is equivocal. Some studies found support for this link (e.g. Marra et al. 1998; Gunnarsson et al. 2005; Goodenough et al. 2017), some found evidence in some years or only for a specific group of individuals (e.g. Rockwell et al. 2012; Drake et al. 2013; López-Calderón et al. 2017), while other studies found no support for this association (Drake et al. 2014; Pedersen et al. 2016; Briedis et al. 2018). In contrast, there is growing evidence for strong relationships between consecutive events as well as for buffering capacity of the non-breeding period that may prevent the accumulation of carry-over effects within the annual cycle (Senner et al. 2014; van Wijk et al. 2017; Briedis et al. 2018; Gow et al. 2019). Despite extensive efforts to identify the most important carry-over effects, there is still a lack of knowledge of delayed

fitness consequences of non-breeding habitat seasonality or habitat conditions during the moult period (Sultan and Janicot 2003; Buttemer et al. 2019).

The spatiotemporal organization of annual cycles can differ between males and females as well as with geographic origin (Conklin et al. 2010; Briedis et al. 2019). This may lead to sex-specific differences in habitat use (Marra and Holmes 2001; Catry et al. 2004) and exposure to harsh environmental conditions, inducing delayed fitness costs different for females and males (Briedis et al. 2017; Lerche-Jørgensen et al. 2018). The current evidence for sex-specific carry-over effects within the annual cycle is inconclusive, supporting all possible combinations of effects such as stronger effects in males (López-Calderón et al. 2017), stronger effects in females (Saino et al. 2017) or mixture of sex-specific differences in different links (Norris et al. 2004). Moreover, breeding latitude seems to have only a weak impact on the strength of carry-over effects (Gow et al. 2019). Consequently, sex differences in carry-over effects can have density-dependent impacts on population dynamics (Briedis and Bauer 2018) and spatial patterns in carry-over effects can explain geographic patterns in population trends (Hanzelka et al. 2019).

The breeding and migration ecology of the great reed warbler (*Acrocephalus arundinaceus*), a Palearctic-African long-distance migratory passerine, is well known (Lemke et al. 2013; Koleček et al. 2016; Hasselquist et al. 2017). Great reed warblers from a single breeding population spread across large areas within the non-breeding range covering a substantial part of sub-Saharan Africa (Koleček et al. 2016). The majority of individuals undertake intra-tropical movements during the non-breeding period in relation to habitat suitability (Koleček et al. 2018) in the highly seasonal regions of sub-Saharan Africa (Sultan and Janicot 2003). Moreover, the timing of these intra-tropical movements often coincides with the end of complete moult, which starts shortly after arrival at the non-breeding grounds (Pearson 1975; Hedenström et al. 1985; Bensch et al. 1991; Sorensen et al. 2016). Finally, there is a strong positive relationship between early breeding site arrival and the number of fledglings and recruits (Hasselquist 1998; Tarka et al. 2015).

Here, we aim at identifying the carry-over effects in great reed warblers and testing for differences in carry-over effects between sexes and populations. We focus on the effects of the non-breeding and moulting period habitat conditions on individual performance in subsequent annual cycle stages. In order to identify the carry-over effects, we use a robust dataset of full-annual tracks in combination with multiple metrics of non-breeding habitat quality and seasonality.

Predictions

1. We predict strongest relations between consecutive events (Piersma 1987; Gow et al. 2019).
2. The non-breeding period will buffer against carry-over effects between the autumn and spring migration periods (Senner et al. 2014; Briedis et al. 2018; Gow et al. 2019).
3. Low quality and high seasonality of non-breeding habitats will delay subsequent annual cycle phases (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004).
4. Weak links between timing of events will be more frequent in males than in females due to their earlier timing and thus higher probability of encountering adverse environmental conditions during spring migration (Lemke et al. 2013; Briedis et al. 2017, 2019; Lerche-Jørgensen et al. 2018). Moreover, impacts of non-breeding habitat conditions will be stronger on females under the scenario of sexual habitat segregation favouring males (Marra and Holmes 2001).
5. Weak relations between timing of events and strong impacts of non-breeding habitat conditions on timing of subsequent events will be more frequent in populations breeding at higher latitudes. This pattern will arise from larger migration distances, more stopovers and higher probability of unfavourable environmental conditions *en route* (Briedis et al. 2017). These differences will diminish the effects of timing and the impacts of non-breeding habitat conditions compared with populations from lower breeding latitudes.
6. Low habitat quality experienced during the complete moult will delay subsequent events more than the overall non-breeding habitat conditions as moult is a physiologically demanding life cycle event (Murphy 1996; Buttemer et al. 2019).

