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ORIGINAL ARTICLE

Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird

Rien E. van Wijk[1,2,3] · Michael Schaub[1,4] · Silke Bauer[1]

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Abstract
Migrating birds have to incorporate migration into their annual cycle, next to breeding and moult. This presents the challenge to arrive at the right place at the right time at any given moment during the year to maximize fitness. Although many studies have investigated the timing of specific (life-history) activities of migrating birds, it is poorly studied how the timing and duration of these activities depend on each other and, ultimately, how they affect fitness. Therefore, we investigated variability and dependencies in the timing and duration of successive activities throughout the annual cycle and assessed their fitness consequences in hoopoes (*Upupa epops*), a long-distance migratory bird, using geolocator and breeding phenology data of five consecutive years. We found that the timing and duration of seasonal activities generally depended on the timing and duration of the preceding activity; yet, the strength of these dependencies and the degree of variability varied between activities. The strongest dependencies were found between the end of breeding and departure from the breeding grounds as well as between the arrival in the breeding grounds and the onset of breeding. We also found fitness consequences of timing and duration but only for specific activities: spring migration and particularly the duration of the pre-breeding period influenced the quality of the territory acquired as well as the total number of fledglings. Consequently, we suggest that our study species has the flexibility to adjust the timing and duration of activities but to varying degrees. This is a step forward in understanding the time-constraints that migratory animals face and in identifying their fitness consequences.

Significance statement
To date, few studies have investigated the timing and dependencies of seasonal activities in migrating birds throughout the annual cycle and their fitness consequences. However, understanding temporal constraints and identifying sensitive—fitness-relevant—periods within the annual cycle is crucial to understand the population dynamics of migrating species. We investigated the timing and duration of life-history activities in a long-distance migratory bird and assessed their fitness consequences. Our results clearly show that seasonal activities were generally linked to the previous activities but that this dependency ceased relative to activities further in the past. We also found clear fitness consequences but only for the timing and duration of specific activities. Thus, our study shows that migrants can adjust the timing and duration of activities to a certain degree but also that this flexibility is more constrained for specific activities.

Keywords Autumn migration · Spring migration · Reproductive success · Geolocator · *Upupa epops* · Non-breeding

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✉ Rien E. van Wijk
rienvanwijk@gmail.com

[1] Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

[2] Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

[3] Present address: Universitetsparken 15, 2100 Copenhagen, Denmark

[4] Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

Introduction

Migrating birds face the challenge of having to time both breeding and migration during the annual cycle such that they can profit from (food) resources that peak at specific yet different times at the places they visit throughout a year (McNamara et al. 1998; Alerstam 2011). Arriving outside the best times incurs penalties. Such penalties and thus, selective pressures, likely differ throughout the annual cycle. For instance, arrival on the non-breeding grounds is probably under much lower selective pressure than arrival on the breeding grounds, since the latter strongly correlates with a component of fitness, reproductive success (Kokko 1999; Gienapp and Bregnballe 2012).

It is generally thought that the flexibility in timing activities is low, e.g. that deviations from the 'optimal' timing of an activity can only be corrected to a very limited extent (Sutherland 1998; Bell et al. 2009; Stanley et al. 2012). Consequently, when we compare successive (life-history) activities in the annual cycle, we would expect their timing to be linked, e.g. a late onset of one activity should lead to a delayed onset of the following activity (Marra et al. 2015). However, there might be differences in the strength of these links with some activities more loosely connected than others.

Linking the timing of activities throughout the annual cycle and investigating their consequences on fitness requires data on both migration and breeding, which easily becomes a complex endeavour in migratory birds. The latter might explain why most studies to date have focussed on the timing of particular parts of the annual cycle, mostly spring migration (Hüppop and Hüppop 2003; Jonzén et al. 2006; Tøttrup et al. 2010), occasionally also in relation to reproductive success (Weatherhead 2005; Gordo et al. 2013; Clausen et al. 2015). Recent technological advances in tracking techniques (Bridge et al. 2011) have tremendously increased the availability of data on year-round whereabouts, particularly also for smaller bird species, which thus allow for an annual cycle perspective, e.g. Lindström et al. (2016) and Briedis et al. (2016). However, to date, no study has identified the timing of activities and their dependencies on each other throughout the annual cycle as well as established a link to their ultimate effect on reproductive success.

