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

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35 (Abstract)

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

52

## 53 **Introduction**

54 Events occurring during an individual's life history can explain their current performance and are  
55 defined as carry-over effects (COEs) (O'Connor et al. 2014). COEs can explain individual differences  
56 in fitness traits such as survival and breeding success (Festa-Bianchet 1998, Harrison et al. 2011,  
57 Ceriani et al. 2015). Recently, Senner et al. (2015) proposed a unifying framework to understand such  
58 individual differences, which suggested that condition experienced during early-life would have  
59 irreversible effects on fitness while conditions encountered during adulthood should have reversible  
60 effects. Consequently, such "reversible state effects" can carry-over to affect individual fitness during  
61 subsequent life-history stages but can also be compensated for, at least partially, i.e. when a period  
62 with abundant resources allows individuals to mitigate negative effect of a previous period  
63 ("compensation hypothesis", Conklin et al. 2013, Senner et al. 2014, Clausen et al. 2015).

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

76 Investigating COEs over full annual cycles poses several major challenges. First, year-round  
77 data are needed on breeding performance, migratory behavior, location of the non-breeding site and  
78 environmental conditions at all places visited, which requires tracking of individuals throughout the

79 year (Harrison et al. 2011). Second, it is often difficult to disentangle the effect of intrinsic and  
80 extrinsic factors and processes (Daunt et al. 2014, Saino et al. 2017). For instance, environmental  
81 conditions in the non-breeding sites may influence individual (body-)condition prior to spring  
82 migration (Norris et al. 2004, Sedinger et al. 2006), which, in turn, may influence the timing of spring  
83 migration, arrival in the breeding site and breeding success (Low et al. 2015). Finally, another critical  
84 challenge is to analyze the different events and processes jointly within the same framework. A  
85 powerful and promising approach that can meet these challenges is the use of structural equation  
86 models (SEMs, Grace et al. 2010) – probabilistic models that evaluate multiple causal pathways and  
87 include both direct and indirect effects (Grace 2006). SEMs use conceptual (‘latent’) variables that  
88 are constructed by one or more observed variable(s), and thus account for measurement uncertainty  
89 (Grace 2006).

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

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

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

108

## 109 **Material and methods**

### 110 *Model species*

111 We investigated a population of hoopoes breeding in south-western Switzerland (46°14'N 7°22'E),  
112 in a study area of about 62 km<sup>2</sup> (Arlettaz et al. 2010) with currently ~550 nest boxes. Hoopoes are  
113 long-distance Palearctic-African migrants, which spend the non-breeding season (hereafter referred  
114 to as 'wintering') in the Sahelian belt south of the Sahara (Bächler et al. 2010). Birds typically return  
115 to the breeding grounds in early April, start breeding in late April, and the last nestlings fledge in  
116 early August (van Wijk et al. 2016). Most hoopoes in our study population produce one clutch per  
117 year, but one third has two or more clutches (Hoffmann et al. 2015).

118

### 119 *Data collection*

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

127

## 128 **Characterization of Migration**

129 Based on geolocator data, we determined individual migration schedules and location of wintering  
130 areas (Schmaljohann et al. 2016, van Wijk et al. 2017). Autumn and spring migration schedules were  
131 characterized by both start date and duration. We used the normalized difference vegetation index  
132 (NDVI) to characterize conditions in wintering areas as these correlate with weather conditions  
133 (temperature and rainfall) and vegetation openness and thus, most likely, also with food availability  
134 (Trierweiler et al. 2013). We retrieved NDVI values from U.S Geological Survey Famine Early  
135 Warning System network (eMODIS NDVI data <http://earlywarning.usgs.gov/fews>) and used the  
136 median NDVI values over the months October to February as a proxy of general conditions and the  
137 difference between median NDVI values in October and February ( $\Delta\text{NDVI} = \text{NDVI}_{\text{Feb}} - \text{NDVI}_{\text{Oct}}$ ) as  
138 an index of their variation.

