Environmental conditions during winter predict age- and sex-specific differences in reproductive success of a trans-Saharan migratory bird

C. López-Calderón, K. A. Hobson, A. Marzal, J. Balbontín, M. Reviriego, S. Magallanes, L. García-Longoria, F. de Lope & Anders P. Møller

Previous studies have linked winter habitat with subsequent breeding phenology and physical condition of migratory birds, but few have found delayed effects of winter habitat on subsequent reproductive success. The aim of this study was to test if African winter habitat is related to subsequent reproductive success of house martins (Delichon urbicum) breeding at a colony in Spain. We measured stable isotope (δ2H, δ13C, δ15N) values from feathers moulted in West Africa and used confirmatory path analysis to test if isotopic values of winter-grown feathers were related to reproductive success through the mediation of breeding phenology and body condition. We conducted separate analyses for males, females and age classes (yearlings vs ≥ 2 years old). Experienced males wintering in habitats of higher rainfall (as inferred from lower feather δ2H values) were in better body condition and produced more offspring during the subsequent breeding season. In contrast, we did not find any effect of winter habitat on reproductive success of young males or females. These findings provide evidence consistent with a complex causal link between winter habitat quality and subsequent breeding success of long-distance migratory songbirds.

In an ecological context, carry-over effects occur when the previous history and experience of an individual explains its current performance in a given situation. Many studies of migratory birds have found that environmental conditions experienced during winter have carry-over effects in terms of subsequent body condition and breeding phenology. However, few studies have found carry-over effects of environmental conditions from winter areas on final reproductive success. For instance, older barn swallows (Hirundo rustica) arrived earlier to their breeding grounds after winters with favorable environmental conditions and, as a result of increased frequency of second broods, their reproductive success was higher in those years.

Given the difficulty in tracking migratory songbirds with exogenous instruments or markers, analyses of stable isotopes on feathers can provide an alternate or complementary means of studying carry-over effects. For instance, populations of godwits (Limosa limosa islandica) wintering in 13C-enriched (i.e., high quality marine) habitats have higher reproductive success than populations wintering in 13C-depleted (lower quality terrestrial) habitats.

Environmental conditions experienced in winter may first affect physical condition during winter, timing of departure from wintering sites and timing of arrival to breeding areas. Then, arrival time to breeding areas could determine the start of breeding and this in turn directly influence the number of offspring produced. In addition, physical condition upon arrival and during the breeding season could be related to breeding performance. Structural Equation Models (hereafter: SEM) and path analysis (a kind of SEM with only measured variables) provide a powerful statistical method to study complex natural systems, since multiple predictor and response variables can be analyzed in a single causal network. Specifically, these kinds of analyses can be especially useful in dealing with carry-over effects in migratory birds since the above-mentioned variables flow...
in a time series fashion from wintering to breeding period and vice versa. However, despite the great potential of SEM to detect carry-over effects in migratory birds, it has rarely been used for this purpose. For instance, an indirect carry-over effect of winter habitat quality (inferred from δ13C measurements) on reproductive success in American redstart (Setophaga ruticilla), was elegantly disentangled by the use of path analysis. In that study, the use of path analysis was essential for discerning that arrival, laying and fledging date, as mediated by the effect of winter habitat quality, determined the number of fledglings finally reared during the subsequent breeding season. A similar result was found for yearling female yellow warblers (Setophaga petechia) overwintering in Mexico and breeding in Canada, utilizing general linear models in a path-like analysis. Recently, the complex associations among phenology, winter ecology and breeding performance in the barn swallow have been analyzed by means of partial least squares path modeling (which is related to SEM).

The house martin (Delichon urbicum) is a small colonial hirundine distributed across Europe, Asia and Africa. In the Palearctic, this species breeds across Europe and winters throughout Africa south of 20°N, where the single complete annual moult occurs. House martins breeding in Western Europe tend to winter in Western Africa and those breeding in Eastern Europe tend to winter in Eastern Africa. Like many aerial insectivores and long-distance migrants, the Palearctic population of house martin has declined during 1990–2000 and the global population is also declining. However, causes of these declines and the degree of migratory connectivity in this species are poorly understood. We previously analyzed stable isotope (δ2H, δ13C, δ15N) values from feathers of house martins breeding in southwestern Spain and proposed two winter areas in West Africa with different environmental conditions (savannah and broadleaf forest). We also found that experienced males winter in savannas at higher probability than females, whereas young males winter in savannas at lower probability than females. By contrast, experienced and young females winter in both areas with similar probabilities. Furthermore, we showed that winter area choice was related to clutch initiation date in the subsequent breeding season. However, we did not detect a final carry-over effect on the number of fledglings produced.