Materials and methods

Tracking data and feather samples

We used light-level geolocator data covering full annual cycles of 103 adult great reed warblers (38 females, 64 males and 1 of unknown sex). The birds tracked between 2010 and 2018 come from three European breeding populations – Sweden (SE; northern; $n = 37$; 59°N, 15°E), Czech Republic (CZ; central; $n = 35$; 49°N, 18°E), Bulgaria (BG; southern; $n = 21$; 44°N, 26°E), and two Asian breeding populations – Turkey (TR; $n = 4$; 42°N, 36°E) and Kazakhstan (KZ; $n = 6$; 44°N, 77°E; Fig. 1). The tracked individuals have been recaptured in the vicinity of their breeding/tagging sites and the archived data thus reflect migratory behaviour of surviving individuals that did not disperse outside the study sites. For details on the number of recaptured individuals and geolocator specification see Electronic Supplementary Material (ESM) 1. During geolocator recovery, we collected either the distal part of a fifth primary (BG), a third tail feather (SE, KZ and TR), or a second tertial (CZ) for stable isotopic analyses. These feathers are assumed to be moulted in Africa during the first part of the non-breeding period (Hedenström et al. 1985; Bensch et al. 1991). We also collected each of these three feather types from 30 individuals in the SE, CZ and BG populations in 2018 to check for intra-individual variation in stable carbon isotope signatures. We found no differences in the stable isotopic signal between feather types ($F_{2,58} = 0.26$; $P = 0.772$) using a linear mixed-effect model with feather type as a fixed effect and individual identity as random intercept.

Spatiotemporal information on annual cycles

We determined the timing of annual cycle events, migration speed and geographic locations of the non-breeding sites using data from light-level geolocators. To this end, we estimated sunrises and sunsets from the log-transformed light-level recordings using *preprocessLight* function from *twGeos* package (Wotherspoon et al. 2016). For further analysis, we used functions from *GeoLight* package version 2.0.0 (Lisovski and Hahn 2012): we filtered unlikely sun events (*loessFilter* function; $k = 2$), identified stationary and migratory periods (*changeLight* function; quantile = 0.9; days = 2) and

calculated geographic positions of stationary periods using in-habitat calibration estimating the sun elevation angle (SEA) from the known breeding period.

When the resulting positions were unreliable (e.g. in the sea or desert; $n = 11$ individuals), we replaced in-habitat calibration by Hill-Ekstrom calibration estimating SEAs by minimising variation of the latitude estimates. Subsequently, we used the SEA to calculate positions of all stationary sites for each individual. For each stationary period, we defined the mode of the raw positions as a site and considered all sites south of 20°N and lasting more than 23.5 days (longer than 90% of all stationary locations north of 20°N) as individual non-breeding sites. Timing of first and last position estimates represent individual stationary site arrivals and departures. The impact of geolocator attachment on event timing is considered negligible (Brlík et al. 2020). It was not possible to record data blind because our study involved focal animals in the field.

In 10 individuals from SE and CZ for which the arrival back to the breeding site was not recorded, we used the individual date of the first colour-ring resighting at the breeding site as the geolocator-derived and observed breeding site arrivals are highly correlated in these populations (Pearson's correlation test: $\rho = 0.99$, $df = 25$, $P < 0.001$).

Habitat quality assessment

Habitat conditions at individual non-breeding sites were described using two approaches – by extracting remotely sensed Normalized Difference Vegetation Index (NDVI) values at geolocator-derived sites and by stable carbon isotope analysis from feathers moulted in Africa.

Firstly, we used NDVI data as a proxy for primary productivity and seasonality of vegetation (Pettorelli et al. 2005) and abundance of insects (Lassau and Hochuli 2008; Deveson 2013; Sweet et al. 2015), the main diet of the great reed warblers (Cramp 1992; Dyrce 1995), in a buffer surrounding the non-breeding sites of tracked individuals. For each individual, we extracted a series of weekly mean NDVI values in the region surrounding the non-breeding site (44×44 km) using pre-processed, noise- and cloud-free NDVI measurements with 4-km resolution (accessed from:

ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blended_VH_4km/geo_TIFF/). The time period for NDVI acquisition was set by the occupation period of the respective site from geolocators. We determined three habitat characteristics: (i) the 'greenness' as the average of weekly values, (ii) 'greenness trend' as the sum of between-week differences and (iii) the 'greenness seasonality' as the average of absolute between-week differences (ESM 2). We calculated a weighted average of the non-breeding site habitat characteristics in individuals with multiple non-breeding sites with a number of weeks spent at these sites as a weight. Due to the low accuracy of latitude estimates derived from geolocators (Fudickar et al. 2012; Lisovski et al. 2012), we collected NDVI measurements from two extended non-breeding regions – 144×44 km and 244×44 km (latitude × longitude) – and calculated path models employing the path structure from the set of path models 3 (described below). Since the results did not differ (ESM 3), we use the most precise data from the 44×44-km non-breeding region.

