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Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects

Martins Briedis [1,2] · Miloš Krist [1,3] · Miroslav Král [1] · Christian C. Voigt [4] · Peter Adamík [1,3]

Abstract

Annual cycles of animals consist of distinct life history phases linked in a unified sequence, and processes taking place in one season can influence an individual's performance in subsequent seasons via carry-over effects. Here, using a long-distance migratory bird, the collared flycatcher *Ficedula albicollis*, we link events throughout the annual cycle by integrating breeding data, individual-based tracking, and stable-carbon isotopes to unravel the connections between different annual phases. To disentangle true carry-over effects from an individuals' intrinsic quality, we experimentally manipulated the brood size of geolocator-tracked males prior to tracking. We did not find unambiguous differences in annual schedules between individuals of reduced and increased broods; however, in the following spring, the latter crossed the Sahara and arrived at the breeding grounds earlier. Individuals with higher absolute parental investment delayed their autumn migration, had shorter non-breeding residency period but advanced spring migration compared to individuals with lower breeding effort. Neither the local non-breeding conditions (as inferred from $\delta^{13}C$ values) nor the previous breeding effort was linked to the timing of the following breeding period. Furthermore, while on migration, collared flycatchers showed a pronounced "domino effect" but it did not carry over across different migration seasons. Thus, the non-breeding period buffered further accumulation of carry-over effects from the previous breeding season and autumn migration. Our results demonstrate tight links between spatially and temporally distinct phases of the annual cycles of migrants which can have significant implications for population dynamics.

Significance statement

Timing is everything! This holds true also for migratory animals which must time their annual movements, breeding and non-breeding seasons according to the environment they live in. However, perfect timing of a particular event can be hampered by past events. We studied connections between spatially and temporarily distinct annual phases in collared flycatchers, a small bodied bird which twice a year migrates between Europe and sub-Saharan Africa. We found tight links between individual's parental investment and timing of autumn migration, but not spring migration. Similarly, the timing of autumn migration did not translate to influence the timing of spring migration. Thus, our results demonstrate that the non-breeding period may serve as a buffer to overcome high energy expenditure during the previous breeding season and prevent further accumulation of carry-over effects in migratory birds.

✉ Martins Briedis
   martins.briedis@vogelwarte.ch

1 Department of Zoology, Palacký University, tř. 17. listopadu 50, 77146 Olomouc, Czech Republic

2 Department of Bird Migration, Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

3 Museum of Natural History, nám. Republiky 5, 77173 Olomouc, Czech Republic

4 Leibniz Institute for Zoo and Wildlife Research, Evolutionary Ecology, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

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Introduction

Annual cycles of migratory animals consist of various spatially and temporally distinct phases, such as reproduction, moult, migration, and non-breeding residency. Nevertheless, these events are linked to each other physiologically and ecologically, and preceding events may have profound consequences on the following life history phases (Harrison et al. 2011). For long-distance migratory birds, this means that experiences at their tropical non-breeding grounds may carry over across seasons and continents to influence events taking place at their temperate breeding grounds and vice versa. For instance, residing in sub-optimal habitat at non-breeding areas can result in delayed spring migration, consequently negatively affecting breeding performance the following season (Marra et al. 1998; Norris et al. 2004; Catry et al. 2013; Low et al. 2015). Such events and processes taking place in one season which result in individuals making the transition between seasons in different physical conditions and ultimately affecting their performance are defined as carry-over effects (Norris and Marra 2007; Harrison et al. 2011). Habitat quality, social status, population density and breeding effort have been identified among the main drivers of carry-over effects (Harrison et al. 2011).

Negative consequences of carry-over effects are often exhibited as delays in timing of annual events (Harrison et al. 2011). In annual migrations, it has often been shown that delays in one phase of migration (i.e. onset of migration) translate into delays in the following migration phases (i.e. end of migration)—a so-called domino effect (Piersma 1987). Such patterns can have significant consequences for individual fitness and population dynamics revealing links between different parts of the annual cycle (Bauer et al. 2015).

Carry-over effects can influence individual condition not only in the following season but also across years. For example, successful breeding in one year can negatively influence breeding probability and fecundity in the following year (Gustafsson and Sutherland 1988; Inger et al. 2010); but it is important to note that the interaction between individual quality and the environment may also play a significant role (Souchay et al. 2018). Furthermore, parental investment can affect migration timing as well as the geographical distribution of individuals during the non-breeding season. In Cory's shearwaters *Calonectris diomedea*, birds with experimentally reduced breeding effort started autumn and the following spring migration earlier and were more likely to engage in long-distance migration than their conspecifics which had naturally higher breeding effort (Catry et al. 2013). This suggests that energetic and time-dependent costs of reproduction can influence subsequent migration episodes via carry-over effects. On the other hand, carry-over effects of delayed autumn migration could also be overcome during the non-breeding period as found in Hudsonian godwits *Limosa haemastica* (Senner et al. 2014). Hence, we still lack a comprehensive assessment of carry-over effects across full annual cycles.

Just as parental effort influences migration and the non-breeding period, experiences at the non-breeding areas have consequences for the following spring migration and breeding season. Non-breeding conditions are known to influence spring migration phenology and individual fitness (Marra et al. 1998; Norris et al. 2004; Saino et al. 2004; Gunnarsson et al. 2005; Balbontín et al. 2009; Drake et al. 2013; López-Calderón et al. 2017). For instance, individuals residing in better habitats arrive at the breeding sites earlier and in better condition (Marra et al. 1998). For such studies, stable isotope ratios of winter-grown tissues have been increasingly used to evaluate the local conditions individual birds experience at their distant non-breeding areas. Thus far, stable-carbon isotope ($\delta^{13}C$) signatures have been used most often to discriminate between higher (i.e. mesic) and lower quality (i.e. xeric) sites (e.g. Bearhop et al. 2004; Norris et al. 2004; Procházka et al. 2008) as $\delta^{13}C$ values allow for the discrimination between habitats with C3 and C4 plants.