139

#### 140 **Breeding performance**

141 At the breeding grounds in Switzerland, nest boxes were surveyed every two weeks from the  
142 beginning until the end of the breeding season. Occupied nest boxes were subsequently visited every  
143 three days to obtain the number of eggs, hatchlings and fledglings, and the timing of incubation,  
144 hatching and fledging. For each individual, we recorded the number of clutches and the number of  
145 fledglings, (see Table 1 and Appendix 2 for a full description of the dataset).

146

147 *Investigating causal hypotheses using structural equation model*

#### 148 **Causal framework**

149 Structural equation models combine a measurement model that defines latent variables from one or  
150 more observed variables with a structural regression model that links these latent variables (Grace  
151 2006). This structural regression model can represent causal relations between latent variables.

152 Following the approach in Grace et al. (2012) we aimed at explaining current breeding success  
153 in the hoopoe population assuming causal links to the following latent variables: previous breeding  
154 success, timing of autumn and spring migration, location and conditions of the wintering areas and

155 timing of the wintering period (Fig. 1). Current breeding success was thus the terminal latent variable  
156 in our model.

157 Our causal framework followed a chronological pathway (Fig.1) and hypothesized that  
158 dependencies between successive activities in the annual cycle. In particular, we assumed that (i)  
159 previous breeding success could directly affect current breeding success (black arrows in Fig.1), (ii)  
160 autumn and spring migration, wintering timing and conditions have direct effects on breeding success,  
161 (iii) autumn migration has an effect on winter timing and conditions, and (iv) these could, in turn,  
162 affect spring migration. Thus, the model not only tested the direct influences of previous events on  
163 current breeding success but also their indirect effects, e.g. whether previous breeding success  
164 influenced current breeding success via changes autumn migration, wintering and spring migration  
165 (grey arrows in Fig.1).

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

175

## 176 **Implementation of our structural equation model**

177 Following the notation from Grace (2006), the measurement model is:

$$178 \quad x_{ij} = \lambda_i \xi_j + \delta_j$$

$$179 \quad y_{ik} = \lambda'_i \eta_k + \varepsilon_k$$

180 Where  $x_{ij}$  and  $y_{ik}$  are measured variables associated to independent latent variable  $j$  and the dependent  
181 latent variable  $k$ , respectively  $\lambda_i$  and  $\lambda_i'$  are the loading factors linking the measured variable  $i$  to an  
182 independent and dependent latent variable, respectively,  $\xi_j$  is the independent latent variable  $j$ ,  $\eta_k$  the  
183 dependent latent variable  $k$ , and  $\delta_j$  and  $\varepsilon_k$  are measurement and residual errors, respectively.

184 Our structural model (Fig.2) is:

$$185 \eta_k = \gamma_{kj} \xi_j + \zeta_k$$

186 With  $\gamma_{kj}$  being the structural coefficient describing the effect of the independent latent variable  $\xi_j$  on  
187 the dependent latent variable  $\eta_k$  and  $\zeta_k$  the residual variance.

188 Due to the relatively restricted sample size (54 individual annual cycles) and the inclusion of  
189 both categorical and continuous variables in the dataset, we estimated the parameters of the  
190 measurement and structural model using Markov Chain Monte Carlo (MCMC) simulations within a  
191 Bayesian framework, which is a robust method even with low sample sizes (Grace et al. 2012). For  
192 all parameters to be estimated, we specified non-informative prior distributions (see Appendix 3: R  
193 script for a complete specification of the model and priors used). The model was implemented in  
194 WinBUGS (Lunn et al. 2000) called from R (R Development Core Team 2010) with package  
195 R2WinBUGS (Sturtz et al. 2005).

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

204

## 205 **Results**

206 Our data fitted the SEM expectations generally well (Bayesian p-value = 0.49) and explained around  
207 75% of the variance in current breeding success ( $1 - \zeta$ , Fig. 3).