The aim of this study was to investigate the relationship between winter habitat of house martins wintering in West Africa and subsequent reproductive success in the temperate breeding area in southwestern Spain. We used as a proxy of winter habitat the isotopic values of feathers moulted at the wintering grounds, and confirmatory path analysis to discriminate between some of the likely mediator variables involved in this migratory system. We predicted that environmental conditions in winter areas, as reflected by multiple feather isotopes (δ2H, δ13C, δ15N), indirectly affect the subsequent reproductive success of individuals through effects on subsequent breeding phenology and body condition. Specifically, we hypothesized that open habitats dominated by C4 vegetation with high seasonal rainfall are more suitable for our study species to overwinter than equatorial closed forests dominated by C3 vegetation. This is caused by higher rainfall being correlated with higher abundance of flying insects, but also because open habitats may provide a better habitat for aerial insectivores to forage. Therefore, we expected that lower feather δ2H and higher feather δ13C and δ15N values would be correlated with earlier breeding phenology, improved physical condition and thus higher reproductive success in the subsequent breeding season. We separately analyzed young (i.e., one-year-old birds migrating for the first time) from experienced birds (i.e., two-years or older birds that have previously migrated successfully), and males from females, since we predicted such carry-over effects operate differently according to age and sex. Each breeding season, we performed more than one hundred capture sessions from March to July, capturing more than 90% of the colony. Breeding dispersal is negligible for house martins, while recruitment and first reproduction occurs at the age of one year. Thus, we could assign the age of individuals accurately, assuming un-ringed adult birds being yearlings at first capture originating from outside the study area, and assuming that disappearance of ringed breeders from the colony indicated mortality rather than dispersal.

Results

Winter habitat features carried over to affect reproductive traits more strongly in males than in females. Breeding performance was affected by different winter habitat features depending on age class. For experienced males, confirmatory path analysis showed that rainfall amount as inferred by feather δ2H had a significant direct effect on body condition [estimate (SE) = −0.33 (0.15), p = 0.04], and also that body condition had a significant direct effect on the number of fledglings produced during the breeding season [estimate (SE) = 0.45 (0.16), p = 0.01]. For young males, confirmatory path analysis showed that vegetation type as indexed by feather δ13C and δ15N had significant direct effects on body condition [δ13C: estimate (SE) = 0.36 (0.14), p = 0.01; δ15N: estimate (SE) = 0.40 (0.14), p < 0.01] and laying date [δ13C: estimate (SE) = −0.29 (0.13), p = 0.05; δ15N: estimate (SE) = −0.29 (0.13), p = 0.04]. For females, we only found that feather δ13C had a significant direct effect on the laying date of young females [estimate (SE) = 0.21 (0.09), p = 0.03], possibly related to diet (i.e. trophic position) or foraging micro-habitat. Therefore, confirmatory path analyses showed strong differences in path coefficients across age and sex categories (Fig. 1, Table 1).

Laying date and body condition were not significantly correlated in any of the confirmatory path analyses [experienced males: estimate = 0.23, p = 0.08; young males: estimate = 0.19, p = 0.09; experienced females: estimate = −0.13, p = 0.75; young females: estimate = −0.17, p = 0.93]. Feather δ13C and δ15N values were not significantly correlated for young males (estimate = −0.37, p = 0.99). We used d-separation test to quantify the goodness of fit of our models, which tests the assumption that all variables are conditionally independent. All models provided robust fit to data (experienced males: Fisher’s C = 7.7, df = 6, p = 0.26; young males: Fisher’s C = 3.59, df = 6, p = 0.73; experienced females: Fisher’s C = 7.65, df = 6, p = 0.26; young females: Fisher’s C = 6.66, df = 6, p = 0.35). We did not find any significant association among unconnected variables in any of our models. Thus, we concluded that the hypothesized relationships we examined were consistent with the data. By examining “qq plots”, we determined that every single linear mixed model was well fitted with the only exception of the linear model built for the number of fledglings in experienced females.
Since for experienced males we found that feather $\delta^{2}H$ had an indirect effect on the number of fledglings mediated through body condition, we used standardized path coefficients from this model to predict how final reproductive success shifts in response to the change in feather $\delta^{2}H$ (Fig. 2). We quantified that the increase by one SD of $\delta^{2}H$ decreases the number of fledglings by 0.2 SD.