Habitat characteristics during the moulting period were defined as those from the first non-breeding sites in individuals with more than one non-breeding site. In individuals with one non-breeding site only, we extracted the habitat characteristics for the period between the arrival at the non-breeding grounds and average departure from the first non-breeding site in the individuals with more than one non-breeding site (7th December, SD = 22 days, n = 79). High greenness values are assumed to reflect high-quality habitats, high greenness seasonality values represent habitats with high temporal variability of greenness values and high positive greenness trend values reflect habitats with a high increase in greenness measurements over time.

Secondly, we used stable carbon isotope ratios from feathers presumably grown at the first non-breeding site to estimate habitat quality during the moulting period. Stable isotopes are transported in food webs and archived in metabolically inert tissues during their synthesis. The stable isotopic signal then reflects the diet as well as the habitat where the feather was grown (Hobson 2011). The $^{13}\text{C}/^{12}\text{C}$ values differ between C_3 and C_4 plants (Tippie and Pagani 2007), which have specific temperature and humidity optima for growth (Collatz et al. 1998; Sage et al. 1999). The

resulting stable carbon isotope ratio can thus be used as a proxy for habitat quality on the dry–moist gradient (Bearhop et al. 2004) or used as a proxy for arthropod biomass (Studds and Marra 2005). Stable isotope analysis of feather samples in our study followed the procedure detailed in Procházka et al. (2018). Obtained sample $^{13}\text{C}/^{12}\text{C}$ ratios are expressed in delta notation ($\delta^{13}\text{C}$; mean = -15.56‰ ; SD = 3.20; range: $[-22.31; -10.45]$) relative to the Vienna Pee Dee Belemnite standard. Repeated measures of internal laboratory standards (Institute of Limnology, University of Konstanz, Germany) indicate that our measurement error was $\pm 0.05\text{‰}$ (SD). More negative $\delta^{13}\text{C}$ values reflect C_3 -dominated and thus more moist habitats.

Carry-over effects calculation

We employed partial least square path models (hereafter ‘path models’), to identify the direction and quantify the strength of carry-over effects (Dijkstra and Henseler 2015; Hair et al. 2017) adopting *plspm* function from *plspm* R package (Sanchez et al. 2017). We used the timing of events, migration speed and non-breeding habitat characteristics as states of the individual annual cycle events for developing an initial path diagram based on predictions 1–3 ($n = 103$ individuals, Table 1, ESM 4).

We then prepared a set of reduced initial path models testing predictions 4–6 and using data differing in sample sizes as we used data from European populations where both sexes were tracked (prediction 4) and where a sufficient number of tracks enabled comparisons (prediction 5), or all individuals with available feather sample $\delta^{13}\text{C}$ values (prediction 6), respectively. Therefore, we also adjusted the number of relationships within the initial path model following the rule of a minimum of 10 observations per explanatory variable (Cohen 1992; Barclay et al. 1995). In total, we prepared four sets of path models examining:

1. Carry-over effects within all stages of the annual cycle (path model 1; predictions 1–3; $n = 103$ individuals; ESM 4).

2. Sex-specific differences in carry-over effects (set of path models 2; predictions 1–4; European populations only; females = 38, males = 54).
3. Population-specific differences in carry-over effects (set of path models 3; predictions 1–3 and 5; European populations only: SE = 37, CZ = 35 and BG = 21).
4. Impact of environmental conditions experienced during moult vs. the entire non-breeding period on the subsequent phases (set of path models 4; predictions 1–3 and 6; n = 86; see ESM 5 for all reduced initial path models).

We refer to path coefficients >0.5 as strong effects, $0.3\text{--}0.5$ as moderate effects and coefficients <0.3 as weak effects (Cohen 1977). We consider path coefficients statistically important when 95% confidence intervals (bootstrapped with 1×10^4 iterations) do not overlap zero. We scaled and centred all variables within a population prior to fitting path model 1, and the sets of path models 2 and 4. As we found little or no inter-annual differences in explanatory variables, we do not incorporate year into path models (see ESM 6). The group average of path coefficients was calculated from absolute values using *vglm* function (following folded normal distribution) from VGAM R package (Yee 2019).

