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Research

Identifying drivers of breeding success in a long-distance migrant using structural equation modelling

Guillaume Souchay, Rien E. van Wijk, Michael Schaub and Silke Bauer

G. Souchay (http://orcid.org/0000-0003-0214-9362) (guillaume.souchay@oncfs.gouv.fr), R. E. van Wijk (http://orcid.org/0000-0002-6887-3153), M. Schaub (http://orcid.org/0000-0003-2745-0557) and S. Bauer (http://orcid.org/0000-0002-0844-164X), Swiss Ornithological Inst., Sempach, Switzerland. Present address for GS: ONCFS – DRE Unité Faune de Plaine, Parc d'Affaires la Rivière 8 Bd Albert Einstein Bât. B – CS 42355, FR-44323 Nantes, France. REVW also at: Inst. of Evolutionary Biology and Environmental Studies, Univ. of Zürich, Zürich, Switzerland. MS also at: Inst. of Ecology and Evolution, Division of Conservation Biology, Univ. of Bern, Bern, Switzerland.

In migrant animals, conditions encountered at various times and places throughout their annual cycle may affect breeding success. Yet, most studies so far have only investigated the effect of specific parts of the annual cycle, despite the importance to understand how different stages can interact and how these stages compare to intrinsic quality to properly modulate breeding success. Using a structural equation modelling approach, we investigated drivers of breeding success (migration cycle, individual quality, breeding conditions) in hoopoes *Upupa epops*, a long-distant migrant. Our causal framework explained 75% of the variation in breeding success. The effect of the migration schedule was negligible, whereas the previous breeding attempt strongly influenced current breeding success. We suggest that the interplay of individual quality and environmental conditions during both previous and current breeding season may be more important drivers of breeding success than migration schedules, even in a long-distance migrant. We conclude that structural equation modeling is a promising tool to investigate causal relationships. Applied to hoopoes, we demonstrated that current breeding success is strongly linked to previous breeding success. Complementary analysis integrating weather and climate conditions during migration and the breeding season may provide a deeper and wider overview of the annual cycle of hoopoes and additional insights into the existence of carry-over effects in breeding success.

Introduction

Events occurring during an individual's life history can explain their current performance and are defined as carry-over effects (COEs) (O'Connor et al. 2014). COEs can explain individual differences in fitness traits such as survival and breeding success (Festa-Bianchet 1998, Harrison et al. 2011, Ceriani et al. 2015). Recently, Senner et al. (2015) proposed a unifying framework to understand such individual differences, which suggested that condition experienced during early-life would have irreversible effects on fitness while conditions encountered during adulthood should have reversible effects. Consequently, such 'reversible state effects' can carry-over to affect individual fitness during subsequent life-history stages but can also be compensated for,

at least partially, i.e. when a period with abundant resources allows individuals to mitigate negative effect of a previous period ('compensation hypothesis', Conklin et al. 2013, Senner et al. 2014, Clausen et al. 2015).

Carry-over effects have been demonstrated in various taxa, from mammals to invertebrates (Festa-Bianchet 1998, Harrison et al. 2011, Ceriani et al. 2015). They might be particularly prevalent in migratory animals as migratory journeys often imply high energetic costs, adverse weather conditions during the journey and on the non-breeding site, or decreased food availability that may compromise (components of) fitness (Clausen et al. 2015, Cooper et al. 2015, Rushing et al. 2016). In principle, COEs may occur between any successive stages of the annual cycle but those linking environmental conditions in the non-breeding sites and the timing of spring migration have most commonly been investigated to explain current reproductive success (Marra et al. 1998, 2015, Norris 2005). However, links between other events or links embracing full annual cycles have been considered only recently; yet we need a holistic approach considering all periods within a year to improve our understanding of animal movement and life-history evolution (Marra et al. 2015, Saino et al. 2017).

Investigating COEs over full annual cycles poses several major challenges. First, year-round data are needed on breeding performance, migratory behavior, location of the non-breeding site and environmental conditions at all places visited, which requires tracking of individuals throughout the year (Harrison et al. 2011). Second, it is often difficult to disentangle the effect of intrinsic and extrinsic factors and processes (Daunt et al. 2014, Saino et al. 2017). For instance, environmental conditions in the non-breeding sites may influence individual (body-)condition prior to spring migration (Norris et al. 2004, Sedinger et al. 2006), which, in turn, may influence the timing of spring migration, arrival in the breeding site and breeding success (Low et al. 2015). Finally, another critical challenge is to analyze the different events and processes jointly within the same framework. A powerful and promising approach that can meet these challenges is the use of structural equation models (SEMs, Grace et al. 2010) – probabilistic models that evaluate multiple causal pathways and include both direct and indirect effects (Grace 2006). SEMs use conceptual ('latent') variables that are constructed by one or more observed variable(s), and thus account for measurement uncertainty (Grace 2006).