**Discussion**

We found direct and indirect effects of environmental conditions experienced in the winter areas on different breeding traits in our migratory study population of house martins. Interestingly, we found that environmental conditions experienced during winter in Africa affected reproductive success depending on the age and sex of individuals. We found for experienced males that amount of rainfall, as inferred by feather $\delta^{2}H$, directly affected physical condition, and that physical condition directly affected the number of fledglings produced in the first brood. This amounted to a difference of one fledgling reared across the range of feather $\delta^{2}H$ values. In ecological terms, experienced males wintering in habitats of higher rainfall (i.e. indicated by lower $\delta^{2}H$) were in better body condition and raised a larger number of fledglings during the subsequent breeding season than experienced males wintering in drier habitats (i.e. higher $\delta^{2}H$). In contrast, vegetation type as indexed by feather $\delta^{13}C$ and $\delta^{15}N$ values, affected body condition and breeding phenology of young males. In ecological terms, young males wintering in C4-dominated savannah (i.e. enriched in $^{13}C$) were in better body condition during the subsequent breeding season and reproduced earlier than young males wintering in broadleaf forest (i.e. depleted in $^{13}C$). However, the change in these reproductive variables did not translate into a final change in the number of fledglings. This could indicate that breeding phenology and body condition are of lower importance for reproductive success of young compared to experienced males. Actually the confirmatory path analysis built for young males revealed some effect of breeding phenology on the number of fledglings, but not sufficiently strongly to reach statistical significance. We hypothesize that young males may invest less in reproduction than experienced males, yet survival rates of young males are much lower. Characterizing winter habitats based on $\delta^{15}N$ values are inherently more difficult due to effects of both natural (e.g. climate) and anthropogenic (e.g. fertilizer use, agricultural intensity)
As wet forests or mangroves2–4,35. In contrast, previous studies on house martins showed that this species mainly
young males and young females. Significant effects are highlighted in bold.
and random effects. Sample size is 38, 28, 52 and 77, respectively, for experienced males, experienced females,
winters in habitats enriched in 13C such as open savannah and grassland29. We found that experienced males win-
δ15N. Because several factors can influence dietary
performance of experienced females.
here are standardized path coefficients (i.e. slopes of effects). R 2 shown here is the conditional R 2, based on fixed
Summary results from confirmatory path analyses built for each age and sex class. Estimates shown
Table 1. Summary results from confirmatory path analyses built for each age and sex class. Estimates shown
Factors34. Mean predicted δ15N values were similar in both isotopic clusters described as winter areas for house
martins breeding in Southern Spain4. Feather δ15N values also affected laying dates of young females, although in
the opposite direction as in young males; young females wintering in habitats of higher δ15N started to reproduce
later than young females wintering in habitats of lower δ15N. Because several factors can influence dietary δ15N
values, including climate, anthropogenic factors and plant nitrogen fixation pathways, it is difficult to predict what
may be driving this pattern34. Finally, we did not find any effect of winter habitat features on the reproductive
performance of experienced females.
Previous studies on Neotropical migratory passerines have found improved reproductive success10,12 and
improved physical condition associated with lower δ13C values expected from more mesic environments such as
wet forests or mangroves2–4,35. In contrast, previous studies on house martins showed that this species mainly
winters in habitats enriched in 13C such as open savannah and grassland29. We found that experienced males win-
tering in habitats of presumed higher seasonal rainfall raised more offspring in the subsequent breeding season,
and also that young males improved body condition and initiated breeding earlier when wintering in habitats of
higher δ13C values. Therefore, our results suggest that savannah in West Africa is a more suitable winter area for	house martins than broadleaf forest. Previous studies have determined that house martins benefit from higher
precipitation on their wintering grounds36,37, and this is in agreement with our results based on feather δ15N values.
We interpret this in terms of higher expected insect production in wet vs dry areas30,32.
To our knowledge, only two previous studies have quantified the indirect effect of isotopic signature from the
wintering areas on the number of fledglings reared by a small passerine in the subsequent breeding season, and
these were both in the New World. The effect of winter habitat on the number of fledglings was stronger for female
than for male American redstarts48, while only young female yellow warblers experienced this carry-over effect12.
We also found that environmental conditions from winter areas affected house martins differently according
to age and sex. Specifically, a final increase of approximately one fledgling was predicted for experienced males