Collared flycatchers *Ficedula albicollis* are long-distance Afro-Palearctic migrants which breed across large areas of the Western Palearctic and migrate to Southern-Central Africa during the Northern Hemisphere winter (Briedis et al. 2016). During their annual cycle, flycatchers spend about 3 months at breeding sites where birds reproduce and undergo a complete body moult before departing for autumn migration (Stresemann and Stresemann 1966). For the greater part of the year, birds reside in sub-Saharan Africa, where approximately 5 months are spent at the non-breeding residency sites (Briedis et al. 2016). During the non-breeding period, the species is assumed to feed solely on invertebrates, but little is known about habitat use and preferences (Cramp and Perrins 1993). However, we might expect that inhabiting mesic habitats should be advantageous over residing in xeric habitats as the former offer better feeding opportunities (Studds and Marra 2007; López-Calderón et al. 2017).

With this study, we aim to narrow the gap in our understanding of full annual cycles in animal ecology by linking summer–winter–summer events in a long-distance migratory bird (Marra et al. 2015). We couple an experimental approach with observational data to unravel the links between different parts of the annual cycle by integrating breeding monitoring, tracking by light-level geolocators, and stable isotope analyses of winter-grown feathers. By doing so, we are able to follow individual birds throughout the full annual cycle and assess the magnitude of carry-over effects from the breeding season to autumn migration, non-breeding period, spring migration, and the following breeding period as well as from the non-breeding season to spring migration and the subsequent breeding season. As the non-breeding period in collared flycatchers

is supposedly less time-constrained (Briedis et al. 2016), we predict that (i) parental investment will affect autumn migration schedules via carry-over effects, but the costs of breeding may be overcome during the non-breeding residency, rather than accumulate further (Senner et al. 2014). Therefore, (ii) spring migration schedules and the consecutive breeding period will be more dependent on the non-breeding habitat conditions, rather than the previous parental investment.

Methods

We studied collared flycatchers at two localities in the Czech Republic approximately 30 km apart (site Dlouhá Loučka: 49° 50′ N, 17° 13′ E, site Kosíř: 49° 32′ N, 17° 04′ E). In spring, flycatchers arrive starting from the second week of April (Briedis et al. 2016) and the earliest clutches are initiated in late April or early May. At both sites, birds breed in nest boxes situated mainly in mixed deciduous woodlands. Nest boxes were regularly monitored throughout the breeding season and nearly all breeding birds were captured and marked with aluminium rings while feeding the nestlings. The flycatchers at Dlouhá Loučka are under heavy predation pressure by edible dormouse *Glis glis*; therefore, we protected the nest boxes by applying approximately 50 cm wide plastic foil around the trees roughly 50 cm above and below the nest boxes.

Data availability The datasets analysed during the current study are available upon request from the MoveBank data repository (project ID 166151488).

Geolocator deployment and retrieval

Field work was carried out during three breeding seasons from 2013 to 2015. In 2013 and 2014, we attached geolocators (model GDL2.0, Swiss Ornithological Institute) to the backs of adult birds using flexible 24 mm long leg-loop harnesses made from 1 mm thick silicone or neoprene cords. Geolocators automatically—thus with a blind method—measured ambient light intensity every minute and stored maximum values in 5 min intervals. To reduce potential shading of the light sensor by birds' feathers, all devices were equipped with a 7-mm long light stalk. Each device weighted approximately 0.6 g including the harness and light stalk (i.e. < 5% of the body mass of collared flycatchers).

In 2013 at Dlouhá Loučka, we deployed a total of 69 geolocators on breeding birds (33 males, 36 females) during late stages of their respective breeding cycles (last days of feeding nestlings in the nest boxes). In 2014, we deployed a total of 165 geolocators (157 males, 8 females) at Kosíř where birds were captured and equipped with the devices upon their arrival at the site before the onset of breeding ($n = 139$) and during nestling provisioning ($n = 26$).

In the years following the deployment of the devices, we conducted extensive re-trappings of the returning birds before and during the breeding season. In 2014 at Dlouhá Loučka, we recovered 28 (40.6%, 14 males, 14 females) of the 69 deployed geolocators. One additional device (male) was recovered in 2015 accounting for a total recovery rate of 42%. In 2015 at Kosíř, we recovered 29 geolocators (17.6%, all males) and one additional device from a male was recovered in 2016 (total recovery rate 18.2%). The relatively low recovery rate at Kosíř may be explained by the deployment of devices on birds before the onset of breeding, as not all birds that were fitted with geolocators bred in the nest boxes in 2014 and/or 2015. The recovery rate was 43.3% when considering only males that were observed breeding in the nestboxes in 2014. Since all captured males were fitted with geolocators at Kosíř in 2014, we were not able to compare return rates of tagged and untagged birds, but typical return rates at this site range between 30% and 50% (MK unpublished data). At Dlouhá Loučka, the geolocators had no apparent effect on return rates of the tagged individuals compared to the control group of ringed-only birds (tagged: 28/69 = 40.6%; control: 29/83 = 34.9%; $\chi^2 = 0.30$, $p = 0.58$).

Brood size manipulation

To disentangle true carry-over effects from the intrinsic quality of individuals, during the 2014 field season at Kosíř, we conducted a brood size manipulation experiment by adding or subtracting one chick to/from the initial brood. Nests with the same hatching date were treated in pairs by randomly moving one chick from one nest to another. The manipulation took place on day 2 or 3 after the eggs had hatched. In total, 104 nests (52 pairs) were experimentally manipulated. At the manipulated nest, we trapped adult males and equipped them with geolocators. In total, we tagged males at 46 nests with increased brood size and 44 nests with decreased brood size. However, this represents only 86 individuals, since four of those males were polygynous and were caught on two nests. We obtained migration and non-breeding residency data from the geolocators of seven males with reduced broods (reduced from 8 to 7 chicks = 1 case, 7/6 = 1, 6/5 = 1, 5/4 = 1, 4/3 = 2, 3/2 = 1) and nine males with increased brood size (increased from 5 to 6 chicks = 2 cases, 6/7 = 7, including one polygynous male that also took care of another nest with increased brood size 3/4).