208 The model coefficients indicate that previous breeding had a direct and positive influence on  
209 current breeding success ( $\gamma_{1.1}=0.62$ ,  $p(\gamma_{1.1}>0)=0.97$ , Table 2) but its indirect effect through the  
210 migration and non-breeding period was negligible. Autumn migration had a slightly positive effect  
211 on winter timing ( $\gamma_3=1.49$ ) but only a weak effect on winter conditions encountered ( $\gamma_4=0.52$ ). Winter  
212 timing and conditions had nearly no effect on spring migration (-0.19 and 0.14, respectively). Finally,  
213 autumn migration, winter timing and conditions, and spring migration had nearly no influence on  
214 breeding success (-0.01, -0.03, -0.02 and 0.02, respectively).

215

## 216 **Discussion**

217 Using a structural equation model, we tested the hypothesis that previous breeding success, migration  
218 bouts and the non-breeding period influenced current breeding success in a long-distance migrant  
219 bird. Surprisingly, none of the migration stages influenced current breeding success suggesting that  
220 carry-over effects were virtually absent and that the influence of adverse environmental factors en  
221 route or in the non-breeding areas could be buffered or equalized. However, we found a direct and  
222 positive relationship between previous and current breeding success, which could be explained by  
223 strong intrinsic effects in determining breeding success.

224

### 225 *No relationship between successive stages*

226 As the annual cycle of migratory birds is thought to be time-constrained, we expected strong  
227 relationships both between consecutive steps/periods (Newton 2008) – especially between spring  
228 migration timing and breeding success, what has been found in many earlier studies (Bêty et al. 2004,

229 Catry et al. 2013, Low et al. 2015). No relationship between stages of the migration cycle is thus a  
230 striking result.

231         One explanation for the unexpected weak link between successive steps of the non-breeding  
232 part of the life cycle might be that there are simply no COEs. In fact, this would be consistent with  
233 the ontogenetic framework and the reversible properties of COEs initiated during the adulthood. The  
234 likely mechanism for fading COEs is compensation, which has previously been found in long-lived  
235 species (Conklin and Battley 2012, Conklin et al. 2013, Clausen et al. 2015) but not in a relatively  
236 short-lived species like hoopoes. Compensation means that, e.g. individuals arriving late on non-  
237 breeding sites increase foraging effort or molt rates to start spring migration at similar times like  
238 early-arriving individuals (Conklin and Battley 2012, Conklin et al. 2013). Such compensation may  
239 also explain the weak link between spring migration and breeding success in our analysis: birds  
240 arriving later on the breeding grounds may shorten the pre-laying period and eventually achieve a  
241 similar breeding performance like birds that arrived earlier (Senner et al. 2014). This is probably the  
242 case in our hoopoe population, in which the arrival date on the breeding ground only marginally  
243 affects the total number of fledglings (van Wijk et al. 2017). Furthermore, the variability in arrival  
244 dates on the breeding ground was generally smaller than the variability in any other dates of the  
245 migration schedule, suggesting that all birds arrive on the breeding ground at similar dates.

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

250         However, there are also methodological issues that may affect our ability to detect a  
251 potentially existing relationship between stages. In the structural equation approach, we did not test  
252 the effect of one observed variable to another but, instead, defined latent migration variables from  
253 departure dates and duration of migratory stages. Furthermore, we added an overdispersion parameter  
254 to account for noise in these latent variables. This noise may be equally or more important than the

255 variance explained by the timing component (departure and duration) and then lead to weak estimates  
256 of the relationship between latent variables. Although it is unknown so far what produces this noise  
257 (residual variance), conditions during migration (e.g. weather or wind conditions, Liechti 2006),  
258 length of migration routes or number of stop-overs (Arlt et al. 2015) likely contribute to it. Such  
259 information might be integrated into latent variables on finer spatial or temporal scales once  
260 information is available and further clarify the relationship between successive stages.