| Model                | Response            | Predictor              | estimate | SE     | P      | R²     |
|----------------------|---------------------|------------------------|----------|--------|--------|--------|
| **Experienced males**| No. fledglings       | Scaled body mass index | 0.455    | 0.160  | 0.010  | 0.340  |
|                      | Laying date          | δH                    | 0.217    | 0.153  | 0.169  | 0.418  |
|                      |                      | δ13C                  | 0.273    | 0.182  | 0.160  | 0.418  |
|                      |                      | δ15N                  | 0.273    | 0.163  | 0.899  | 0.418  |
|                      | Number of fledglings | Scaled body mass index | 0.017    | 0.141  | 0.098  | 0.025  |
|                      | Laying date          | δH                    | 0.249    | 0.141  | 0.099  | 0.350  |
|                      |                      | δ13C                  | 0.293    | 0.132  | 0.034  | 0.350  |
|                      |                      | δ15N                  | 0.293    | 0.134  | 0.037  | 0.350  |
|                      | Number of fledglings | Scaled body mass index | 0.034    | 0.204  | 0.896  | 0.002  |
|                      | Laying date          | δH                    | 0.229    | 0.197  | 0.279  | 0.205  |
|                      |                      | δ13C                  | 0.293    | 0.206  | 0.379  | 0.205  |
|                      |                      | δ15N                  | 0.293    | 0.198  | 0.244  | 0.205  |
|                      | Number of fledglings | Scaled body mass index | 0.025    | 0.118  | 0.841  | 0.038  |
|                      | Laying date          | δH                    | 0.017    | 0.204  | 0.939  | 0.002  |
|                      |                      | δ13C                  | 0.229    | 0.197  | 0.279  | 0.205  |
|                      |                      | δ15N                  | 0.229    | 0.198  | 0.244  | 0.205  |
|                      | Number of fledglings | Scaled body mass index | 0.150    | 0.110  | 0.179  | 0.519  |
|                      | Laying date          | δH                    | 0.010    | 0.100  | 0.923  | 0.477  |
|                      |                      | δ13C                  | 0.010    | 0.094  | 0.269  | 0.477  |
|                      |                      | δ15N                  | 0.150    | 0.094  | 0.026  | 0.477  |
|                      | Number of fledglings | Scaled body mass index | 0.144    | 0.103  | 0.273  | 0.519  |
|                      | Laying date          | δH                    | 0.046    | 0.103  | 0.656  | 0.519  |
|                      |                      | δ13C                  | 0.046    | 0.103  | 0.656  | 0.519  |
|                      |                      | δ15N                  | 0.046    | 0.103  | 0.656  | 0.519  |
wintering in areas with lowest δ²H values relative to areas with the highest values. Interestingly, the final shift in breeding success we found for experienced male house martins was similar to the previous studies on Neotropical migrants. Few studies have identified the specific mechanism underlying carry-over effects. We found previously for house martins breeding in Spain that experienced males winter with a much higher probability in high-quality areas (i.e. savannahs) than young males. However, females winter in high quality areas with similar probabilities regardless of their age category. This finding is consistent with the notion that competition over winter habitats occurs among male house martins, and that it is linked to habitat characteristics important to male reproductive success. Previous studies found that competition at the winter grounds or selective pressure to arrive earlier at the breeding areas are stronger for males than for females, which could explain the differences we found among ages and sexes.

We showed a seasonal carry-over effect in a migratory passerine, where environmental conditions experienced in the tropical wintering areas had an indirect effect on reproductive success. Interestingly, we found this carry-over effect to be operating differently according to age and sex, where only the reproductive success of experienced males is sensitive to isotopic signatures of wintering area foodwebs. Confirmatory path analysis allowed us to identify body condition as a mediator for the observed carry-over effect on reproductive success. The analysis of stable isotopes from feathers has proven very useful for understanding the migratory ecology of this long-distance aerial insectivore, which is difficult or impossible to track by other methods. Further research, ideally involving the ground-truthing of feather isotope values compared to model predictions is recommended.

Methods

Field procedures. We studied a single colony of house martins in Badajoz, Southern Spain (38°53'N 7°01'W), during 2005–2013 (excluding 2006). From February to July, we followed reproductive events every second day to determine laying date (i.e., the date the first egg is laid) and brood size (i.e., the number of fledglings in the first brood). Adult house martins were captured and identified with numbered metal rings. Our original sample size was 195 adults and we only took one observation per individual. We categorized our original data in two different age-classes: young birds (i.e., one-year old individuals that have migrated for the first time that year; n = 129), and experienced birds (i.e., two-years or older individuals that were at least in their second migration year; n = 66). We categorized as young birds, individuals ringed as nestlings/fledglings that were recaptured in the next year (n = 41), and also individuals ringed for the first time as adults (n = 88). We categorized as experienced birds, individuals ringed as nestlings/fledglings that were recaptured two years or more after their first capture (n = 20), and also individuals ringed for the first time as adults that were recaptured in subsequent years (n = 46). From each adult we removed the outermost rectrix for isotopic analysis, recorded tarsus length with a digital caliper to the nearest 0.01 mm and body mass with a Pesola spring balance to the nearest 0.5 g. To estimate body condition we used the scaled mass index, which standardizes body mass at a fixed value of a linear body measurement (tarsus) based on the scaling relationship between mass and body length.