SEMs appear well-suited for investigating COEs in migrants as they can consider the whole migration process and quantify relationships between several latent variables and breeding success. For instance, previous breeding performance can affect current breeding through intrinsic factors such as individual quality (McCleery et al. 2008) or by a series of COEs triggered by events on the journeys between breeding and non-breeding sites (Shoji et al. 2015). Thus, to clearly distinguish between causal pathways and assess the relative importance of potential factors, we need to consider a direct influence of previous breeding on current breeding success (reflecting individual history) as well as the influence of events occurring outside the breeding periods.

In the present study, we investigated COEs during the annual cycle in a long-distance migrant – the hoopoe *Upupa epops*. We reconstructed the annual cycle of more than 50 individuals between consecutive breeding bouts from geolocator data, characterized breeding success, timing of migration (both in autumn and spring) and location of non-breeding sites. Using SEMs, we quantified the relationships between each step of the annual cycle and breeding success, and thus, quantified the degree to which breeding success was shaped by previous breeding performance, autumn migration, condition at the non-breeding sites, and spring migration.

As a study recently demonstrated dependencies between successive stages in the annual cycle of hoopoes (van Wijk et al. 2017), we expected strong relationships between each stage throughout the year but, given the ontogenetic framework, only weak COEs on breeding success.

Material and methods

Model species

We investigated a population of hoopoes breeding in southwestern Switzerland (46°14′N, 7°22′E), in a study area of about 62 km² (Arlettaz et al. 2010b) with currently ~550 nest boxes. Hoopoes are long-distance Palearctic–African migrants, which spend the non-breeding season (hereafter referred to as 'wintering') in the Sahelian belt south of the Sahara (Bächler et al. 2010). Birds typically return to the breeding grounds in early April, start breeding in late April, and the last nestlings fledge in early August (van Wijk et al. 2016). Most hoopoes in our study population produce one clutch per year, but one third has two or more clutches (Hoffmann et al. 2015).

Data collection

Hoopoes were caught in or at nest boxes and equipped with geolocators of type SOI-GDL1 (Bächler et al. 2010, van Wijk et al. 2017). The tracking devices had no effects on reproduction, condition and survival in hoopoes (van Wijk et al. 2016). From 2008 to 2013, 328 breeding hoopoes were equipped with geolocators, of which 54 were retrieved in the following year (Supplementary material Appendix 1 Table A1 for details by year and sex). For these birds, we determined timing of migration, location of wintering areas and breeding performance (number of clutches and the number of fledglings of the first clutch, see Supplementary material Appendix 2 for a full description of the dataset).

Characterization of migration
Based on geolocator data, we determined individual migration schedules and location of wintering areas (Schmaljohann et al. 2016, van Wijk et al. 2017). Autumn and spring

migration schedules were characterized by both start date and duration. We used the normalized difference vegetation index (NDVI) to characterize conditions in wintering areas as these correlate with weather conditions (temperature and rainfall) and vegetation openness and thus, most likely, also with food availability (Trierweiler et al. 2013). We retrieved NDVI values from US Geological Survey Famine Early Warning System network (eMODIS NDVI data <http://earlywarning.usgs.gov/fews>) and used the median NDVI values over the months October to February as a proxy of general conditions and the difference between median NDVI values in October and February ($\Delta NDVI = NDVI_{Feb} - NDVI_{Oct}$) as an index of their variation.

Breeding performance

At the breeding grounds in Switzerland, nest boxes were surveyed every two weeks from the beginning until the end of the breeding season. Occupied nest boxes were subsequently visited every three days to obtain the number of eggs, hatchlings and fledglings, and the timing of incubation, hatching and fledging. For each individual, we recorded the number of clutches and the number of fledglings, (see Table 1

and Supplementary material Appendix 2 for a full description of the dataset).