261

262 *Carry-over effect on breeding success?*

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

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

273 Alternatively (or in addition to intrinsic quality), conditions during the breeding season can  
274 influence reproductive output in hoopoes (Martín-Vivaldi et al. 1999, Arlettaz et al. 2010), with rain  
275 and low temperatures decreasing, and higher temperatures increasing breeding success. Spring  
276 conditions in the breeding grounds were quite variable over the last 5 years (van Wijk *unpublished*  
277 *data*). Yet, despite these fluctuations in breeding conditions, breeding performances in consecutive  
278 years remained positively related suggesting that weather has less influence on breeding success than  
279 individual quality. However, we could not clearly distinguish between both sources of variation  
280 (intrinsic quality or breeding conditions) of breeding success due to lack of available data.

281

282 *Structural equation model as a tool to investigate the annual cycle*

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

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

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

305

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

309

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315

## 316 **References**

- 317 Arlettaz, R. et al. 2010. Impact of weather and climate variation on Hoopoe reproductive ecology  
318 and population growth. - J. Ornithol. 151: 889-899.
- 319 Arlettaz, R. et al. 2010. From publications to public actions: when conservation biologists bridge  
320 the gap between research and implementation. - Bioscience 60: 835-842.
- 321 Arlt, D. et al. 2015. Prolonged stopover duration characterises migration strategy and constraints of  
322 a long-distance migrant songbird. - Animal Migration 2.
- 323 Bächler, E. et al. 2010. Year-round tracking of small trans-Saharan migrants using light-level  
324 geolocators. - Plos One 5: e9566.
- 325 Bêty, J. et al. 2004. Individual variation in timing of migration: causes and reproductive  
326 consequences in greater snow geese (*Anser caerulescens atlanticus*). - Behav. Ecol. Sociobiol. 57:  
327 1-8.
- 328 Cam, E. et al. 2013. Looking for a needle in a haystack: inference about individual fitness  
329 components in a heterogeneous population. - Oikos 122: 739-753.

330 Catry, P. et al. 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance  
331 migrant: an experimental demonstration. - Ecology 94: 1230-1235.

332 Ceriani, S. et al. 2015. Carry-over effects and foraging ground dynamics of a major loggerhead  
333 breeding aggregation. - Mar. Biol. 162: 1955-1968.

334 Clausen, K. K. et al. 2015. Carry-Over or Compensation? The Impact of Winter Harshness and  
335 Post-Winter Body Condition on Spring-Fattening in a Migratory Goose Species. - PLoS ONE 10:  
336 e0132312.

337 Conklin, J. R. and Battley, P. F. 2012. Carry-over effects and compensation: late arrival on non-  
338 breeding grounds affects wing moult but not plumage or schedules of departing bar-tailed godwits  
339 *Limosa lapponica baueri*. - J. Avian Biol. 43: 252-263.

340 Conklin, J. R. et al. 2013. Absolute Consistency: Individual versus Population Variation in Annual-  
341 Cycle Schedules of a Long-Distance Migrant Bird. - PLoS ONE 8: e54535.

342 Cooper, N. W. et al. 2015. Experimental reduction of winter food decreases body condition and  
343 delays migration in a long-distance migratory bird. - Ecology 96: 1933-1942.

344 Cubaynes, S. et al. 2012. Testing hypotheses in evolutionary ecology with imperfect detection:  
345 capture-recapture structural equation modeling. - Ecology 93: 248-255.

346 Daunt, F. et al. 2014. Longitudinal bio-logging reveals interplay between extrinsic and intrinsic  
347 carry-over effects in a long-lived vertebrate. - Ecology 95: 2077-2083.

348 Festa-Bianchet, M. 1998. Condition-dependent reproductive success in bighorn ewes. - Ecol. Lett.  
349 1: 91-94.

350 Grace, J. B. 2006. Structural equation modeling and natural systems. - Cambridge University Press.

351 Grace, J. B. et al. 2010. On the specification of structural equation models for ecological systems. -  
352 Ecol. Monogr. 80: 67-87.

353 Grace, J. B. et al. 2012. Guidelines for a graph-theoretic implementation of structural equation  
354 modeling. - Ecosphere 3: 73.

355 Grimm, A. et al. 2015. Earlier breeding, lower success: does the spatial scale of climatic conditions  
356 matter in a migratory passerine bird? - *Ecol. Evol.* 5: 5722–5734.