Figure 2. Relationship between feather δ²H and reproductive success of experienced male house martins from Badajoz (southwestern Spain). Points represent observed values. The line shows predicted values obtained from the standardized path coefficients of the confirmatory path analysis fitted for experienced males. The increase across feather δ²H range of values is predicted to decrease one fledgling reared by experienced males. Predicted values were obtained leaving δ¹³C and δ¹⁵N constant at their means, and taking into account only fixed effects.
Stable isotope analysis. All feathers were cleaned of surface oils in 2:1 chloroform:methanol solvent rinse and prepared for δ2H, δ13C and δ15N analysis. Deuterium abundance in the non-exchangeable hydrogen of feathers was determined following standard procedures42, and using three calibrated keratin hydrogen-isotope reference materials (CBS = −197‰; SPK = −121.6‰; KHS = −54.1‰). Deuterium measurement was performed on H2 gas derived from high-temperature (1350 °C) flash pyrolysis of 350 ± 10 µg feather subsamples and keratin standards. Measurement of the three keratin laboratory reference materials, corrected for linear instrumental drift, were both accurate and precise with typical within-run (n = 5) SD values of <2‰. For feather δ13C and δ15N analyses, between 0.5 and 1.0 mg of feather material was combusted online using a Eurovector 3000 elemental analyzer (Eurovector, Milan, Italy). The resulting CO2 and N2 was separated by Gas Chromatograph (GC) and introduced into a Nu Horizon (Nu Instruments, Wrexham, UK - www.nu-ins.com) triple-collector isotope-ratio mass-spectrometer via an open split and compared to CO2 or N2 reference gas. Using previously calibrated internal laboratory C and N standards [powdered keratin (BWBIII; δ13C = −20‰; δ15N = 14.4‰) and gelatin (PUGEL; δ13C = −13.6‰; δ15N = 4.73‰)], within run (n = 5), precisions for δ15N and δ13C measurements were ~±0.15‰. Stable isotope ratios are reported in standard delta (δ) notation relative to VSMOW for δ2H, VPDB for δ13C, and AIR for δ15N analyses.

Environmental conditions in the wintering areas of house martins. House martins have feather δ2H values reflecting long-term, amount-weighted, average δ2H from precipitation prior to moult according to established calibration equations43,44, while δ13C and δ15N values are associated more directly from inorganic and organic sources to primary production following isotopic discrimination 44,45. Feather keratin is metabolically inert after synthesis46 and so isotopic values in feathers reflect the environmental conditions where they were grown (i.e. the wintering areas). Considerable literature has emphasized that foodweb δ2H, δ13C and δ15N values are strongly influenced by climate47. Lower values of δ2H in rain are linked to higher amount of precipitation in tropical latitudes48,49 (i.e. the so-called “amount effect”). Higher values of δ13C are associated with environments dominated by C4 plants as well as C3 plants adapted to hydric stress50. Finally, xeric/cultivated habitats tend to be relatively enriched in 15N relative to mesic/uncultivated habitats44.