Therefore, we investigated the timing of the full annual cycle and its consequences on reproductive success and on the quality of established territories using geolocator and breeding phenology data of hoopoes (*Upupa epops*). Overall, we expected that the variability in the timing of activities differed over the annual cycle, that the timing and durations of consecutive activities depended on each other, and finally, that the timing of activities had fitness consequences.

Methods

Study population and study set-up

We conducted our study in a population of hoopoes that breed in southern Switzerland (46°14′ N, 7°22′ E) and migrate to the Sahel region of west Africa for the non-breeding season (Bächler et al. 2010; van Wijk et al. 2016a). The study area is roughly 62 km^2 and approx. 700 nestboxes had been installed prior to this study (Arlettaz et al. 2010). To investigate the timing of seasonal activities, their dependencies and consequences, we equipped birds with geolocators and recorded their reproductive performance.

Data collection

Between 2009 and 2014, 328 breeding hoopoes were equipped with geolocators of type SOI-GDL1 (Bächler et al. 2010). These geolocators, including a leg-loop harness, weigh on average 1.32 g (roughly 2% of a hoopoe's body mass) and had no negative effects on body condition, physiological state, reproductive success or survival (van Wijk et al. 2016b). We retrieved 81 geolocators, of which 71 had usable data, 13 had data gaps and thus only parts of their annual cycle could be used in subsequent analyses. Since hoopoes are consistent in their individual spatial and temporal migration patterns (van Wijk et al. 2016a), we only used data from the first recorded annual cycle of each individual resulting in a dataset of 57 unique tracks. Captured hoopoes were sexed by inspecting their uropygial gland.

We obtained data on breeding phenology and success by regularly inspecting all broods. Every 14 days, we checked all nestboxes in our study area, and occupied nestboxes were inspected every third day to obtain dates for egg laying and hatching and the numbers of broods and fledglings per individual (see also Hoffmann et al. 2015). Fledging dates were defined as 28 days after hatching (Martín-Vivaldi et al. 1999). We used territory occupancy, i.e. the proportion of years a nestbox was occupied, as a measure of territory quality (Tschumi et al. 2014; Guillod et al. 2016). For each individual, we determined the number of fledglings in the first brood as well as the total number of fledglings (in one season).

Data analysis—geolocator data

To determine the timing of activities outside the breeding grounds, we analysed light-level geolocator data to identify the locations and periods over which individuals were stationary. To this end, we followed a stepwise procedure, using functions of the R-package *GeoLight* (Lisovski and Hahn 2012) in combination with scripts described in Schmaljohann et al. (2016), both using R (version 3.1, R Core Team 2014). We first defined the timing of sun events, i.e. sunrise and sunset, as the times when light levels exceeded or fell below thresholds. Subsequently, we filtered 'false' sun events, e.g. when birds entered or left the nestbox, using the *loessFilter* with $k = 2$ and *runningMax* filter set to $k = 25$. We defined stationary periods with the function *trendLight*, which uses the difference in sun events between successive days and is thus independent from location estimates. Since *trendLight* was set to be very sensitive for changes in sun events, sometimes additional stationary periods were defined that in fact belonged to the same site. Therefore, preliminary positions were calculated with a fixed sun elevation angle of −5°, and sites were merged when the modi of their positions were either ≤250 km apart for the migratory period (i.e. from *end of breeding* until 14 October and from 16 February until retrieval of geolocators) or ≤400 km for the non-breeding period outside the equinoxes (i.e. from 15 October until 15 February). Final positions were calculated using a sun elevation angle identified from an in-habitat calibration (Schmaljohann et al. 2016).

To detect site changes, we used the following settings in the *trendLight* function: a window of 13 backward- and forward-days and a minimum stationary period of 2 days during migration, compared to 11 backward- and forward-days and a minimum period of 3 days for the non-breeding period.

The main non-breeding site was defined as the site, where birds stayed for the longest time between October and February. In a few cases, individuals used two non-breeding sites on which they stayed at least 2 months each between October and February. For these, we delimited the non-breeding period by the arrival in the first, and departure from the second non-breeding site.