Moreover, we employed linear mixed-effects models to test for sex-specific differences in habitat characteristics: We ran separate models for greenness, greenness trend and greenness seasonality as response variables, each with sex as an explanatory variable and population identity as random intercept (*lmer* function from lme4 R package; Bates et al. 2015). We used R version 3.5.3 for the analyses (R Core Team 2019).

Results

We found the strongest positive relationships within migration periods, i.e. between the departure from the breeding sites and the arrival at the non-breeding grounds (path coefficient = 0.62; 95% confidence interval (CI) [0.49; 0.76]), and between the departure from the non-breeding sites and

arrival at the breeding sites (0.78 [0.65; 0.92]). Long stopovers during both migration periods were associated with late arrival at the non-breeding sites (0.39 [0.23; 0.53]), and to the breeding sites (0.34 [0.16; 0.52]), respectively. The later birds departed from the non-breeding grounds the shorter were the stopovers during the spring migration (-0.38 [-0.55 ; -0.20]; Fig. 2). In contrast, we detected only weak links between autumn and spring periods (Fig. 2, ESM 7).

The assessment of non-breeding habitat quality and seasonality effects on subsequent annual cycle stages revealed only weak effects. However, individuals spending the non-breeding period in places with positive greenness trend over time departed later than individuals from deteriorating habitats (0.26 [0.06; 0.43]; Fig. 2; ESM 7).

We did not find differences in either direction or strength of carry-over effects between males and females (Fig. 3A). Moreover, the sex differences in habitat quality and seasonality of non-breeding sites were negligible (Table 2).

We detected the strongest carry-over effects in the annual cycle events of birds from the southern breeding population (BG, mean of absolute path coefficient values = 0.48, 95% CI [0.16; 0.79]) compared to the central (CZ, 0.26 [-0.10 ; 0.60]) and northern (SE, 0.28 [-0.02 ; 0.59]) European populations. These differences were consistent in relationships between the timing of annual cycle events (SE, 0.42 [0.24; 0.61]; CZ, 0.36 [0.12; 0.60]; BG, 0.61 [0.30; 0.93]) as well as in the impacts of the non-breeding habitat quality on the subsequent phases (SE, 0.08 [-0.18 ; 0.35]; CZ, 0.16 [-0.09 ; 0.41]; BG, 0.30 [0.15; 0.45]). Individuals from the southern breeding population (BG) using non-breeding habitats with high average greenness departed earlier from their non-breeding grounds (path coefficient = -0.49 ; 95% CI [-0.75 ; -0.17]). In contrast, we found a negligible relationship between average greenness and the departure from non-breeding grounds for the central and northern European breeding populations but higher average greenness was related to shorter stopovers during spring migration in these two populations (Fig. 3B).

While longer autumn stopovers were positively related to the departure from the breeding site in the northern population (SE, path coefficient = 0.41; 95% CI [0.09; 0.67]), these were

negatively related in both the central (CZ, -0.39 [-0.61; -0.07]) and the southern (BG, -0.69 [-0.87; -0.43]) European breeding populations (Fig. 3B). In all three populations, we detected strong positive relationships between departure from the breeding site and arrival at the non-breeding grounds as well as between departure from the non-breeding grounds and arrival at the breeding site. The highest variation in this relationship was observed in the southern population and the lowest variation in the northern European population (Fig. 3B).

Higher greenness seasonality during moult entailed longer spring migration and slightly delayed event timing (mean of absolute path coefficient values = 0.25; 95% CI [0.23; 0.27]) compared to greenness seasonality during the entire non-breeding period (0.16 [0.10; 0.23]). In contrast, greenness trend during the entire non-breeding period had a slightly stronger effect on the timing of departure from the non-breeding grounds and arrival at the breeding site as well as on the duration of spring stopovers (0.18 [0.08; 0.29]) than greenness trend during the moulting period (0.04 [-0.97; 1.06]). We found a more negative feather $\delta^{13}\text{C}$ values (reflecting moist habitats) related to later departures from the non-breeding grounds (path coefficient = -0.28; 95% CI [-0.53; -0.04]; Fig. 3C).