357 Harrison, X. A. et al. 2011. Carry-over effects as drivers of fitness differences in animals. - *J. Anim.*  
358 *Ecol.* 80: 4-18.

359 Hoffmann, J. et al. 2015. Factors influencing double brooding in Eurasian Hoopoes *Upupa epops*. -  
360 *Ibis* 157: 17–30.

361 Kéry, M. and Schaub, M. 2012. Bayesian Population Analysis using WinBUGS. A hierarchical  
362 perspective. - Academic Press.

363 Liechti, F. 2006. Birds: blowin' by the wind? - *J. Ornithol.* 147: 202-211.

364 Low, M. et al. 2015. Delayed timing of breeding as a cost of reproduction. - *J. Avian Biol.* 46: 325-  
365 331.

366 Lunn, D. J. et al. 2000. WinBUGS - A Bayesian modelling framework: Concepts, structure, and  
367 extensibility. - *Statistics and Computing* 10: 325-337.

368 Marra, P. P. et al. 2015. A call for full annual cycle research in animal ecology. - *Biol. Lett.* 11.

369 Marra, P. P. et al. 1998. Linking Winter and Summer Events in a Migratory Bird by Using Stable-  
370 Carbon Isotopes. - *Science* 282: 1884-1886.

371 Martín-Vivaldi, M. et al. 1999. Determinants of reproductive success in the Hoopoe *Upupa epops*, a  
372 hole-nesting non-passerine bird with asynchronous hatching. - *Bird Study* 46: 205-216.

373 McCleery, R. et al. 2008. Age-specific reproduction in a long-lived species: the combined effects of  
374 senescence and individual quality. - *Proc. R. Soc. B* 275: 963-970.

375 Newton, I. 2008. *The Migration Ecology of Birds*. - Elsevier.

376 Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. - *Oikos* 109:  
377 178-186.

378 Norris, D. R. et al. 2004. Tropical winter habitat limits reproductive success on the temperate  
379 breeding grounds in a migratory bird. - *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 271: 59-64.

380 O'Connor, C. M. et al. 2014. Biological carryover effects: linking common concepts and  
381 mechanisms in ecology and evolution. - *Ecosphere* 5.

382 Ockendon, N. et al. 2013. Climatic effects on breeding grounds are more important drivers of  
383 breeding phenology in migrant birds than carry-over effects from wintering grounds. - *Biol. Lett.* 9.

384 R Development Core Team. 2010. R: a language and environment for statistical computing. - R  
385 Foundation for Statistical Computing.

386 Rushing, C. S. et al. 2016. Winter habitat quality but not long-distance dispersal influences apparent  
387 reproductive success in a migratory bird. - *Ecology* 97: 1218-1227.

388 Saino, N. et al. 2017. Sex-dependent carry-over effects on timing of reproduction and fecundity of a  
389 migratory bird. - *J. Anim. Ecol.* 86: 239-249.

390 Schmaljohann, H. et al. 2016. Proximate causes of avian protandry differ between subspecies with  
391 contrasting migration challenges. - *Behav. Ecol.* 27: 321-331.

392 Sedinger, J. S. et al. 2006. Effects of El Nino on distribution and reproductive performance of Black  
393 Brant. - *Ecology* 87: 151-159.

394 Senner, N. R. et al. 2015. An ontogenetic perspective on individual differences. - *Proc. R. Soc. B*  
395 282.

396 Senner, N. R. et al. 2014. An Exception to the Rule: Carry-Over Effects Do Not Accumulate in a  
397 Long-Distance Migratory Bird. - *PLoS ONE* 9: e86588.

398 Shoji, A. et al. 2015. Breeding phenology and winter activity predict subsequent breeding success in  
399 a trans-global migratory seabird. - *Biol. Lett.* 11.

400 Sturtz, S. et al. 2005. R2WinBUGS: a package for running WinBUGS from R. - *J. Stat. Softw.* 12:  
401 1-16.

402 Trierweiler, C. et al. 2013. A Palaearctic migratory raptor species tracks shifting prey availability  
403 within its wintering range in the Sahel. - *J. Anim. Ecol.* 82: 107-120.