The winter areas we previously identified for house martins breeding in southwestern Spain7 were defined by multi-isotopic clusters described for Africa 44. These isotopic clusters were closely associated with different African biomes, broadleaf forest in the so-called “Cluster 1” and savannah in “Cluster 2” (Fig. 3). Values of feather δ2H and δ13C differed markedly between the two areas of West Africa7, reflecting foodwebs in savannahs relatively enriched in 13C and depleted in 2H. In this wintering area, the savannah receives more rainfall during the rainy season than the broadleaf forest to the south51. Thus, we expect the foodweb to be relatively enriched in 13C here due to expected C4-dominated grasslands46, but depleted in 2H due to greater seasonal rainfall48,49. Indeed, that pattern was shown previously in the multi-isotopic cluster analysis for Africa44.
Confirmatory path analysis. Structural equation models (SEMs) are probabilistic models that hypothesize a causal network with multiple variables that can appear as both predictor and response variables. SEMs are usually represented as path diagrams in which one-headed arrows represent causal direct relationships from the independent variable to the dependent variable. Path analysis is a type of SEM that only takes into account observed variables, omitting latent variables (i.e., not measured variables). We used confirmatory path analysis to examine how feather isotope values reflecting winter habitats could explain reproductive success in the subsequent breeding season through mediation of breeding phenology and body condition. We refer to “confirmatory path analysis” as directed acyclic, or piecewise, SEM based on applications from graph theory. In piecewise SEM, the path diagram is translated to a set of linear equations (e.g., linear mixed models), which are then evaluated individually thus allowing a wide range of distributions and sampling designs. Another advantage of this methodology is that it allows fitting models with relatively small sample sizes. In addition, the goodness of fit of the entire causal network can be quantified by a directed separation test (“d-separation test”), which tests the assumption that all variables are conditionally independent (i.e., that there are no missing relationships among unconnected variables).

To control the effect of age and sex on breeding success, we developed different path models for each age and sex category. We split our original data set in four subsets: experienced males (n = 38), experienced females (n = 28), young males (n = 52) and young females (n = 77). We included six variables in our models: feather δ13H, δ13C, δ15N, body condition, first-egg laying date and number of fledglings in the first brood. Isotopic values were considered independent (exogenous), while the rest were considered dependent (endogenous) variables. Every observed variable included in our models had the same sample size (i.e., listwise deletion).

The structure of the path analysis was designed based on previous knowledge of the migratory ecology of our study population, but also on hypotheses to be tested. Exploratory analyses indicated that δ13C and δ15N values were negatively correlated for young males. We found in a previous study that breeding phenology (i.e., first egg laying date) depends on wintering area inferred from stable isotope analysis. It is also well known that breeding phenology is related to reproductive success in migratory passerines. Different studies have found an effect of wintering habitat (inferred from δ13C values) on body condition before departure to the breeding areas, and during spring migration. Therefore, we included as hypotheses to be tested causal paths from winter-grown feather δ13C and δ15N to body condition during the breeding season. We measured body condition when we first captured the individual. Within our original data set, 140 birds were first captured after they had already started breeding, whereas 55 birds were first captured before they started breeding. For this reason, we assumed correlated errors between the laying date and body condition, i.e., a relationship that is bidirectional and assumed to be caused by a shared underlying driver. For instance, arrival time to breeding areas could determine the start of breeding but also the physical condition during the breeding season. The R library piecewiseSEM implements a crude approximation of correlated errors by excluding them from the basis set (since there is no presumed direction of causality), and then running a simple test of significance on the bivariate correlation. Finally, body condition may influence the potential foraging of adults and hence the quantity of prey delivery they could afford for their progeny, and this, in turn, may influence the number of fledglings reared. In all cases, we captured adults and measured body condition before we recorded the number of fledglings. Each of our path analyses was made up of three linear mixed models, one for each dependent variable. Isotopic values were the independent variables of the linear mixed models built for body condition and first-egg laying date, while these were in turn the independent variables of the linear mixed model built for number of fledglings. In every linear mixed model we included “year” as the random effect, to statistically control for inter-annual effects. Finally, we examined the “q q plots” to visually test for normality of residuals in every individual linear mixed model. We conducted all our analyses with the library piecewiseSEM using R version 3.3.1.

Ethics statement. Methods were evaluated and approved by institutional Commission of Bioethics of University of Extremadura (CBUE 49/2011) and by Junta de Extremadura Local Government (CN0008/11/ACA and CN11/0388). All efforts were made to ameliorate suffering of animals and minimize handling time according to Guidelines to the Use of Wild Birds in Research (J. Fair, E. Paul, and J. Jones, Eds. 2010. Washington, D.C.: Ornithological Council). All the experiments comply with the current laws of Spain, where the experiments were performed.

Data availability. The dataset analysed during the current study is available from the corresponding author on reasonable request.