Discussion

In this study, we describe a network of carry-over effects within the whole annual cycle of great reed warblers from across their breeding range. Our results support the prediction of the strongest relationships between consecutive events and the buffering capacity of the non-breeding period hypothesis. Surprisingly, we did not find evidence for strong or moderate effects of various environmental characteristics during the non-breeding period on subsequent stages of the annual cycle. However, spending the moult period in habitats with higher seasonality entailed slower spring migration and later arrival at the breeding sites. We found no profound differences in strength of carry-over effects between males and females. However, carry-over effects were strongest for individuals from the southern European breeding population (BG).

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363 **Carry-over effects within the full annual cycle**

364 Consecutive events within the migration periods were most closely linked, supporting our
365 prediction 1 based on the previously proposed ‘domino effect’ hypothesis (Piersma 1987). This
366 temporal pattern likely arises from an ‘optimal migration strategy’ which minimizes time spent on
367 migration (Hedenström 2008). The strong links within the spring migration period correspond with
368 strong selection for early arrivals in both male and female great reed warblers (Tarka et al. 2015).
369 The positive relationships between migration speed and subsequent events suggest co-effects of
370 environmental conditions or habitat quality at stopover sites causing delay or fitness costs in
371 subsequent phases (Briedis et al. 2017; Rakhimberdiev et al. 2018; Lindström et al. 2019). In
372 contrast, we detected no firm links between timing of autumn and spring migration periods
373 suggesting a large buffering capacity of the non-breeding period (Briedis et al. 2018; Gow et al.
374 2019). This effect may be further reinforced by intra-tropical movements which usually occur when
375 habitats deteriorate (Koleček et al. 2018).

376 In contrast to our prediction 3, we did not detect strong relationships between any spring
377 migration timing and any non-breeding habitat quality or seasonality measures. The absence of such
378 links may be explained by the non-breeding habitat use and intra-tropical movements. Firstly,
379 observational studies have highlighted the species’ preference for small-scale habitat patches with
380 higher water availability throughout the non-breeding period (Becquaert 1952; Ruwet 1965; De Roo
381 and Deheegher 1969; Sorensen et al. 2015). Under such conditions, non-breeding habitat quality
382 with coarser resolution used in our study may not be a decisive limiting factor, and thus not result in
383 measurable habitat-induced carry-over effects to subsequent phases. However, the range of $\delta^{13}\text{C}$
384 values measured in feathers (see Materials and Methods section) suggests that great reed warblers
385 use both C_3 - and C_4 -plant habitats during the moulting period. Secondly, many great reed warblers
386 undertake intra-tropical movements that could further reduce the impact of non-breeding habitat
387 quality on subsequent phases (Koleček et al. 2018). Importantly, the non-breeding habitat quality at

the first site was found to carry over to the final non-breeding period affecting the body condition of great reed warblers but only in a dry year and the habitat conditions did not carry over into the non-breeding period before departure (Sorensen et al. 2016).

Importance of habitat conditions during the moulting period

We found that the seasonality of habitats during the moulting period had stronger carry-over effects on subsequent phases than seasonality during the entire non-breeding period, although the carry-over effects only differed slightly between these two periods.

These findings correspond to a previously observed carry-over effect of habitat quality at the first non-breeding site to the final non-breeding site, and the absence of such a relationship in the period of the departure from the non-breeding grounds (Sorensen et al. 2016). Importantly, links between autumn migration, non-breeding and spring migration periods could be stronger in smaller bird species (Martin et al. 2020) and in species with a higher sensitivity to non-breeding habitat conditions, as compared to the larger, habitat-specialist species in this study (Cramp 1992). In addition, our results suggest slight differences in broad-scale average habitat quality NDVI metric and $\delta^{13}\text{C}$ derived from feathers.

In contrast to our prediction, we found a negative relationship between feather $\delta^{13}\text{C}$ values and departure from the non-breeding grounds suggesting that individuals depart later from more mesic habitats than from xeric habitats. This contrasts with the results of previous studies unveiling a positive link between $\delta^{13}\text{C}$ in bird tissues and timing of spring migration (e.g. Marra et al. 1998). Despite a common use of the $\delta^{13}\text{C}$ value as a marker of habitat quality in migratory birds (Hobson 2011), only few studies have evaluated the relationship between the $\delta^{13}\text{C}$ values measured in vegetation and in tissues of insectivorous bird species collected in the same area (so far conducted only in Central America; Marra et al. 1998; Bearhop 2004; Studds and Marra 2005). As long as the mechanisms of $\delta^{13}\text{C}$ transport between vegetation, insects and bird tissues are not firmly established, the links between $\delta^{13}\text{C}$ ratios and subsequent timing should be interpreted cautiously.