Investigating causal hypotheses using structural equation model

Causal framework

Structural equation models combine a measurement model that defines latent variables from one or more observed variables with a structural regression model that links these latent variables (Grace 2006). This structural regression model can represent causal relations between latent variables.

Following the approach in Grace et al. (2012) we aimed at explaining current breeding success in the hoopoe population assuming causal links to the following latent variables: previous breeding success, timing of autumn and spring migration, location and conditions of the wintering areas and timing of the wintering period (Fig. 1). Current breeding success was thus the terminal latent variable in our model.

Our causal framework followed a chronological pathway (Fig.1) and hypothesized that dependencies between successive activities in the annual cycle. In particular, we

Table 1. Short description of the measured variables.

Measured variable	Description	Biological meaning	Source	latent variable	Median (range) [calendar date]
Departure date (Dep)	date (in Julian day) of the beginning of the migration for the followed individual	early or late departure	from geolocator data[1]	AU	227.5 (203;258) [22 Jul;15 Sep]
				SP	68.5 (46;111) [15 Feb;21 Apr]
Arrival date (Arr)	date (in Julian day) of the end of the migration phase for the followed individual	early or late arrival	from geolocator data[1]	WiT	266 (236;306) [24 Aug;2 Nov]
Duration (Dur)	arrival date – departure date	length of the seasonal period	from geolocator data[1]	AU	35 (5;76)
				WiT	169 (132;198)
				SP	24 (5;63)
Number of brood (Br)	no. of brood per individual each breeding season	proxy for breeding success	from breeding survey in Switzerland	PB	1 (1;3)
				BS	2 (1;4)
Number of fledglings (Fl)	no. of fledgling in the first brood per individual	proxy for breeding success	from breeding survey in Switzerland	PB	5 (0;8)
				BS	5 (0;8)
NDVI	median value of stretched NDVI values from October to February	indicator of vegetation cover and prey accessibility	USGS FEWS NET data portal[2]	WiC	0.21 (0.08;0.53)[3]
ΔNDVI	difference in stretched NDVI values between February and October	indicator of seasonal change in vegetation cover and prey accessibility	USGS FEWS NET data portal[2]	WiC	–0.14 (–0.40;0.01)[3]

[1]see van Wijk et al. (2017) for detailed information about determination of individual migration schedules and location of wintering areas
[2]eMODIS NDVI data obtained for West Africa from <https://earlywarning.usgs.gov/fews/product/115>.
[3]unstretched values are presented to easy comparison with other studies and were obtained as follows:
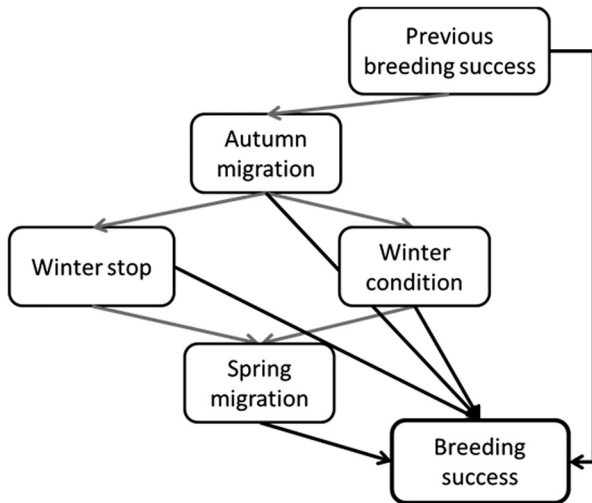unNDVI = (value – 100)/100
unΔNDVI = (value)/100

Figure 1. Conceptual diagram of how variables were linked to each other in our model. Directional arrows refer to the direction of the causal relationship. Grey and black arrows represent indirect and direct effects of variables on breeding success.

assumed that 1) previous breeding success could directly affect current breeding success (black arrows in Fig.1), 2) autumn and spring migration, wintering timing and conditions have direct effects on breeding success, 3) autumn migration has an effect on winter timing and conditions, and 4) these could, in turn, affect spring migration. Thus, the model not only tested the direct influences of previous events on current breeding success but also their indirect effects, e.g. whether previous breeding success influenced current breeding success via changes autumn migration, wintering and spring migration (grey arrows in Fig.1).