References
1. O’Connor, C. M., Norris, D. R., Crossin, G. T. & Cooke, S. J. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere 5, 28 (2014).
2. Marra, P. P., Hobson, K. A. & Holmes, R. T. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282, 1884–1886 (1998).
3. Bearhop, S., Hilton, G. M., Votier, S. C. & Waldron, S. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proc. R. Soc. Lond. B 271, S215–S218 (2004).
4. Studds, C. E. & Marra, P. P. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86, 2380–2385 (2005).
5. Balbontín, J. et al. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. J. Anim. Ecol. 78, 981–989 (2009).
6. Marral, A. et al. Malaria infection and feather growth rate predict reproductive success in house martins. Oecologia 171, 853–861 (2013).
7. López-Calderón, C. et al. Wintering areas predict age-related breeding phenology in a migratory passerine bird. J. Avian Biol. 48, 631–639 (2017).
8. Saino, N. et al. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol. Lett.* **7**, 21–25 (2004).
9. Saino, N. et al. Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. *J. Anim. Ecol.* **86**, 239–249 (2017).
10. Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. & Ratcliffe, L. M. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. R. Soc. Lond. B* **271**, 59–64 (2004).
11. Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. & Sutherland, W. J. Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. R. Soc. Lond. B* **272**, 2319–2323 (2005).
12. Drake, A., Rock, C., Quinlan, S. P. & Green, D. J. Carry-over effects of winter habitat vary with age and sex in yellow warblers *Setophaga petechia*. *J. Avian Biol.* **44**, 321–330 (2013).
13. Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. & Holmes, R. T. Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* **17**, 76–83 (2002).
14. Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. & Bearhop, S. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**, 4–18 (2011).
15. Winkler, D. W. & Allen, P. E. The seasonal decline in Tree Swallow clutch size: Physiological constraint or strategic adjustment? *Ecology* **77**, 922–932 (1996).
16. Smith, R. J. & Moore, F. R. Arrival timing and seasonal reproductive performance in a long-distance migratory land bird. *Behav. Ecol. Sociobiol.* **57**, 231–239 (2005).
17. Marzl, A. et al. A longitudinal study of age-related changes in *Haemoproteus* infection in a passerine bird. *Okoš* **125**, 1092–1099 (2016).
18. Balboti, J. et al. Lifetime individual plasticity in body condition of a migratory bird. *Biol. J. Linn. Soc.* **105**, 420–434 (2012).
19. Shipley, B. *Cause and correlation in biology: a user’s guide to path analysis, structural equations and causal inference with R* (Cambridge University Press, 2016).
20. Lefcheck, J. S. *piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics*. *Methods. Ecol. Evol.* **7**, 573–579 (2016).
21. Turner, A. K. *Family Hirundinidae (swallows and martins)* in *Handbook of the Birds of the World* (eds del Hoyo, J., Elliott, A. & Christie, D.) 602–685 (Lynx Edicions, 2004).
22. Szép, T., Liechti, F., Nagy, K., Nagy, Z. & Hahn, S. Discovering the migration and non-breeding areas of sand martin and house martins breeding in the Pannonian basin (central-eastern Europe). *J. Avian Biol.* **48**, 114–122 (2017).
23. Cramp, S. *The birds of the Western Palearctic, Vol. 5.* (Oxford University Press, 1988).
24. Turner, A. & Rose, C. *A Handbook to the Swallows and Martins of the World* (Christopher Helm, 1989).
25. Hobson, K. A., Van Welden, S. L., Piersma, T. & Wassenaar, L. I. Solving a migration riddle using isocapces: House Martins from a Dutch village winter over West Africa. *PLoS ONE* **7**, e45005 (2012).
26. Nebel, S., Mills, A., McCracken, J. & Taylor, P. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conserv. Ecol.* **5** (2010).
27. Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & Van Bommel, P. P. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Cons.* **131**, 93–105 (2006).
28. BirdLife International. *Delichon urbicum. The IUCN Red List of Threatened Species* https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T130811886A87468519.en (2016).
29. Evans, K. L., Newton, J., Mallord, J. W. & Markman, S. Stable isotope analysis provides new information on winter habitat use of declining avian migrants that is relevant to their conservation. *PLoS ONE* **7**, e34542 (2012).
30. Denlinger, D. L. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica* **77**, 922–932 (1996).
31. Cumming, G. S. & Bernard, R. T. F. Rainfall, food abundance and timing of parturition in African bats. *Ecology* **111**, 309–317 (1997).
32. Frampton, G. K., Van Den Brink, P. J. & Gould, P. J. Effects of spring drought and irrigation on farmland arthropods in southern Britain. *J. Appl. Ecol.* **37**, 865–883 (2000).