Assessment of non-breeding conditions

Upon geolocator retrieval, we collected feather samples from all previously tagged birds. We used stable isotope ratios of carbon ($\delta^{13}C$) measured from tertial feathers moulted at the

non-breeding sites (Svensson 1992) to assess the non-breeding conditions. Lower $\delta^{13}C$ values identify cooler and moister habitats which accommodate increased quantities of invertebrates providing better feeding opportunities, while higher $\delta^{13}C$ values are associated with hotter and drier habitats with more C_4 plants (Marra et al. 1998; Marshall et al. 2007). Lab procedures of stable isotope analyses are detailed in the Online Resource 1.

Data analyses

We determined sunrise and sunset times within the recorded geolocator light data using 'GeoLocator' software (Swiss Ornithological Institute). Non-breeding sites and migratory departure and arrival times were determined with the R-package 'GeoLight' v 1.03 following the standard procedures outlined by Lisovski and Hahn (2012) and setting the 'changeLight' function parameters to $q = 0.85$, days $= 3$. Unfortunately, due to high variability in the recorded light data during the migration and proximity of the equinox, we were not able to identify specific migratory stopover sites. Geographic coordinates of the individual non-breeding sites were calculated using Hill-Ekstrom calibration. The derived sun elevation angles ranged between +8.6 and −0.7. We determined time of Sahara crossing by carefully inspecting daily patterns of raw light recordings and searching for days with periods of uninterrupted maximal light intensities throughout the day, which indicate non-stop diurnal flight, characteristic of a desert crossing (Adamík et al. 2016; Ouwehand and Both 2016). Migration distance for each individual was measured as a great circle (orthodromic) distance between the respective breeding and non-breeding sites (using the median coordinates within the non-breeding residency period).

We used general linear models to identify if there was an effect of study year (and accordingly study site), birds' age and sex on the timing of annual events (e.g. breeding, onset of migration, Sahara crossing, etc.). Analyses revealed that study year was a significant predictor for timing of breeding, departure from the breeding site, arrival at the non-breeding site, and breeding the following year (Online Resource 2), while age was a significant predictor only for the timing of breeding in the first year. Sex had no effect on the dependent variables (i.e. no protandry); therefore, we pooled male and female data. For further analyses, we centred the timing of annual events relative to the average first egg's laying date in each year (2013: 10 May, SD = 8.53, $n = 115$, 2014: 4 May, SD = 7.33, $n = 125$), thus compensating for the year effect on the consecutive parts of the annual cycle. Only the first clutch of each individual was considered.

To test for carry-over effects of breeding effort on the timing of consecutive parts of the annual cycle, we categorized all birds according to their breeding performance. This was done due to the relatively low variation in the number of fledged nestlings, and a skewed distribution (but see Online Resource 3 for regression analyses of the number of fledglings against the annual schedule variables). Each individual was assigned to one of the two groups depending on the number of nestlings fledged—above or below the average (5.4 ± 1.4 SD fledged nestlings, $n = 30$). Further analyses on how breeding effort influenced the timing of consecutive parts of the annual cycle were done using these two categories. We excluded all individuals that fledged zero nestlings due to adverse weather or predation as the nest losses may have happened at different stages of the breeding season and the further whereabouts of these individuals were unknown. Some individuals may have attempted to have a replacement clutch (outside of our nest boxes) while others may not, thus not allowing for the accurate evaluation of their breeding effort. Sample sizes of timing data for different stages of the annual cycle differ due to technical issues with the geolocators (typically lower sample sizes for spring events due to limitations of the geolocators' batteries' life span) or the inability to determine the timing of certain events due to high noise in the recorded light data ($n = 2$ cases).

We used confirmatory path analyses (R-package 'lavaan'; Rosseel 2012) to examine direct and indirect effects of how timing of one annual cycle event is linked to the timing of all subsequent events. Path analysis is a type of structural equation models where only the measured variables are considered ignoring latent variables. In structural equation models, components can appear both as predictors and response variables generating a causal network. We included timing of eight annual cycle events in our model: onset of egg laying in the first year, breeding site departure, Sahara crossing in autumn, non-breeding site arrival, non-breeding site departure, Sahara crossing in spring, breeding site arrival, and onset of egg laying in the second year. Since the timing of all events in the animals' annual cycle are linked in a unified sequence via carry-over effects (Harrison 2011), we structured the path model so that the timing of each event was dependent on the timing of all preceding events. The final path diagram was plotted using R-package 'semPlot' and one-headed arrows represent causal relationship between the variables. The given path coefficients are standardized partial regression coefficients.

Due to multiple testing, p values should be interpreted against a threshold level of alpha = 0.008 for the timing of migration, and alpha = 0.017 for the duration of annual stages (autumn migrations, non-breeding residency, and spring migration). We assessed the timing of spring events in relation to the non-breeding conditions ($\delta^{13}C$ values) and previous parental investment using general linear models (GLM) with normal error structure and an identity link function:

Timing/duration of migration event $\sim \delta^{13}C$ + previous parental investment.

We calculated the unbiased Cohen's d values and their confidence intervals according to Nakagawa and Cuthill (2007) accounting for small sample sizes. Statistical tests were performed in R version 3.3.1 (R Core Team 2016).

Results

Brood size manipulation

The comparison of annual migration schedules of experimentally manipulated birds revealed no significant differences in timing at any stage of the annual cycle between the males whose brood size was increased (average fledged: 6.1 ± 0.9 SD, $n = 9$) and those with reduced broods (averaged fledged: 4.1 ± 1.9 SD, $n = 7$; Fig. 1a, Online Resource 4). Nor did we

find a statistically significant difference between the two treatment groups regarding migration durations in autumn or spring, non-breeding residency duration or total migration distance.

