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Authors	Tomotani, Barbara M.;van der Jeugd, Henk;Gienapp, Phillip;de la Hera, Iván;Pilzecker, Jos;Teichmann, Corry;Visser, Marcel E.
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Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird

Barbara M. Tomotani[1] | Henk van der Jeugd[1,2] | Phillip Gienapp[1] | Iván de la Hera[1,3] | Jos Pilzecker[4] | Corry Teichmann[1] | Marcel E. Visser[1]

[1]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

[2]Dutch Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

[3]School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[4]Vogelwerkgroep Arnhem, Leuvenheim, The Netherlands

Correspondence
Barbara M. Tomotani, Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands.
Email: b.tomotani@nioo.knaw.nl

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Abstract

Shifts in reproductive phenology due to climate change have been well documented in many species but how, within the same species, other annual cycle stages (e.g. moult, migration) shift relative to the timing of breeding has rarely been studied. When stages shift at different rates, the interval between stages may change resulting in overlaps, and as each stage is energetically demanding, these overlaps may have negative fitness consequences. We used long-term data of a population of European pied flycatchers (*Ficedula hypoleuca*) to investigate phenological shifts in three annual cycle stages: spring migration (arrival dates), breeding (egg-laying and hatching dates) and the onset of postbreeding moult. We found different advancements in the timing of breeding compared with moult (moult advances faster) and no advancement in arrival dates. To understand these differential shifts, we explored which temperatures best explain the year-to-year variation in the timing of these stages, and show that they respond differently to temperature increases in the Netherlands, causing the intervals between arrival and breeding and between breeding and moult to decrease. Next, we tested the fitness consequences of these shortened intervals. We found no effect on clutch size, but the probability of a fledged chick to recruit increased with a shorter arrival-breeding interval (earlier breeding). Finally, mark–recapture analyses did not detect an effect of shortened intervals on adult survival. Our results suggest that the advancement of breeding allows more time for fledgling development, increasing their probability to recruit. This may incur costs to other parts of the annual cycle, but, despite the shorter intervals, there was no effect on adult survival. Our results show that to fully understand the consequences of climate change, it is necessary to look carefully at different annual cycle stages, especially for organisms with complex cycles, such as migratory birds.

KEYWORDS

breeding, European pied flycatcher, *Ficedula hypoleuca*, fitness, mark–recapture, migration, moult, recruitment

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1 | INTRODUCTION

During the past decades, increases in temperature caused by global warming have affected biological systems in various ways (Walther et al., 2002). One of the most evident effects is the alterations in phenology or timing of annual events across different animal and plant taxa (Brown, Li, & Bhagabati, 1999; Crick, Dudley, Glue, & Thomson, 1997; Parmesan, 2006; Parmesan & Yohe, 2003). For example, timing of flowering, breeding and migration are some of the events known to have advanced in response to the increased temperatures (Charmantier & Gienapp, 2014; Crick et al., 1997; Parmesan, 2007; Thackeray et al., 2016). Such changes make important to understand whether shifts in timing are fast enough to track changes in the optimal timing for stages to occur (Visser, 2008; Visser & Both, 2005).

The use of standardized long-term datasets, especially of the same population, has allowed researchers to track how organisms respond to climate change and to identify potential causes and consequences of these responses (Visser, 2008, 2016). A relatively large number of studies have reported the effects of climate change on timing of breeding, particularly in birds (e.g. Both et al., 2004; Crick et al., 1997). A few studies also have explored if optimal breeding dates shifted with climate change and if animals were able to respond accordingly (Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016; Plard et al., 2014; Reed, Grøtan, Jenouvrier, Sæther, & Visser, 2013; Reed, Jenouvrier, & Visser, 2013; Stoks, Geerts, & De Meester, 2014; Visser, Holleman, & Gienapp, 2006). These studies are crucial to our understanding of whether species can adapt to such rapid changes in the environment or not (Gienapp et al., 2013).

While some organisms present quite simple annual cycles with only a breeding/nonbreeding transition, others have much more complex cycles (Jacobs & Wingfield, 2000; Wingfield, 2008). For example, many species of birds and mammals also migrate, moult their plumage/pelage and/or hibernate. These additional stages of the annual cycle are likewise reported to shift due to climate change (Both & te Marvelde, 2007; Charmantier & Gienapp, 2014; Morrison et al., 2015; Ozgul et al., 2010; Zimova, Mills, & Nowak, 2016). However, all of these stages (including breeding) are not necessarily affected in the same way by changes in temperatures (Both et al., 2009; Serreze & Francis, 2006; Visser, 2008; Visser et al., 2006). Moreover, because temperatures do not change at the same rate in time or space (Easterling et al., 1997; Serreze & Francis, 2006; Stocker et al., 2013; Vose, Easterling, & Gleason, 2005), it is possible that within the same population, different parts of the annual cycle also change at different rates in response to the unequal increase in temperatures (Crozier et al., 2008). In this scenario, we can expect increased or decreased intervals between annual cycle stages. Therefore, climate change will also alter the time constraints across the annual cycle. This could be particularly problematic for organisms with complex annual cycles since they are supposedly more time constrained than organisms with simpler cycles (Jacobs & Wingfield, 2000; Wingfield, 2008).