Data analysis—timing of activities

We characterized the timing of the following key periods and activities (Fig. 1): (a) the *post-breeding* period as defined by the fledging date of the last brood (*end of breeding*) and the departure date from the breeding grounds, (b) *autumn migration* by the departure from the breeding grounds and arrival on the non-breeding grounds, (c) the *non-breeding* period by arrival on, and departure from, the non-breeding grounds, (d) *spring migration* by departure from the non-breeding grounds and arrival on the breeding grounds, (e) the *pre-breeding* period by the arrival on the breeding grounds and the date when the first egg was laid and (f) the *breeding* period by the date of laying the first egg (*onset of breeding*) and the fledging date of the last brood (Fig. 1).

We characterized the timing of activities and their durations with descriptive statistics, separately for males and females. If not stated otherwise, dates that delimit seasonal activities are given as medians ± the interquartile range (i.e. the difference between the first and the third quartile). We choose this measure of statistical dispersion since we had relatively low sample sizes and wanted to reduce bias from large individual deviations compared to the overall population means. Subsequently, we explored the variability between individuals in timing and durations of these activities and their potential changes in the course of the annual cycle using Bartlett's tests (Bartlett 1937).

Data analysis—dependencies in timing and duration of activities

We investigated dependencies in the timing and duration of activities using linear fixed effect models with Gaussian-distributed residuals. In each model, we considered the timing (or duration) of all activities preceding the focal activity starting with previous breeding. Thus, the model for, e.g. the onset of the current breeding contained the highest number of explanatory variables since it required the timing of all activities within an annual cycle. The list of all fitted models is provided in Table S1.

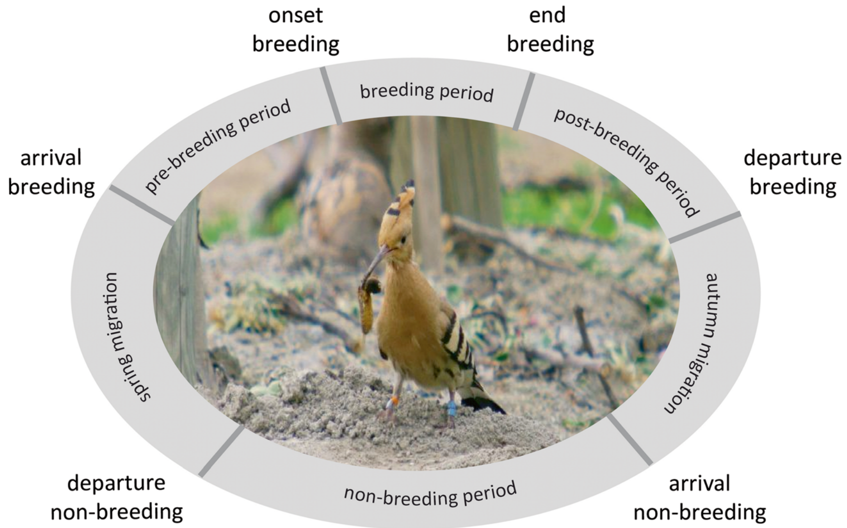

Fig. 1 The annual cycle of a hoopoe consists of several key periods (in boxes), which are delimited by timing (outer variables). In our study, the fledging date of the last brood during the breeding season marks the start of the annual cycle

We performed model selection among all possible models with the given set of explanatory variables. We compared the models using small sample size corrected Akaike information criterion (AICc) (R-package *MuMIn*, Barton 2016) and calculated model averaged regression coefficients. As explanatory and dependent variables had the same units (days), these regression coefficients quantify the direction and magnitude of how the timing (or duration) of a focal activity was changed in response to a late or early timing (or long or short duration) of a previous activity. Thus, a magnitude of the coefficient of around one means that a deviation in timing or duration of the previous activity is directly and unabatedly transferred into the timing or duration of the focal activity.

If dependencies between seasonal activities persisted over the annual cycle, we expected that the regression coefficient would remain relatively high throughout, i.e. even activities that lie further in the past are related to a focal activity. If dependencies weakened over time, we would expect activities to be related but with a diminishing influence of activities further in the past.