Absolute breeding effort

When looking at the absolute fledgling numbers (not considering brood manipulation) as a proxy for breeding effort, we found that individuals that fledged higher than average number of fledglings (6.3 ± 0.5 SD, $n = 18$) underwent all stages of autumn migration later than those fledging fewer than average fledglings (4.0 ± 1.0 SD, n = 12; Fig. 1b, Online Resource 5). The timing difference between the two groups was significant for arrival at the non-breeding site (unpaired t test: $t = 3.1$, $p = 0.004$) with birds fledging more young arriving on average 10 days later. The opposite was observed regarding the timing of spring migration—birds that fledged more young in the previous year underwent all
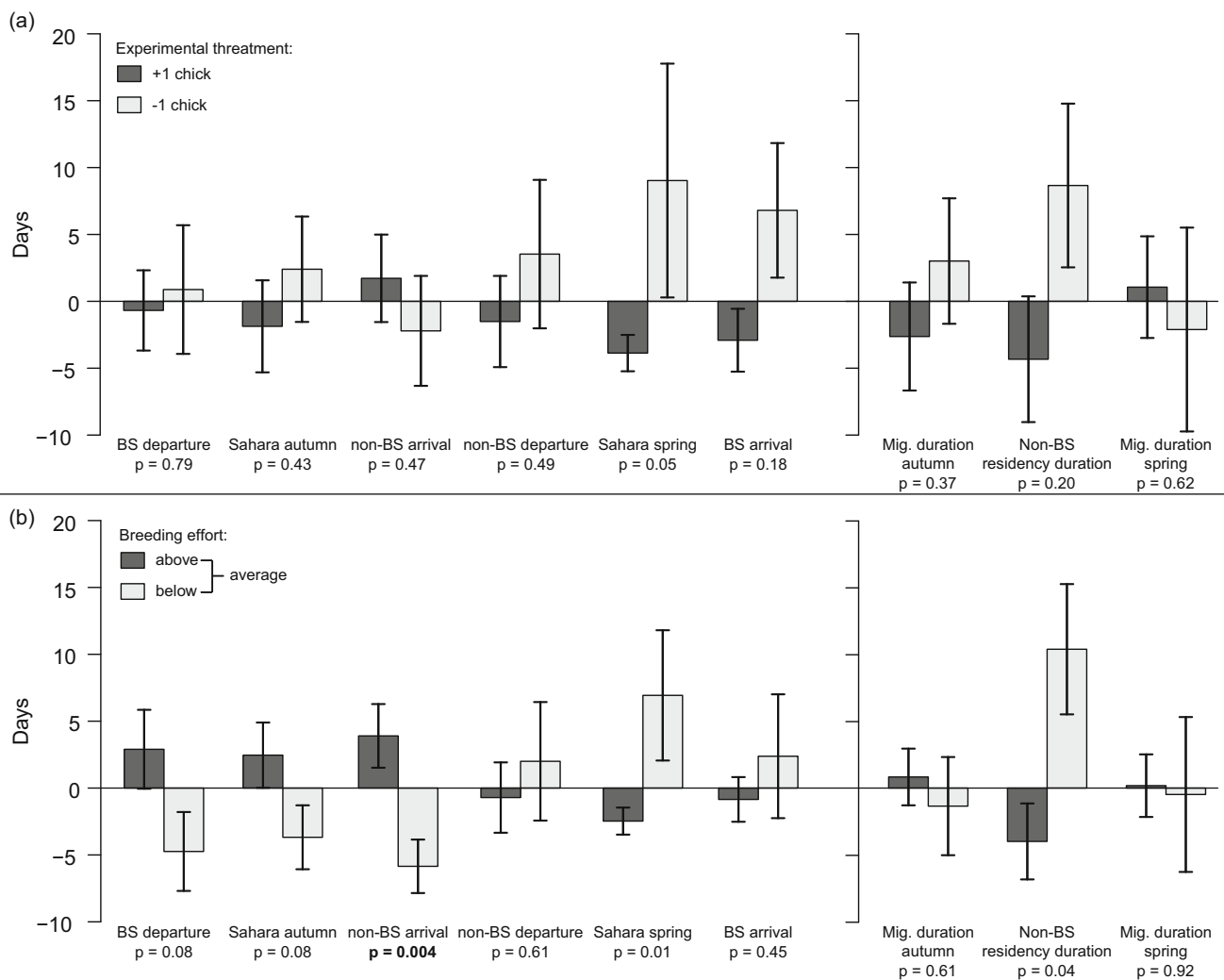