Finally, to delimit the moulting period, we assumed great reed warblers to complete moult at the first non-breeding sites. However, several studies reported rare cases of great reed warblers suspending moult in the southern parts of the breeding range during the post-breeding period (Spina 1990; Copete et al. 1998). Similarly, individuals in our study could have completed moult at their second or third instead of their first non-breeding site. However, none of the studies from sub-Saharan Africa (Pearson 1975; Hedenström et al. 1985; Bensch et al. 1991) reported observations of freshly moulted individuals after the arrival at the non-breeding grounds or during the latter part of the non-breeding period. Furthermore, no individuals with very fresh feathers, indicating completion of moult towards the end of winter, have been found in over 35 years of comprehensive studies of the great reed warbler population breeding in Sweden (DH and BH own observations). Therefore, we encourage future studies on carry-over effects of habitat conditions during complete moult as such relationships might have significant consequences for population dynamics of declining species (Vickery et al. 2014).

Population- and sex-specific differences in carry-over effects

We found the strongest carry-over effects for birds from the southern breeding population (BG) compared to birds breeding in the central and the northern European populations. Despite comparing only three populations, we had sufficient numbers of full annual tracks for each population covering multiple years, which should minimise the effect of between-year variability on the resulting spatial pattern. The most plausible explanation for such a spatial pattern is population-specific migration distances and environmental conditions experienced *en route*. Increasing migration distance and number of stopovers (Koleček et al. 2016) for individuals breeding at higher latitudes might raise the probability of encountering unfavourable environmental conditions *en route*. Such conditions can cause delays of subsequent phases of the annual cycle and override effects of preceding events. In line with our prediction 5, we also detected a strong effect of non-breeding habitat quality on subsequent phases of the annual cycle in the southern European

population (BG) again suggesting the importance of longer migratory distances diminishing the effects of preceding events. Finally, our results indicate that both the direction and the strength of carry-over effects can differ between populations, which should be taken into consideration when interpreting results from single-population studies.

In contrast, carry-over effects were similar for females and males and we did not find any significant sex-specific differences in non-breeding habitat quality suggesting no sex segregation in the non-breeding habitats. Great reed warblers only show limited sex dimorphism in body size (males are on average 4% larger than females; Cramp 1992; Tarka et al. 2014) possibly explaining the absence of dominance-mediated segregation (Marra and Holmes 2001). The lack of sex-specific differences in carry-over effects (prediction 4) further suggests a weak impact of protandry on the strength of carry-over effects. The current evidence for sex-specific differences in carry-over effects is equivocal (Norris et al. 2004; López-Calderón et al. 2017; Saino et al. 2017) and future studies should focus on difference in carry-over effects between the sexes in more species and on impacts of sex-specific habitat use as these differences could have crucial implications for population dynamics (Briedis and Bauer 2018).

Conclusions

Our results complement the knowledge of carry-over effects by uncovering new relationships between the annual cycle events. Furthermore, building a network of links between annual cycle events could enable more robust comparisons of different studies. We detected population-specific differences in carry-over effects and this result might become crucial for understanding regional-scale differences in timing of migration or population trends. Finally, studying full annual cycles provides a better understanding of important links and neglected periods affecting individual performance potentially influencing population dynamics.

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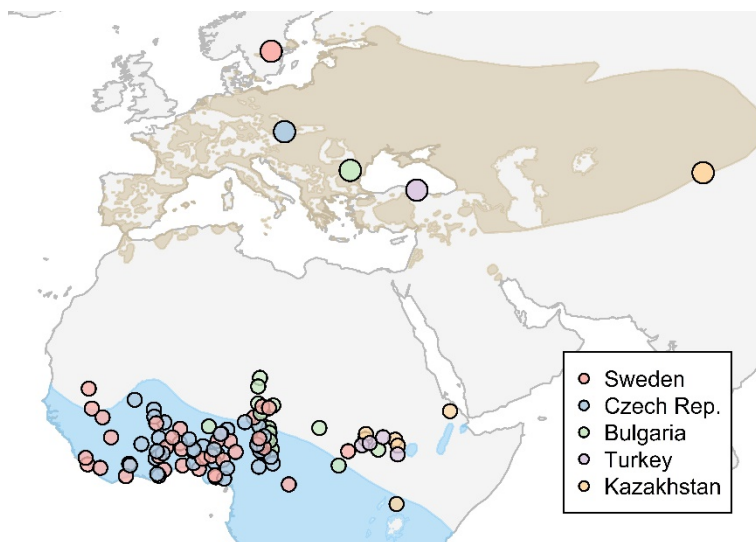
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Figure captions