Data analysis—reproductive success

We used territory quality, number of fledglings in the first brood and total number of fledglings as fitness-relevant measures and linked them to both the timings and durations of (previous) activities using linear models with Gaussian-distributed residuals (for model set-up, see Table S1). Thus, we defined a set of candidate models from all possible combinations of explanatory variables, i.e. timing and duration of each activity, ranked the models using AICc and calculated model averaged regression coefficients as described above.

It was impossible to record data blind because our study involved focal animals in the field.

Results

Timing and duration of activities

We found no significant differences between males and females neither in timing nor in durations of activities (Kruskal-Wallis test, $P > 0.05$ in all cases, Table 1) and therefore pooled the data of both sexes for further analyses. Hoopoes ended breeding overall in mid-July: 13 July ±32 days (Table 1, $N = 57$), but birds still spent 35 ± 26 days in the breeding grounds thereafter during the post-breeding period (Table 1, $N = 54$) and departed for autumn migration on 16 August ±15 days (Table 1, $N = 54$). Arrival on the non-breeding grounds was on 23 September ±20 days ($N = 56$), yielding a median duration of autumn migration of slightly more than 1 month ($N = 54$, Table 1). Departure from the non-breeding grounds was on 10 March ±14 days ($N = 50$) and arrival on the breeding grounds on 5 April ±13 days ($N = 47$), resulting in a spring migration duration of 27 days ($N = 49$, Table 1). Breeding commenced on 25 April ±13 days ($N = 47$), and thus, the pre-breeding period was 18 ± 10 days ($N = 40$, Table 1).

The variability among individuals in timing and durations of activities varied over the annual cycle (Bartlett test, timing: $K = 60.8$, $df = 5$, $P < 0.001$; durations: $K = 39.1$, $df = 6$, $P < 0.001$): while the timing of the end of the breeding season and the duration of the post-breeding period were highly variable, the variability in timing and durations of activities generally decreased towards arrival on the breeding grounds (Fig. 2) and this was not a consequence of individuals being consistently “late” or “early” throughout the annual cycle (Fig. S1).

Table 1 Overview of the timing of activities in male and female Hoopoes, characterized by median date and duration (days), interquartile range (in parentheses) and number of individuals (N). We also provide results of the Kruskal-Wallis test for differences in timing and duration between the sexes

Activity	Males	Females	Both sexes combined	Kruskal-Wallis χ^2	P
End of breeding	14 July (33, $N = 29$)	11 July (24, $N = 28$)	13 July (32, $N = 57$)	<0.01	0.99
Departure breeding	18 August (13, $N = 29$)	15 August (16, $N = 27$)	15 August (14.8, $N = 54$)	0.28	0.60
Arrival non-breeding	23 September (19.5, $N = 23$)	25 September (18, $N = 28$)	23 September (19.5, $N = 56$)	0.36	0.55
Departure non-breeding	10 March (12, $N = 24$)	10 March (14.3, $N = 26$)	10 March (13.5, $N = 50$)	0.05	0.83
Arrival breeding	6 April (14.5, $N = 23$)	4 April (14, $N = 25$)	5 April (14, $N = 47$)	0.41	0.52
Onset breeding	24 April (11, $N = 24$)	27 April (14, $N = 25$)	25 April (13.5, $N = 47$)	0.37	0.54
Duration post-breeding	32 (25.5, $N = 27$)	37 (31, $N = 27$)	35 (25.5, $N = 54$)	< 0.01	0.97
Duration autumn migration	34 (19.5, $N = 27$)	35 (21, $N = 27$)	35 (21.8, $N = 54$)	0.29	0.59
Duration non-breeding	167 (16, $N = 28$)	163 (24.3, $N = 28$)	165 (20, $N = 56$)	0.02	0.90
Duration spring migration	22 (12.5, $N = 24$)	26 (17.5, $N = 25$)	24 (15, $N = 49$)	0.06	0.80
Duration pre-breeding	17 (7.5, $N = 16$)	21 (18, $N = 24$)	18 (10, $N = 40$)	0.35	0.55
Duration breeding	58 (42, $N = 28$)	78 (43, $N = 28$)	76 (42, $N = 56$)	0.02	0.89