Fig. 1 Average deviation of migration timing in collared flycatchers depending on **a** experimental treatment of brood size manipulation, and **b** absolute breeding effort (expressed as below or above the study average of 5.4 fledglings). Bars denote the average difference in timing of migration events relative to the mean of the compared groups. Error bars denote standard errors
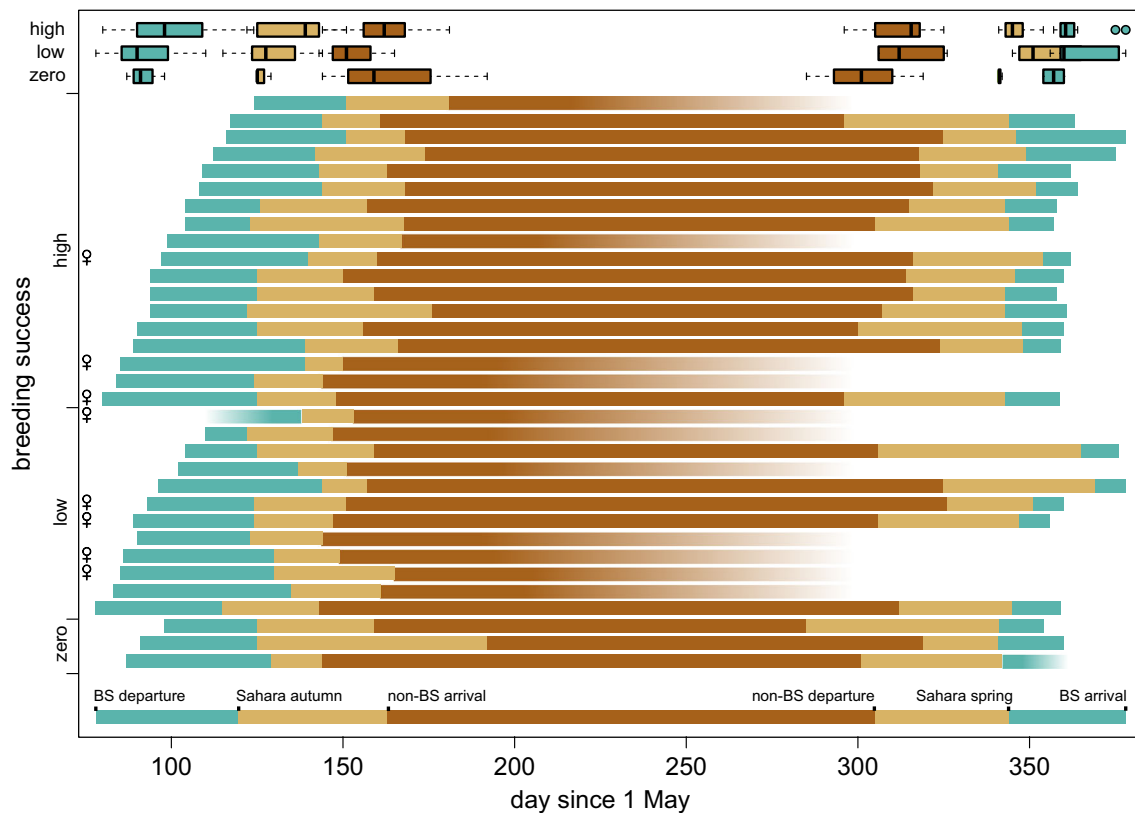
Fig. 2 Migration schedules of the 33 geolocator-tracked collared fly-catchers according to their breeding effort (number of fledglings below or above the average). Individual level (solid lines) and pooled category level (boxplots showing median, interquartile range (IQR)—boxes; whiskers extend to values within 1.5 times the IQR and dots depict outliers) data are presented. Migration schedules include departure from the breeding site, Sahara crossing in autumn, arrival at the non-breeding site, departure from the non-breeding site, Sahara crossing in spring, and arrival at the breeding site. Faded lines indicate lack of data due to failure of the geolocator's battery or uncertainty of the timing of a particular event. Only individuals with known fledgling numbers are shown

stages of the spring migration earlier. We did not find significant differences in migration durations in autumn or spring, nor in total migration distance. However, birds that fledged more young spent on average 14 days less at the non-breeding residency areas (unpaired t test: $t = -2.5$, $p = 0.04$, Fig. 1b, Online Resource 5) and, thus, on average migrated earlier in spring (individual schedules are summarized in Fig. 2).

Confirmatory path analyses between the timing of different annual events revealed no significant effects of the breeding time on the timing of any of the further stages throughout the annual cycle, nor the timing of breeding next year (Fig. 3). There was a significant positive effect of breeding site departure, non-breeding site arrival, and breeding site arrival on the timing of following breeding, while timing of Sahara crossing in autumn had a negative effect on the timing of breeding the following year. Significant positive effects were also found between timing of breeding site departure and Sahara crossing in autumn, as well as Sahara crossing in spring and breeding site arrival (Fig. 3; Online Resource 6).

We found a pronounced 'domino effect' where the timing of each annual stage had the strongest impact on the timing of the following one and the interactions got weaker with increasing timespan between the events ($F_{1,26} = 11.48$, $r^2 = 0.28$, $p = 0.002$, Fig. 4; individual linear regressions are available at Online Resource 7). Thus, there was a stronger relationship in timing of intra-seasonal events compared to timing of inter-seasonal events (autumn–spring).

Stable isotopes

GLM analyses relating spring migration schedules to local habitat conditions at the non-breeding areas and previous breeding effort revealed that $\delta^{13}C$ values were strong predictors only for the non-breeding site departure (Fig. 5, Table 1). There was no indication that either of the factors carried over to influence the timing of the following breeding (Fig. 5d, Table 1d).