404 van Wijk, R. E. et al. 2017. Dependencies in the timing of activities weaken over the annual cycle  
405 in a long-distance migratory bird. - *Behav. Ecol. Sociobiol.* 71.

406 van Wijk, R. E. et al. 2016. No detectable effects of lightweight geolocators on a Palaeartic-  
407 African long-distance migrant. - J. Ornithol. 157: 255-264.

408

409 **Supplementary Material (Appendix oik.XXXXXX at**  
410 **<[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1-3**

411

412 **Figure Caption**

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

416  
417 Figure 2: Structural equation model with all measured variables for each latent variable. Circles  
418 represent latent variables. Squares are measured variables. Arr = arrival date; Dep = departure date;  
419 Dur = duration of the migration; NDVI = median value of NDVI over the wintering period (from  
420 October to February);  $\Delta$ NDVI = difference between February and October values of NDVI; #Br =  
421 number of broods for each individual in the previous (PBr) or the current breeding season (BsBr);  
422 #Fl = number of fledglings raised in first brood in the previous (PFl) or the current breeding season  
423 (BsFl); PB = previous breeding attempt, AU = autumn migration, WiT = winter timing, WiC =  
424 winter condition, SP = spring migration, BS = breeding success. Grey and dark arrows represent  
425 indirect and direct effects, respectively, of latent variables on breeding success with associated  
426 parameters.  $\zeta$  refers to the residual variance of the latent breeding success variable.

427  
428 Figure 3: Estimates of standardized path coefficients from the structural equation model for the  
429 annual cycle of hoopoes.

430

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 <sup>1</sup>	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 <sup>1</sup>	WiT	266 (236;306) [24-Aug;2-Nov]
Duration (Dur)	Arrival date – departure date	Length of the seasonal period	From geolocator data <sup>1</sup>	AU	35 (5;76)
				WiT	169 (132;198)
				SP	24 (5;63)
Number of Brood (Br)	Number 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)	Number 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 <sup>2</sup>	WiC	0.21 (0.08;0.53) <sup>3</sup>

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$\Delta$ NDVI	Difference in stretched NDVI values between February and October	Indicator of seasonal change in vegetation cover and prey accessibility	USGS FEWS NET Data Portal <sup>2</sup>	WiC	-0.14 (-0.40;0.01) <sup>3</sup>
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<sup>1</sup> See van Wijk et al. (2017) for detailed information about determination of individual migration schedules and location of wintering areas

<sup>2</sup> eMODIS NDVI data obtained for West Africa from <https://earlywarning.usgs.gov/fews/product/115>.

<sup>3</sup> Unstretched values are presented to easy comparison with other studies and were obtained as follows:

$$\text{unNDVI} = (\text{value} - 100)/100$$

$$\text{un}\Delta\text{NDVI} = (\text{value})/100$$

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:		$\theta$	Posterior Distribution				P( $ \theta >0$ )
From	To		mean	sd	2.5%	97.5%	
Previous Breeding success (PB)	Autumn migration (AU)	$\gamma_2$	0.01	0.36	-0.70	0.77	0.51
Autumn migration (AU)	Winter Timing (WiT)	$\gamma_3$	1.49	1.16	-1.31	3.24	0.86
Autumn migration (AU)	Winter Condition (WiC)	$\gamma_4$	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