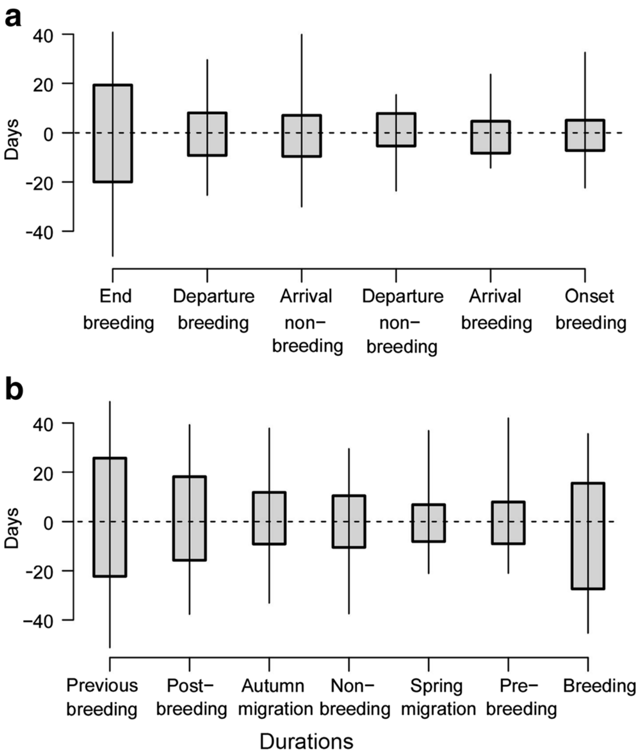

Fig. 2 The variability in **a** the timing of activities and **b** the durations of periods throughout the annual cycle. The medians are standardized to 0, the *whiskers* indicate the 1st and 3rd quartile and the limits of the *vertical lines* show ranges

Dependencies in timing and duration of activities and their fitness-relevance

The timing of an activity was generally positively related to the timing of the activity directly preceding it, but this dependence already ceased for the penultimate activity and was virtually nonexistent for any other prior activities (Fig. 3a, Table S2). Timings with the strongest dependency were those between the end of breeding and the departure from the breeding grounds as well as between the arrival on the breeding grounds and the onset of breeding. The generally positive regression coefficients thus indicate that, e.g. a late arrival on the breeding grounds leads to a late onset of breeding; yet, their magnitudes were always smaller than one, indicating that deviations in timing were only carried on to the next activity to a 'lower-than-original' extent.

The durations of subsequent activities were generally negatively related, yet at a higher magnitude than for the timings above (Fig. 3b, Table S3). The magnitude of the coefficients found (typically <0 and >−1) indicates that, e.g. a longer non-breeding period leads to a shorter spring migration, but that a 1-day change during one period translates into a smaller than 1-day change in the next period. Like above, these relations ceased over time, i.e. durations of activities further back in time had no or only very slight influence on the duration of a focal activity. The strongest relationship existed between the durations of the pre-breeding and breeding period (Fig. 3b).