To construct the measurement model that underlies the causal framework, we assumed starting date and duration of a given period to be good indicators of a common latent variable. This allowed us to build latent variables for the timing of each step of the non-breeding life-cycle: autumn migration (AU) from the departure date from the breeding grounds and the duration of autumn migration; winter timing (WiT) from arrival date on wintering ground and duration of wintering; and spring migration (SP) from departure from the wintering grounds and the duration of spring migration. We used median NDVI and ΔNDVI for the latent variable characterizing resource conditions in the wintering area (WiC). Furthermore, we used number of broods and number of fledglings in the first brood to define latent variables for both previous (PB) and current breeding success (BS) (Fig. 2).

Implementation of our structural equation model
Following the notation from Grace (2006), the measurement model is:

$$x_{ij} = \lambda_i \xi_j + \delta_j$$

$$y_{ik} = \lambda_i' \eta_k + \varepsilon_k$$

Where x_{ij} and y_{ik} are measured variables associated to independent latent variable j and the dependent latent

variable k, respectively λ_i and λ_i' are the loading factors linking the measured variable i to an independent and dependent latent variable, respectively, ξ_j is the independent latent variable j, η_k the dependent latent variable k, and δ_j and ε_k are measurement and residual errors, respectively.

Our structural model (Fig. 2) is:

$$\eta_k = \gamma_{kj} \xi_j + \zeta_k$$

With γ_{kj} being the structural coefficient describing the effect of the independent latent variable ξ_j on the dependent latent variable η_k and ζ_k the residual variance.

Due to the relatively restricted sample size (54 individual annual cycles) and the inclusion of both categorical and continuous variables in the dataset, we estimated the parameters of the measurement and structural model using Markov chain Monte Carlo (MCMC) simulations within a Bayesian framework, which is a robust method even with low sample sizes (Grace et al. 2012). For all parameters to be estimated, we specified non-informative prior distributions (see Supplementary material Appendix 3: R script for a complete specification of the model and priors used). The model was implemented in WinBUGS (Lunn et al. 2000) called from R (<www.r-project.org>) with package R2WinBUGS (Sturtz et al. 2005).

Since we wanted to compare their relative influence, we standardized independent variables and estimated coefficients, i.e. we quantified the change in a dependent variable relative to changes in the independent latent variable(s). The total effect on a latent variable is the sum of both direct and indirect effects (black and grey arrows in Fig. 1– indirect effect is derived as the product of all coefficients through the pathway). The total explained variance of breeding success R^2 can be derived easily from the unexplained variance of breeding success (ζ) as $R^2 = 1 - \zeta$ (Grace 2006). A Bayesian p-value was computed to assess the fit between model and data, where values close to 0 or 1 are suspicious (Kéry and Schaub 2012).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3j8rr> (Souchay et al. 2017).

Results

Our data fitted the SEM expectations generally well (Bayesian p-value = 0.49) and explained around 75% of the variance in current breeding success ($1 - \zeta$, Fig. 3).