Discussion

In this study, we linked events across the entire annual cycle in the long-distance migratory collared flycatcher and evaluated carry-over effects of parental investment and local non-
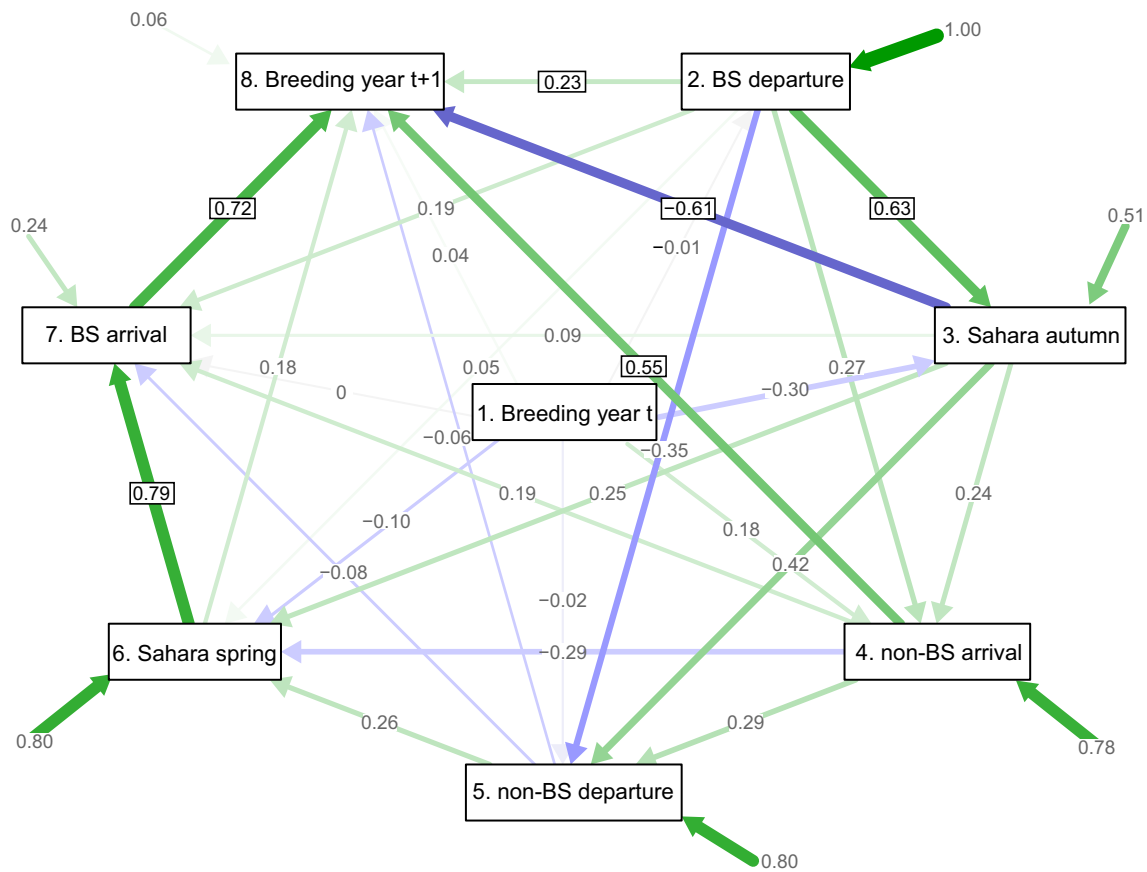
Fig. 3 Path diagram of the model showing causal relationship between different parts of the annual cycle in collared flycatchers. Arrows indicate casual effects of one event (independent variable) on the subsequent events (dependent variables). Green arrows indicate positive effects, blue arrows—negative effects. The width and colour intensity of the arrows represent the values of standardized path coefficients. The significant interactions are highlighted with standardized path coefficients given in boxes

breeding conditions. Our hypothesis that the experimental increase of brood size would result in delayed autumn migration was not supported as we found no difference in migration schedules between the males whose brood sizes were reduced and males with enlarged brood sizes. However, when looking at the absolute parental investment (measured as the total number of fledglings), we found that higher parental investment was associated with delayed autumn migration, shorter non-breeding residency, and advanced spring migration. The magnitude of carry-over effects from one stage to another faded with increasing timespan between the stages along the annual cycle and the non-breeding period served as a buffer not allowing for carry-over effects to accumulate. Hereof, we also showed that neither local non-breeding conditions nor the previous breeding effort was linked to the timing of spring migration and the following breeding period.

Reproduction is an energy- and time-consuming process. Rearing a lower number of chicks should be less energy-demanding, but the total amount of time necessary to complete the breeding cycle should be similar. Previous experimental manipulations of clutch size in the collared flycatcher have shown that an enlarged clutch carries consequences for male secondary

sexual traits and results in the reduction of subsequent fecundity (Gustafsson and Sutherland 1988; Gustafsson et al. 1995). A study of Cory's shearwaters showed that experimentally induced breeding failure resulted in the early onset of autumn migration (Catry et al. 2013). Experimentally manipulated birds were freed from energetic and time-dependent costs of reproduction alike and theoretically could engage in southbound migration before their conspecifics had completed their respective breeding cycles. These results contradict our findings since we did not observe differences in autumn migration schedules between our two experimental groups. This raises the question of whether changing brood size by one chick in a multi-egg laying species carries consequences for the annual schedules of migrants. It could be that the total number of chicks fledged may better reflect the costs of breeding if they carry over to the subsequent annual cycle phases. Another reason for the lack of unambiguous differences between the two experimental groups may be the limited sample size in our study. Furthermore, we looked only at male annual schedules in relation to our experimental manipulation and parental investment through provisioning of young may differ between the sexes.
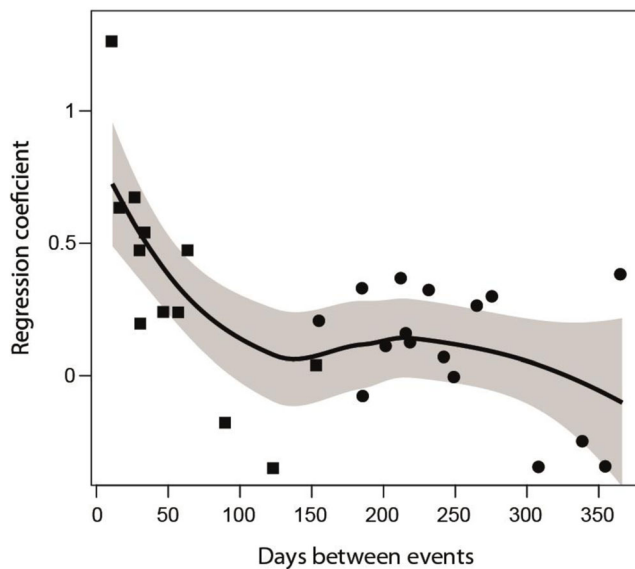
Fig. 4 The strength of the "domino effect" between consecutive parts of the annual cycle expressed as the relationship between regression coefficients of the timing of different parts of the annual cycle and the timespan between the events. Squares (■) denote regression coefficients of intra-seasonal events and circles (●) denote regression coefficients of inter-seasonal events. The black line depicts fitted loess curve ± SE (shaded area)

Table 1 Summary statistics of models showing a relationship between the timing and duration of spring events and non-breeding conditions (δ^{13}C) and parental investment (above or below the population average) in the previous breeding season