Fig. 1 Breeding sites (large dots) and the first non-breeding sites of 103 individuals (small dots). Shaded areas represent the breeding (beige) and the assumed non-breeding (blue) range of the great reed warbler (BirdLife International and NatureServe 2014)

Fig. 2 Direction (green – positive, red – negative) and strength (line width) of carry-over effects between annual cycle events in great reed warblers ($n = 103$ individuals). Only paths with path coefficients >0.1 are depicted. All path coefficients with 95% confidence intervals are presented in Electronic Supplementary Material 7

Fig. 3 Differences in carry-over effects between males and females (A), breeding populations (B) and periods of non-breeding period (C). The directions and strengths of carry-over effects (bars) are derived from the set of path models 2 (A; females = 38, males = 64), set of path models 3 (B; northern = 37 (SE), central = 35 (CZ) and southern = 21 (BG) and set of path models 4 (C; $n = 86$). Error bars depict the 95% confidence intervals



687

688 Fig. 1

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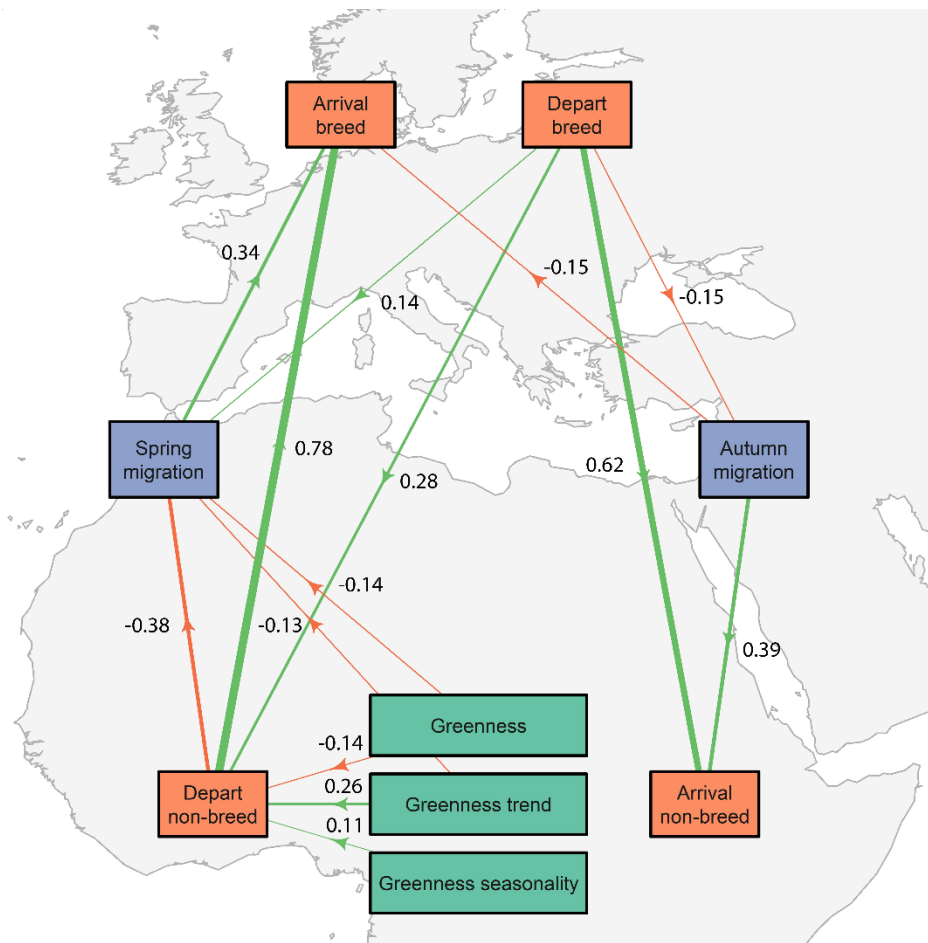