The model coefficients indicate that previous breeding had a direct and positive influence on current breeding success ($\gamma_{1.1} = 0.62$, $p(\gamma_{1.1} > 0) = 0.97$, Table 2) but its indirect effect through the migration and non-breeding period was negligible. Autumn migration had a slightly positive effect on winter timing ($\gamma_3 = 1.49$) but only a weak effect on winter conditions encountered ($\gamma_4 = 0.52$). Winter timing and conditions had nearly no effect on spring migration (–0.19 and
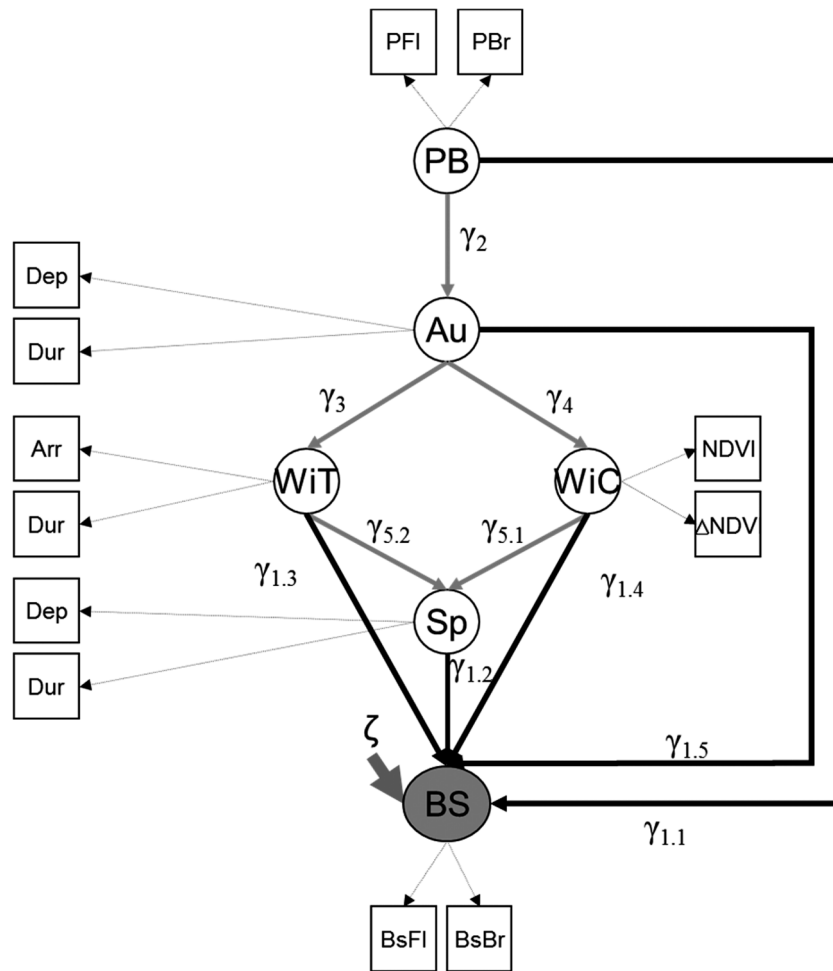
Figure 2. Structural equation model with all measured variables for each latent variable. Circles represent latent variables. Squares are measured variables. Arr = arrival date; Dep = departure date; Dur = duration of the migration; NDVI = median value of NDVI over the wintering period (from October to February); ΔNDVI = difference between February and October values of NDVI; #Br = number of broods for each individual in the previous (PBr) or the current breeding season (BsBr); #Fl = number of fledglings raised in first brood in the previous (PFl) or the current breeding season (BsFl); PB = previous breeding attempt, AU = autumn migration, WiT = winter timing, WiC = winter condition, SP = spring migration, BS = breeding success. Grey and dark arrows represent indirect and direct effects, respectively, of latent variables on breeding success with associated parameters. ζ refers to the residual variance of the latent breeding success variable.

0.14, respectively). Finally, autumn migration, winter timing and conditions, and spring migration had nearly no influence on breeding success (–0.01, –0.03, –0.02 and 0.02, respectively).

Discussion

Using a structural equation model, we tested the hypothesis that previous breeding success, migration bouts and the non-breeding period influenced current breeding success in a long-distance migrant bird. Surprisingly, none of the migration stages influenced current breeding success suggesting that carry-over effects were virtually absent and that the influence of adverse environmental factors en route or in the non-breeding areas could be buffered or equalized. However, we

found a direct and positive relationship between previous and current breeding success, which could be explained by strong intrinsic effects in determining breeding success.

No relationship between successive stages

As the annual cycle of migratory birds is thought to be time-constrained, we expected strong relationships both between consecutive steps/periods (Newton 2008) – especially between spring migration timing and breeding success, what has been found in many earlier studies (Bêty et al. 2004, Catry et al. 2013, Low et al. 2015). No relationship between stages of the migration cycle is thus a striking result.