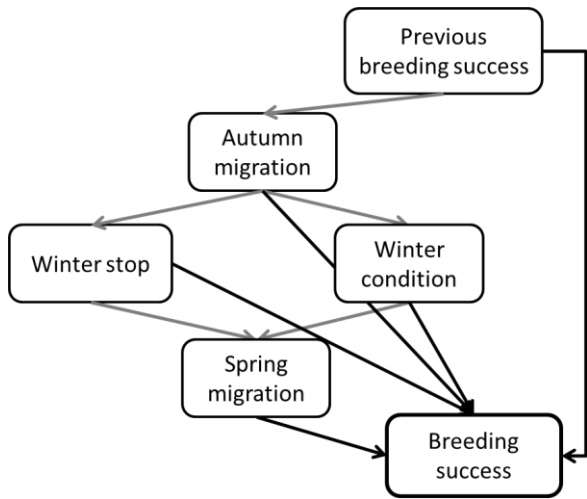


Figure 1

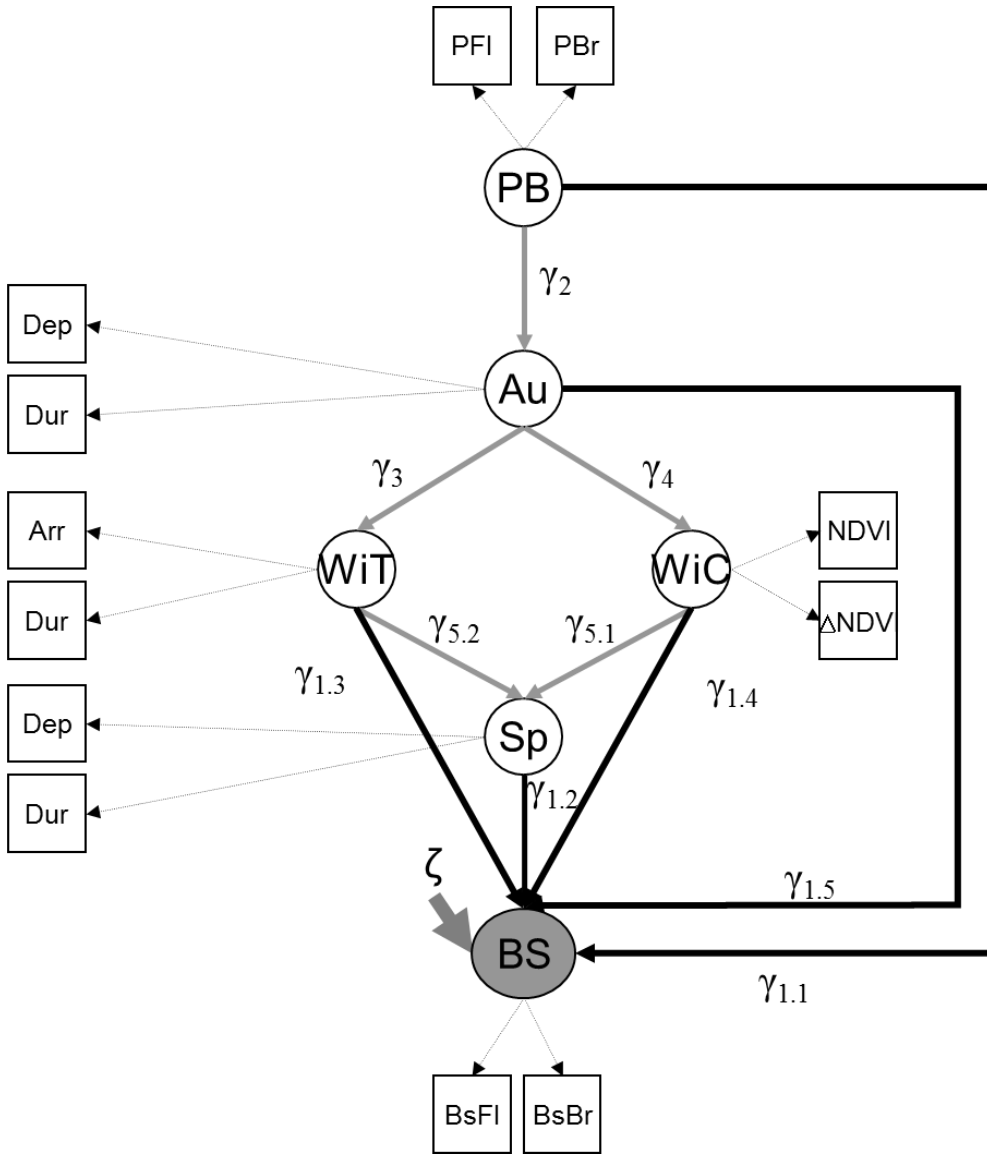