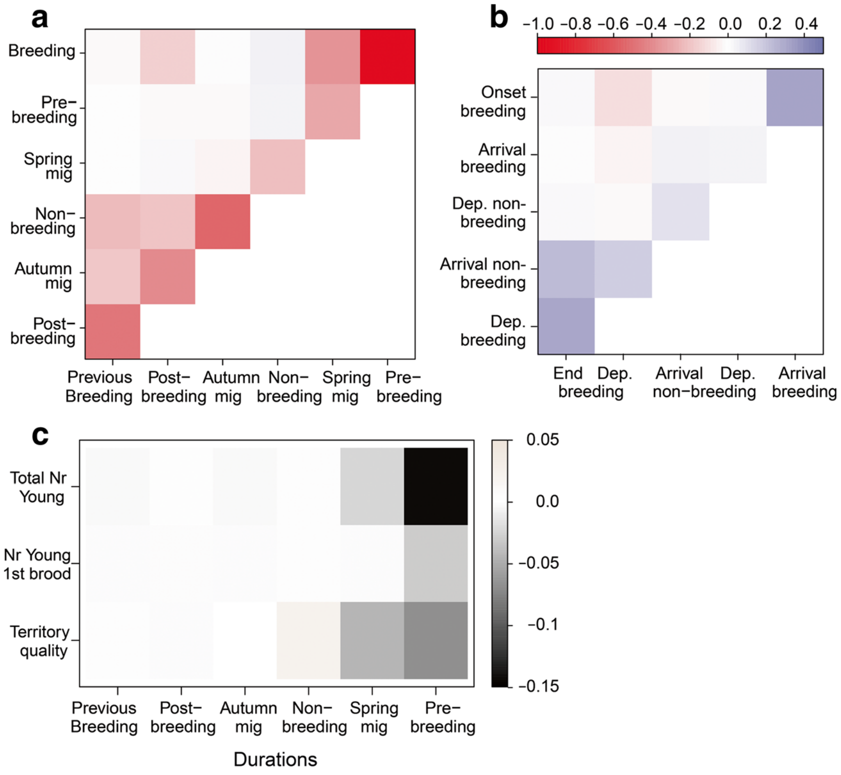

Fig. 3 Dependencies in **a** timing activities and **b** durations within the annual cycle and **c** the fitness consequences of durations. *Colours* indicate the magnitude and direction of model averaged coefficients with *deeper red colours* representing stronger negative dependencies and *deeper blue* stronger positive dependencies. Events on the *x*-axis of panels **a** and **b** are those that occurred further in the past

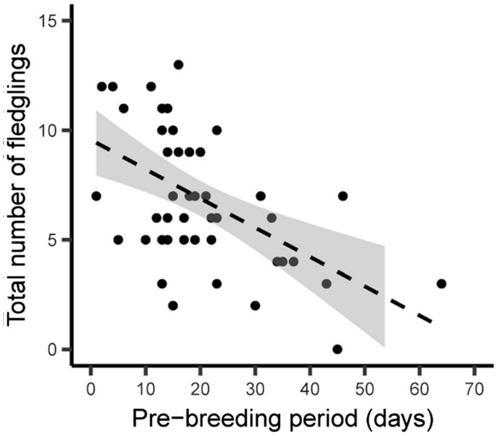

Fig. 4 The duration of the pre-breeding period in relation to the total reproductive output. Individuals are represented by *dots*; the *dashed line* indicates the smoothed conditional means with in *grey* the confidence interval of the estimate depicted by the standard error

The duration (and to a lesser extent, timing) of some activities had fitness consequences (Fig. 3c, Table S4). The duration of spring migration and especially the duration of the pre-breeding period influenced territory choice and the total number of fledglings produced; the number of fledglings in the first brood was only influenced by the duration of the pre-breeding period (Fig. 3c, Table S4). In general, the model coefficients indicate that a longer spring migration or a longer pre-breeding period resulted in occupying a lower-quality territory and fewer fledglings (Fig. 3c, Table S4). Although the coefficients seem to have a relatively low magnitude, they still indicate that, e.g. a 10-day longer pre-breeding period reduces the total number of fledglings approx. by 1.5 (Fig. 4).

Discussion

Our results clearly show that variability and dependencies in timing and duration of (life-history) activities vary within the annual cycle and that timing and duration of specific activities have fitness consequences.

The generally negative relation between successive activities might not be overly surprising—after all, time within a year is limited and thus, if birds take long for one activity, they have to shorten another activity—otherwise, performing specific activities would get fully out of sync with phenology (Wingfield 2008). However, this finding is interesting as it shows that hoopoes are flexible to some extent, register how long they engaged in specific activities and can adjust the duration of activities depending on the duration of the previous activity.

Adjustments in the duration of life-history activities have been shown to exist for, e.g. migration, moult and breeding. For instance, a higher migration speed can be attained with higher flight speeds (Fransson 1995), shorter stopover times (Arlt et al. 2015) or a combination of both. Similarly, many passerines moult in the non-breeding grounds (Jenni and Winkler 1994) and thus, non-breeding duration could be reduced by increasing moult rates (Helm et al. 2005; Barta et al. 2008; Morrison et al. 2015). Finally, an obvious adjustment to the duration of breeding in our study species is the number of breeding attempts—double or triple broods lengthen the breeding period compared to single broods (Hoffmann et al. 2015).