33. de Lope, F. & Da Silva, E. La fidelidad al lugar de nidificación o de nacimiento en el avión común (*Delichon urbicum urbicum*) en Badajoz, España. *Ardeola* **35**, 51–58 (1988).
34. Pardo, L. H. & Nadelhoffer, K. U. Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales in *Isoscapes: understanding movements, pattern and process on Earth through isotope mapping* (eds West, J. B., Bowen, G. J., Dawson, T. E. & Tu, K. P.) 221–249 (Springer, 2010).
35. Smith, J. A., Reitsma, L. R. & Marra, P. P. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. *Ecology* **91**, 2874–2882 (2010).
36. Robinson, R. A., Balmer, D. E. & Marchant, J. H. Survival rates of hirundines in relation to British and African rainfall. *Ringing & Migration* **24**, 1–6 (2008).
37. Ambrosini, R., Otroi, V., Massimino, D. & Bani, L. Identification of putative wintering areas and ecological determinants of population dynamics of common house-martin (*Delichon urbicum*) and common swift (*Apus apus*) breeding in northern Italy. *Avian Conserv. Ecol.* **6**, 3 (2011).
38. Møller, A. P. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). II. Mechanisms of sexual selection. *J. Evol. Biol.* **5**, 603–624 (1992).
39. Lozano, G. A., Perreault, S. & Lemon, R. E. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *Biol. Conserv.* **127**, 164–170 (1996).
40. Hasselquist, D. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* **79**, 2376–2390 (1998).
41. Peig, J. & Green, A. J. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Func. Ecol.* **24**, 1323–1332 (2010).
42. Wassenaar, L. I. & Hobson, K. A. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Jot. Environ. Health S* **39**, 211–217 (2003).
43. Bowen, G. J., Wassenaar, L. I. & Hobson, K. A. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* **143**, 337–348 (2005).
44. Hobson, K. A. et al. A multi-isotope (δ13C, δ15N, δD) feather isoscap to assign Afrotropical migrant birds to origins. *Ecography* **35**, 44 (2012).
45. Vanderklift, M. A. & Ponsard, S. Sources of variation in consumer-diet δ15N enrichment: a meta-analysis. *Oecologia* **136**, 169–182 (2003).
46. Hobson, K. A. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. *Condor* **101**, 799–805 (1999).
47. Hill, J. B., Bowen, G. J., Dawson, T. E. & Tu, K. P. *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping* (Springer, 2010).
48. Dansgaard, W. Stable isotopes in precipitation. *Tellus* **A** **16** (1964).
49. Clark, I. D. & Fritz, P. *Environmental isotopes in hydrogeology*. (CRC press, 1997).
50. Ehleringer, J. R. Carbon isotope ratios and physiological processes in aridland plants in *Stable isotopes in ecological research* (eds Rundel, P. W., Ehleringer, J. R. & Nagy, K. A.) 41–54 (Springer, 1989).
51. Sultan, B. & Janicot, S. The West African monsoon dynamics. Part II: The 'preonset' and 'onset' of the summer monsoon. *J. Climate* 16, 3407–3427 (2003).
52. Grace, J. B. *et al.* Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* 3, 73 (2012).
53. McDonald, R. P. & Ho, M.-H. R. Principles and practice in reporting structural equation analyses. *Psychol. Methods* 7, 64 (2002).
54. R Core Team. The R Project for Statistical Computing. *R Foundation for Statistical Computing* http://www.R-project.org (2016).
55. Allen, J. Land cover classification (1 year). *NASA Earth Observations* http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MCD12C1_T1 (2016).

**Acknowledgements**
This study was funded by research projects of the Spanish Ministry of Economy and Competitiveness (CGL2015-64650-P), Junta of Extremadura (IB16121), Junta of Andalucía (P12-RNM-2144) and University of Extremadura (A7-26). CLC was supported by an operating grant from the Junta of Andalucía (P12-RNM-2144). AM and MR were supported by grants from the Spanish Ministry of Education and Science (JC2011-0405, BES 2004–4886, BES-2007-15549 and BES-2010-030295, respectively). Isotope analyses were supported by an operating grant from Environment Canada to KAH. We want to thank C. Gryba and G. Koehler who assisted with stable isotope analyses.

**Author Contributions**
C.L.C., K.A.H., A.P.M., A.M. and J.B. wrote the first draft of the manuscript. C.L.C. made statistical analyses. C.L.C., K.A.H., A.P.M., J.B. and F.d.L. helped in the design of experimentations. C.L.C., K.A.H., A.P.M., A.M., J.B., F.d.L., S.M., L.G.L. and M.R. substantially helped in the data acquisition, revisions of the manuscript and gave final approval for publication.

**Additional Information**

**Competing Interests:** The authors declare that they have no competing interests.

**Publisher's note:** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2017