	Estimate	SE	t	p
(a) Departure non-breeding site (df = 15)				
Intercept	194.6	57.88	3.36	< 0.01
δ^{13}C	6.85	3.00	2.29	0.04
Breeding effort$_{(below)}$	5.42	4.56	1.19	0.25
(b) Sahara crossing spring (df = 15)				
Intercept	143.15	43.37	3.3	< 0.01
δ^{13}C	2.39	2.25	1.06	0.3
Breeding effort$_{(below)}$	10	3.42	2.93	0.01
(c) Arrival breeding site (df = 15)				
Intercept	135.19	45.3	2.98	0.01
δ^{13}C	1.18	2.35	0.5	0.62
Breeding effort$_{(below)}$	4.71	3.57	1.32	0.21
(d) Onset of egg laying year $t + 1$ (df = 22)				
Intercept	124.67	63.75	1.96	0.06
δ^{13}C	0.03	3.31	0.01	0.99
Breeding effort$_{(below)}$	3.03	3.94	0.77	0.45
(f) Timespan arrival breeding site–onset of egg laying (df = 14)				
Intercept	− 54.95	98.56	− 0.56	0.59
δ^{13}C	− 6.08	5.12	− 1.19	0.25
Breeding effort$_{(below)}$	0.15	7.72	0.02	0.98
(e) Timespan departure non-breeding site–onset of egg laying (df = 14)				
Intercept	3.84	47.92	0.08	0.94
δ^{13}C	− 0.44	2.49	− 0.18	0.86
Breeding effort$_{(below)}$	0.82	3.75	0.22	0.83

When looking at parental investment as the total number of fledglings, we found a negative effect of the absolute number of chicks fledged on autumn migration schedules. Higher parental investment has been reported to delay autumn migration in numerous water birds, e.g. Cory's shearwater (Catry et al. 2013), brent goose *Branta bernicla* (Inger et al. 2010), and black-legged kittiwake *Rissa tridactyla* (Bogdanova et al. 2011), but there is little evidence of this effect in passerines (but see Mitchell et al. 2012). Theoretical models indicate that the onset of migration highly depends on an individual's body condition (McNamara et al. 1998). It is important to note that collared flycatchers undergo a complete body moult before commencing autumn migration (Stresemann and Stresemann 1966). Feather moult is a highly energetically demanding process and there must be trade-offs between shortening the duration of moult and increasing the quality of newly grown feathers (Vágási et al. 2012). It is likely that the energy expenditure of parental care has consequences which influence moult, further affecting the onset of autumn migration. Such interactions could explain why the individuals fledging more young departed later from the breeding sites.

Interestingly, we found no significant relationship between the timing of breeding and other parts of the annual cycle (Fig. 3, Online resources 7). Mitchell et al. (2012), Saino et al. (2017), and van Wijk et al. (2017) reported positive correlation between the completion of breeding and autumn migration departure in savannah sparrows *Passerculus sandwichensis*, barn swallows *Hirundo rustica*, and hoopoes

Upupa epops, respectively. Similarly, an elongated breeding period was associated with delayed autumn departure in Manx shearwaters *Puffinus puffinus* (Fayet et al. 2016), highlighting the time-dependent costs of reproduction. Late-nesting wood thrushes *Hylocichla mustelina* initiated their post-breeding moult later than early-breeding conspecifics, possibly resulting in delayed departure for autumn migration, but no effect was found on the timing of arrival in the tropics (Stutchbury et al. 2011). In wood thrushes, late breeding was also associated with higher reproductive success. The positive relationship between high breeding effort and delayed autumn departure coincides with our findings. Thus, energetic and time-dependent carry-over effects of parental investment could be more important determinants for the onset of autumn departure than the timing of the onset of breeding.

A pivotal finding in our study was that higher parental investment not only delayed autumn migration schedules, but was also associated with shorter non-breeding residency neglecting the delays in autumn migration schedules. Fayet et al. (2016) have shown that experimentally increasing the duration of provisioning for young delayed autumn migration

departure and resulted in a shorter non-breeding residency period in Manx shearwaters. The length of the non-breeding residency period might not be as time-constrained as other parts of the annual cycle and thus could be a subject to adjustments if needed. We have shown earlier that collared flycatchers breeding in Sweden spend ca. 10% less time at the non-breeding sites than birds from our study site in the Czech Republic, suggesting more relaxed schedules and the buffering effect of this period on other parts of the annual cycle (Briedis et al. 2016).

We also observed a pronounced "domino effect" (Piersma 1987) between consecutive parts of the annual cycle. Such a pattern is expected to arise under the time-minimization migration strategy (Hedenström 2008). When adopting this strategy, individual birds should travel as fast as possible given their body condition and environmental conditions, therefore making it difficult to overcome the costs of being late at a particular stage within a single migration season. However, we also observed that the relationship was stronger between annual cycle stages directly following each other and

gradually faded along the annual cycle with increasing timespan between the stages (Fig. 4). The strong links found within rather than across migration seasons suggest that the domino effect and carry-over effects from the breeding season can be overcome during the non-breeding season. Collared flycatchers that had higher breeding effort migrated later in autumn, but earlier in spring, supporting the hypothesis that non-breeding period buffers accumulation of carry-over effects. Van Wijk et al. (2017) also reported strong relationship between the timing of annual stages directly following each other in hoopoes. The dependencies of the timing decreased with increasing timespan between the annual cycle events. Similarly to our results, van Wijk et al. (2017) found the strongest relationship between the timing of breeding site arrival and the onset of breeding, highlighting the importance for timely spring arrival (Kokko 1999).

Conditions at the non-breeding areas have been shown to influence the spring migration schedule and following breeding period in several species (Marra et al. 1998; Norris et al. 2004; Saino et al. 2004; Studds and Marra 2005; Tonra et al.