Generally, we also found that the duration of only successive activities was related, but there were some notable exceptions: in addition to the previous activity, autumn migration and the duration of the non-breeding period were also related to the penultimate activity, but this was not the case anymore for spring migration or the pre-breeding period. Also, the magnitude of coefficients indicated that the strength of dependencies varied and was particularly weak for the relation between spring migration and the non-breeding period as well as between the timing of departure from the non-breeding grounds and arrival on the breeding grounds. The non-breeding period could thus be seen as a buffer, during which dependencies in timing loosen, similar to earlier findings in ducks and shorebirds (Oppel et al. 2008; Senner et al. 2014).

Similar to differences in dependencies, we also found considerable differences in the *variability* of timing and duration of activities. The end of breeding was by far the most variable date, whereas the date of arrival on the breeding grounds and the date of departure from the non-breeding grounds seemed least variable. Similarly, the duration of breeding and post-breeding were found to be the most variable, whereas the duration of spring migration and the pre-breeding period were the least variable activity in the annual cycle, and all other activities showed similar variation. If we assume that variation can be indicative of selection, durations of spring migration and pre-breeding period as well as arrival on the breeding grounds would be subject to strong selection, acting towards timely arrival on the breeding grounds, early onset of breeding and therefore, higher reproductive output (Kokko 1999; Gienapp and Bregnballe 2012).

The duration of spring migration was considerably shorter than autumn migration with 24 compared to 35 days. Although we lacked detailed-enough data to determine stopover times during migration, this finding suggests that birds migrate at higher speed in spring, possibly attained with higher flight speeds (Fransson 1995), shorter stopover times (Arlt et al. 2015) or a combination of both.

Furthermore, we could show that the timing and duration of particular activities had fitness consequences: the durations of spring migration and the pre-breeding period influenced the quality of the territory occupied and especially the total number of fledglings. Specifically, a longer spring migration or a longer pre-breeding period led to the occupation of lower-quality territories and to fewer offspring raised, the latter mainly resulting from fewer breeding attempts rather than from fewer fledglings per clutch. Intraspecific competition might be the main reason why individuals that had a longer spring migration or pre-breeding period occupied territories of lower quality.

Another factor that might explain differences in fitness consequences are specific (weather) conditions on the breeding grounds. In years with generally favourable conditions, reproductive output might not differ greatly between territories of different quality, i.e. all territories provide sufficient resources, and differences in reproductive output will be small. Under such benign conditions, differences in arrival times on the breeding grounds or differences in the duration of the pre-breeding period will not be fully reflected in reproductive success, i.e. there are only slight differences in reproductive success between individuals arriving early or late, or with a long or short pre-breeding period. Likewise, the opposite will apply to years with adverse, harsh or otherwise detrimental conditions on the breeding grounds that will pronounce differences in arrival times or pre-breeding durations regarding their consequences for reproductive success. Thus, the joint effect of arrival time and pre-breeding duration on reproductive success is likely strongly modulated by environmental conditions—an interaction that should be investigated in more detail but requires the inclusion of many more study years with a greater variety of environmental conditions.

The prominent influence of the pre-breeding period for the total number of fledglings indicates that a short pre-breeding period might not be sufficient for female hoopoes as they are likely income breeders and thus acquire body resources from local foraging (Langin et al. 2006). In that respect, it might be important to note that we have differentiated between fledglings of the first brood and overall number of fledglings, because the fitness contribution of broods differs—fledglings produced early in the season have a higher survival, i.e. are more likely to return in the subsequent year compared to fledglings of later broods (Hoffmann et al. 2015) and therefore, yield a higher fitness-payoff than fledglings from late(r) broods.

Identifying constraints in the timing of (life-history) activities as well as their consequences on migrants' fitness is crucial to estimate the consequences of ongoing and future climate-driven changes on the population dynamics of migratory species. Our study has contributed to this by showing that long-distance migrants have the flexibility to correct deviations in timing and duration of life-history activities, but that the extent of this flexibility is limited for specific activities that have clear fitness consequences.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All capture and handling of hoopoes complied with contemporary laws regulating the treatment of animals in Switzerland and was approved by the appropriate management agencies and ethical committees.

Informed consent Informed consent is not applicable in this study.

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