Figure 2

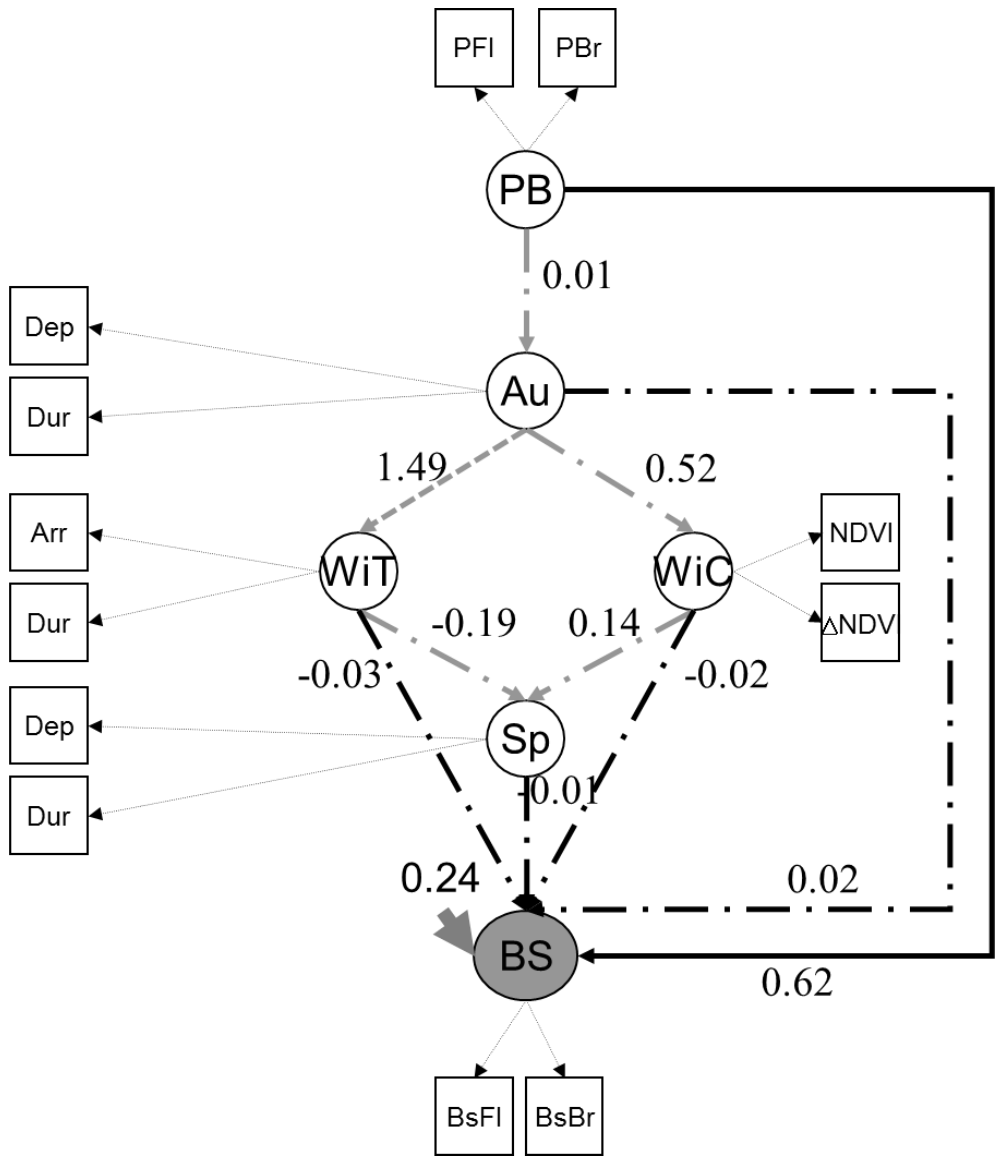


Figure 3