Fig. 5 Relationship between $\delta^{13}C$ values of collared flycatcher feathers grown at the African non-breeding grounds and the timing of spring events. The timing of events is given as Julian dates from 1 January (**a**–**d**), and timespans between events in number of days (**e**–**f**). Diamonds (♦) denote data from 2013 to 2014 and circles (●) denote data from 2014 to 2015 non-breeding seasons. Linear models are depicted by solid lines with 95% CI (shaded area)
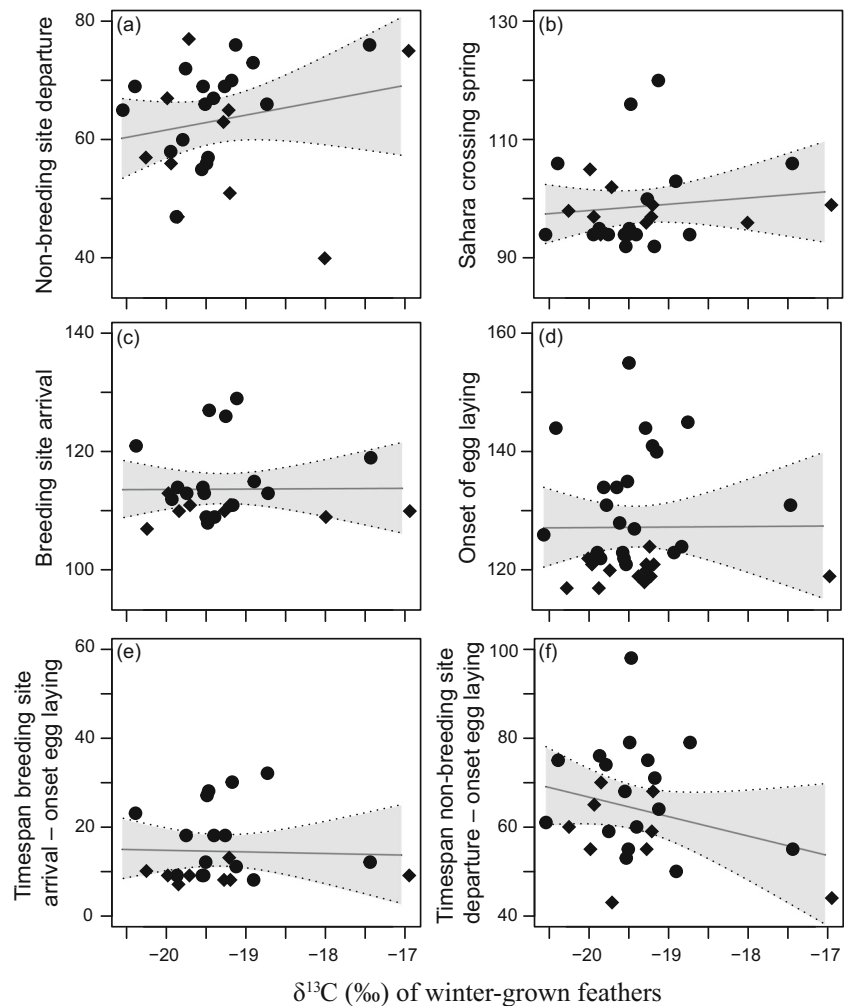
2011; Rockwell et al. 2012; Paxton and Moore 2015; López-Calderón et al. 2017), while we found no such links in our study system (Fig. 5). Pedersen et al. (2016) also found no carry-over effects of local non-breeding habitat conditions on the late stages of spring migration and the following breeding period in red-backed shrikes *Lanius collurio* using $\delta^{13}C$ values as a proxy. Similarly, no carry-over effects of non-breeding habitat quality were found in yellow warblers *Setophaga petechial* (Drake et al. 2014), magnolia warblers *S. magnolia* (Boone et al. 2010), and Hudsonian godwits (Senner et al. 2014). Such contradicting results across species suggest that carry-over effects of non-breeding conditions may not be limiting for all species and populations, or may vary in their detectability via isotope signatures in winter-grown tissues.

Spring migration and the following breeding season might be affected by a combination of factors, like previous breeding effort and conditions experienced during the non-breeding residency. In the present study, we showed that the previous breeding effort and local non-breeding habitat conditions had negligible influence on the timing of the following breeding period. Similarly, Bogdanova et al. (2011) reported no differences in spring migration schedules caused by previous breeding experience. Ouwehand and Both (2017) demonstrated that the rank order of birds from autumn migration was disrupted during the non-breeding period and the timing of spring migration was not related to the timing of autumn migration in the closely related pied flycatchers *Ficedula hypoleuca*. On the contrary, long-lasting carry-over effects of previous breeding effort have been shown to influence following breeding attempts in long-lived migratory birds (Inger et al. 2010; Catry et al. 2013). Carry-over effects from various parts of the annual cycle may play different roles in population dynamics of species with different life history strategies. Therefore, it is important to consider full annual cycles to gain a better understanding of carry-over effects operating in animal populations.

It is likely that the recent decline of long-distance migrants (Vickery et al. 2014) has been caused by the complex interaction of events and processes taking place at temperate breeding grounds, tropical non-breeding areas and during migration between them. Our results indicate that energetic and time-dependent costs of reproduction play a key role in altering autumn migration schedules and defining individual variation via carry-over effects but we also highlight the importance of non-breeding period as a buffer for further accumulation of the carry-over effects. Linking events throughout the entire annual cycle can give us an in-depth insight into underlying processes driving animal population dynamics. This may open new perspectives in our understanding of the ecology of migratory animals and further be of service to conservation efforts. We hope that our study will stimulate more comprehensive animal ecology research with respect to full annual cycles.

Compliance with ethical standards

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

Ethical approval This study was carried out in accordance with the Ethical Committee of Palacký University and approved by the Ministry of Education, Youth and Sports of the Czech Republic (Licence number: MSMT-56147/2012-310). All applicable institutional and national guidelines for the care and use of animals were followed.

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