Fig. 2

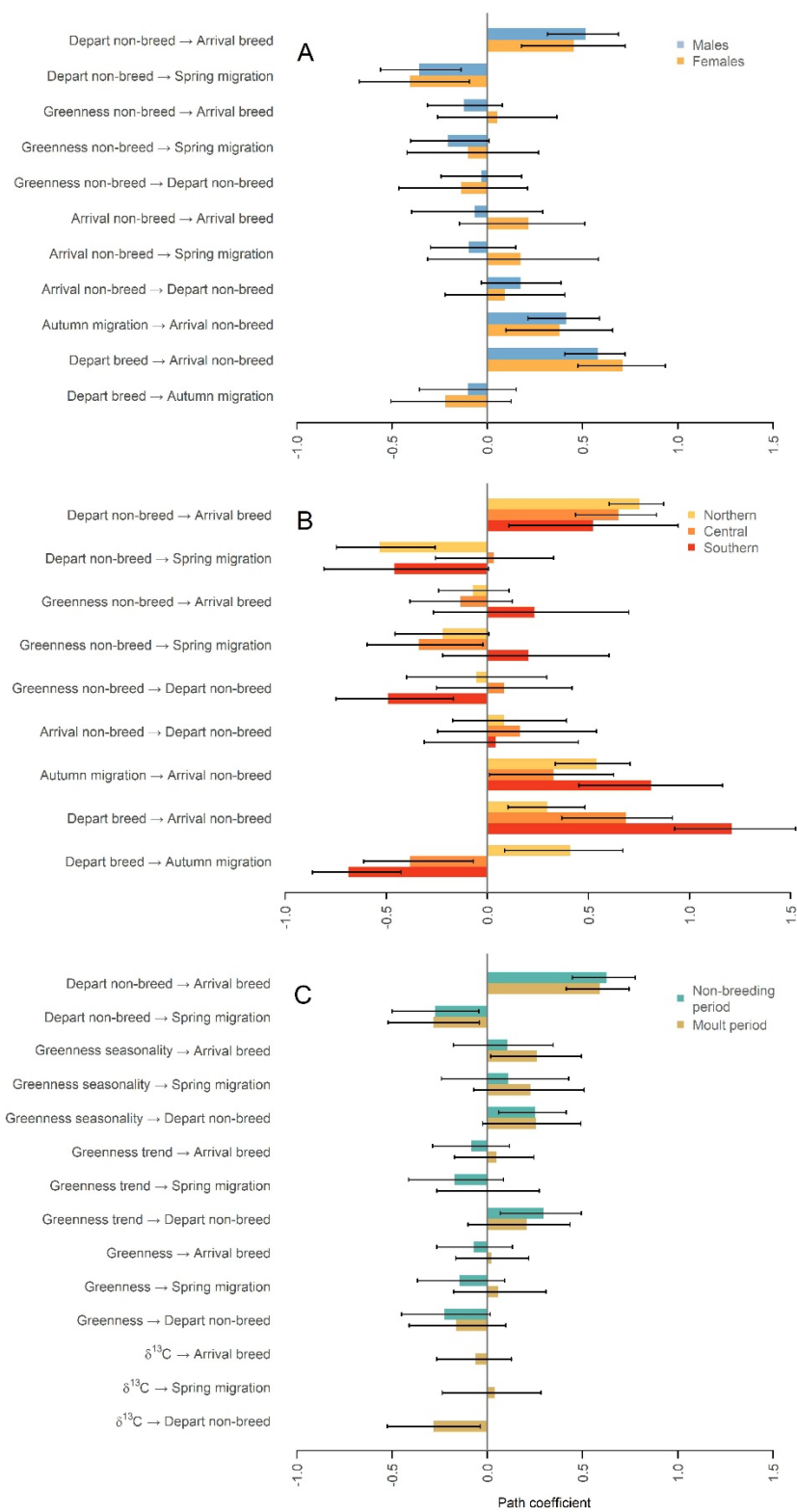


Fig. 3

Table 1 Variables used to describe states of the annual cycle events and abbreviations used in Figs 2, 3

<i>Abbreviation</i>	<i>Description</i>
Depart breed	Departure date from the breeding site
Autumn migration	Ratio of the stationary time to the total duration of the autumn migration
Arrival non-breed	Arrival date at the first non-breeding site
$\delta^{13}\text{C}$	Stable carbon isotope ratio of feathers
Greenness	Mean of weekly NDVI values
Greenness trend	Sum of between-week differences in NDVI
Greenness seasonality	Mean of between-week differences in NDVI
Depart non-breed	Departure date from the non-breeding site
Spring migration	Ratio of the stationary time to the total duration of the spring migration
Arrival breed	Arrival date at the breeding site

701 Table 2 Differences in non-breeding habitat conditions between males and females. Females are the
702 reference level (females = 38, males = 64)

<i>Response variable</i>	<i>Estimate</i>	<i>SE</i>	<i>t</i>	<i>P</i>
Greenness	<0.01	0.01	0.71	0.48
Greenness trend	-0.03	0.02	-1.83	0.07
Greenness seasonality	<0.01	<0.01	-1.04	0.30

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