One explanation for the unexpected weak link between successive steps of the non-breeding part of the life cycle might be that there are simply no COEs. In fact, this would
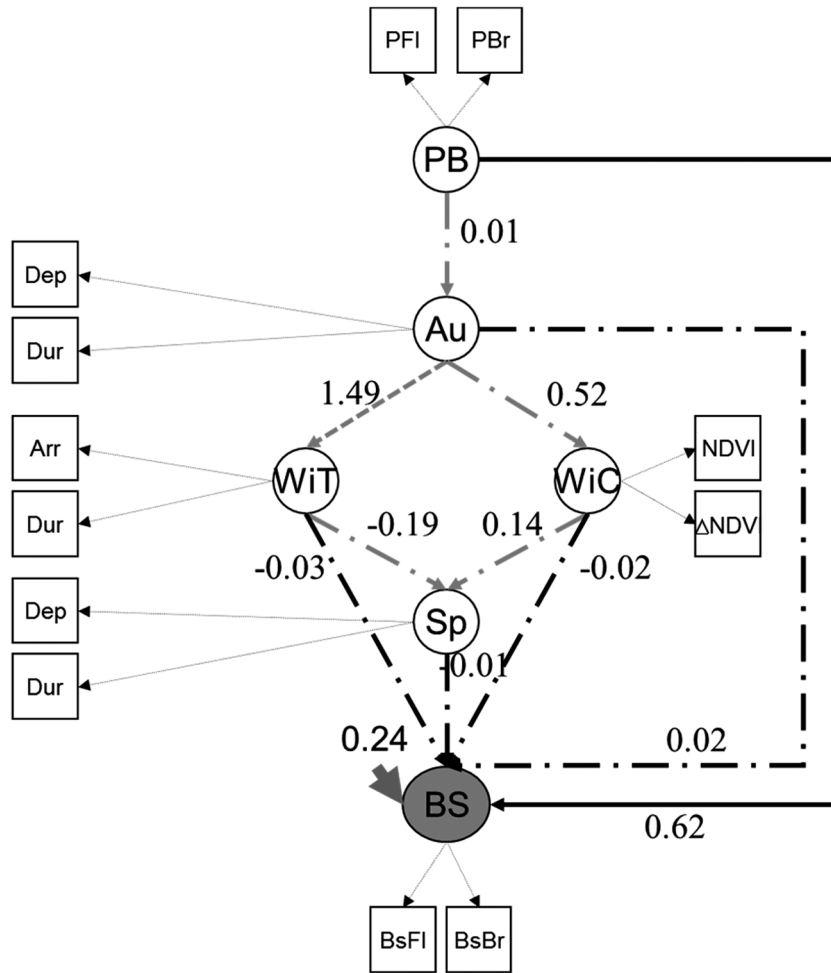
Figure 3. Estimates of standardized path coefficients from the structural equation model for the annual cycle of hoopoes.

be consistent with the ontogenetic framework and the reversible properties of COEs initiated during the adulthood. The likely mechanism for fading COEs is compensation, which has previously been found in long-lived species (Conklin and Battley 2012, Conklin et al. 2013, Clausen et al. 2015) but not in a relatively short-lived species like hoopoes. Compensation means that, e.g. individuals arriving late on non-breeding sites increase foraging effort or molt rates to start spring migration at similar times like early-arriving individuals (Conklin and Battley 2012, Conklin et al. 2013). Such compensation may also explain the weak link between spring migration and breeding success in our

Table 2. Summary of the standardized estimates of the relationships between latent variables from our structural equation model. For each parameter we provide the summary of the Bayesian posterior distribution (mean, standard deviation [SD], limits of the credible intervals [2.5%, 97.5%]) and the probability that the parameter is strictly positive.

Relationship:			Posterior distribution				
From	To	θ	mean	SD	2.5%	97.5%	$p(|\theta|>0)$
Previous breeding success (PB)	autumn migration (AU)	γ_2	0.01	0.36	−0.70	0.77	0.51
Autumn migration (AU)	winter timing (WiT)	γ_3	1.49	1.16	−1.31	3.24	0.86
Autumn migration (AU)	winter condition (WiC)	γ_4	0.52	0.92	−1.24	2.41	0.71
Winter condition (WiC)	spring migration (SP)	$\gamma_{5.1}$	0.14	0.41	−0.63	1.08	0.62
Winter timing (WiT)	spring migration (SP)	$\gamma_{5.2}$	−0.19	0.36	−1.07	0.43	0.70
Previous breeding success (PB)	breeding success (BS)	$\gamma_{1.1}$	0.62	0.29	−0.48	1.04	0.97
Autumn migration (AU)	breeding success (BS)	$\gamma_{1.2}$	−0.01	0.21	−0.44	0.41	0.53
Winter timing (WiT)	breeding success (BS)	$\gamma_{1.3}$	−0.03	0.12	−0.27	0.21	0.62
Winter condition (WiC)	breeding success (BS)	$\gamma_{1.4}$	−0.02	0.09	−0.20	0.16	0.59
Spring migration (SP)	breeding success (BS)	$\gamma_{1.5}$	0.02	0.11	−0.21	0.24	0.56

analysis: birds arriving later on the breeding grounds may shorten the pre-laying period and eventually achieve a similar breeding performance like birds that arrived earlier (Senner et al. 2014). This is probably the case in our hoopoe population, in which the arrival date on the breeding ground only marginally affects the total number of fledglings (van Wijk et al. 2017). Furthermore, the variability in arrival dates on the breeding ground was generally smaller than the variability in any other dates of the migration schedule, suggesting that all birds arrive on the breeding ground at similar dates.

Another explanation for non-existent COEs is that any effects of events and processes during the non-breeding period might be less importance and thus, masked by the dominating effect of the previous breeding season, conditions during the current breeding season or individual quality (Ockendon et al. 2013, Grimm et al. 2015).

However, there are also methodological issues that may affect our ability to detect a potentially existing relationship between stages. In the structural equation approach, we did not test the effect of one observed variable to another but, instead, defined latent migration variables from departure dates and duration of migratory stages. Furthermore, we added an overdispersion parameter to account for noise in these latent variables. This noise may be equally or more important than the variance explained by the timing component (departure and duration) and then lead to weak estimates of the relationship between latent variables. Although it is unknown so far what produces this noise (residual variance), conditions during migration (e.g. weather or wind conditions, Liechti 2006), length of migration routes or number of stop-overs (Arlt et al. 2015) likely contribute to it. Such information might be integrated into latent variables on finer spatial or temporal scales once information is available and further clarify the relationship between successive stages.

Carry-over effect on breeding success?

The absence of COEs from migration might be explained by the great relative importance of the previous on current breeding success. Indeed, we found a strong, positive link between successive breeding attempts, suggesting that current breeding success is highly correlated with previous breeding success.

Following the ontogenetic framework, individual quality is the only type of individual difference that is not reversible, persists over an individual's lifetime (Senner et al. 2015) and may explain the highly correlated performance between successive breeding. Hoffmann et al. (2015) showed intrinsic quality (e.g. ability to occupy a higher quality territory) determined double-brooding and individuals of high quality typically raised more fledglings in the first brood than lower-quality individuals, and also more often produced a second clutch (Hoffmann et al. 2015).

Alternatively (or in addition to intrinsic quality), conditions during the breeding season can influence reproductive output in hoopoes (Martín-Vivaldi et al. 1999, Arlettaz et al. 2010a), with rain and low temperatures decreasing, and higher temperatures increasing breeding success. Spring conditions in the breeding grounds were quite variable over the last five years (van Wijk unpubl.). Yet, despite these fluctuations in breeding conditions, breeding performances in consecutive years remained positively related suggesting that weather has less influence on breeding success than individual quality. However, we could not clearly distinguish between both sources of variation (intrinsic quality or breeding conditions) of breeding success due to lack of available data.

Structural equation model as a tool to investigate the annual cycle

We used a structural equation modelling approach to investigate COEs in the annual cycle rather than classical methods such as generalized linear models or path analysis. We created a causal framework embracing the full annual cycle of a long-distance migrant and separated the effect of individual quality from the effects of migration and non-breeding periods. The low sample size, however, did not permit us to compare and select the most likely of several alternative causal frameworks. For example, instead of using a chronological pathway from one breeding season to the next, an alternative pathway with other conceptual variables, e.g. for all departure dates irrespective of the migration step, length of migration steps, or wintering conditions, etc. could be designed and tested would provide a different perspective and supplement our current findings.

A step forward could be the combination of several datasets (e.g. collected in a systematic way on breeding sites and surveys on breeding sites) and/or combination of models such as capture–recapture models and structural equation models to investigate fitness consequence of individual life history. Such solutions may allow the inclusion of more individuals in the studied population with the integration of imperfect detection (Cubaynes et al. 2012). It could help to distinguish between individual heterogeneity and external sources of variation, a well-known issue in vertebrates (Cam et al. 2013).

Thus, the structural equation model provided a novel tool for testing assumptions within a causal framework and for estimating the relative importance of potential drivers of breeding success. Such models can provide a more general, comprehensive view of multi-step processes with the integration of measurement error and residual variance. When set up within a Bayesian framework with incorporation of prior information and Markov chain Monte Carlo estimations, SEMs deliver reliable results even for low sample sizes (Grace et al. 2012).

Overall, structural equation models are a promising tool to investigate causal relationships such as carry-over effects and can improve our understanding of complex mechanisms such as migration in ecology.

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