Analyses showing how intervals between annual cycle stages are changing are rare in comparison to studies dealing with changes in single stages. To detect such patterns, it is necessary to collect long-term data of not only one but multiple annual cycle stages within a population. It has been reported that some species have gained more time for key intervals. For example, yellow-bellied marmots (*Marmota flaviventris*) advanced both the termination of hibernation and weaning, resulting in more time for growth and fattening for their offspring (Ozgul et al., 2010). In red deer (*Cervus elaphus*), however, reproductive stages of males and females unequally advanced, suggesting that males are unable to track advancements in oestrus of females. Moreover, the termination dates of males' rut advanced more than the initiation dates, which resulted in a shorter breeding window and likely reduced breeding performance (Moyes et al., 2011). Barnacle geese (*Branta leucopsis*) that rapidly expanded their breeding range to temperate areas more than doubled the interval between breeding and moult, resulting in changed body mass dynamics (Eichhorn, van der Jeugd, Meijer, & Drent, 2010; Van der Jeugd et al., 2009). Finally, long-term data on date of arrival and breeding of migratory birds suggest that timing of breeding and migration may not respond the same way to climate change. There are reports of both shorter (Both & Visser, 2001) and longer (Ahola et al., 2004; Valtonen, Latja, Leinonen, & Pöysä, 2016) intervals between arrival and breeding. Thus, for animals with more complex annual cycles, the assessment of the impacts of climate change becomes considerably more challenging, because unequal changes in the timing of stages may impose fitness costs (e.g. reduce the interval between moult and breeding thereby causing more overlap; Hemborg & Lundberg, 1998).

Here, we analysed how climate change affects the timing of different annual cycle stages of a long-distance migratory bird, the European pied flycatcher. We used long-term data (1980–2015) collected from a Dutch population of flycatchers, looking at three important annual cycle stages: spring migration (arrival dates), breeding (egg-laying and hatching dates) and postbreeding moult onset. Furthermore, we included initial information on the variability in timing of autumn migration. Apart from describing the changes in patterns through time, we also investigated the potential environmental causes and fitness consequences of the variation in timing of these important stages.

2 | MATERIALS AND METHODS

2.1 | Study species and study area

Pied flycatchers (*Ficedula hypoleuca* ([Pallas], 1764); Muscicapidae) are long-distance migratory birds that reproduce in Europe and winter in West Africa (Ivory Coast in the case of our study populations; Ouwehand et al., 2016, see also geolocator data in results). These birds readily accept artificial nest boxes and have low nest desertion rates, allowing the precise monitoring of their reproduction. We used long-term data from the breeding population of the forests of the Hoge Veluwe National Park (the Netherlands; 5°51′E 52°02′N). Forested areas in the park are dominated by pedunculate oaks (*Quercus robur*), northern red oaks (*Quercus rubra*), Scots pines (*Pinus sylvestris*), Larches (*Larix* spp.) and birches (*Betula* spp.). For more than 60 years nest boxes are provided year-round in an area of 171 ha, they are occupied in spring by cavity-nesting passerines such as pied

flycatchers, great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), nuthatches (*Sitta europaea*) and coal tits (*Periparus ater*). Voucher material of this pied flycatcher population was deposited in the ornithology collection of the Naturalis Biodiversity Center (Leiden, the Netherlands) under the inventory numbers RMNH 592347, RMNH 592348 and RMNH 592349.

2.2 | Data collection

Data on timing of breeding (egg-laying, chick hatching) was collected for this pied flycatcher population since 1959, timing of migration (arrival dates and, more recently, departure dates) and timing of moult since 2005. We also obtained 35 years of arrival data of pied flycatchers breeding in a nearby location (from the Vogelwerkgroep Arnhem, the dataset used in Both & Visser, 2001, including recent years). For our final dataset, we used 35 years of egg-laying dates, chick-hatching dates, female arrival (nest building) dates (to match the number of years available for arrival dates from the Arnhem dataset), 11 years of male arrival dates collected on our study population, 9 years of moult onset dates and 3 years of departure dates and arrival at the wintering grounds.

2.2.1 | Timing of breeding

Data for timing of breeding were available for 1959 (when the first pied flycatchers started to breed in our study area) and then from 1962 to 2015, but as mentioned above, we used data only from 1980 until 2015 because male arrival data (Arnhem) were available from that year onwards. Every year nest boxes were checked weekly from early March until late July, and information on the progression of nest building and on the date when first eggs were laid was collected. Since eggs are laid in one-day intervals and pied flycatcher clutches typically have six eggs in the Netherlands, we had accurate measurements of individual laying dates. Pied flycatcher females typically incubate for 12–14 days, usually starting at the date when the last egg is laid; thus, after around 13 days of incubation, nests were inspected daily to identify the hatching dates of chicks. In some cases when we missed the actual hatching date, the date could be determined by ageing the chicks based on size and plumage development. When nestlings were 7 days old, they were identified with a uniquely numbered aluminium ring and parents were also caught and identified.

2.2.2 | Arrival dates

From 2005 until 2015, individual arrival date of males was assessed by daily scoring newly arriving males in our study area from early April onwards (Both, Bijlsma, & Ouwehand, 2016; Potti, 1998; Visser et al., 2015). Birds choose a territory upon arrival and advertise their cavity or nest box to the females by singing continuously at or close to the potential nest site. Two or three trained observers walked independently pre-established routes covering the whole study area and visiting all boxes. Routes and direction of the routes were alternated daily among observers in order to prevent any potential bias among them. Detected birds were described in terms of plumage and aluminium/colour ring combinations. Male pied flycatchers display relatively large individual variation in plumage characteristic, which, combined with colour ring combinations, allows an initial recognition in the field without the need of capturing the birds. In our study site, plumage coloration varied from female-brown or light grey to almost entirely black with intermediates of increasing blackness (Drost, 1936). The forehead white patch also varied in size, from absent to a large patch covering most of the forehead, and also in shape from two distinct dots to a rectangular-shaped patch. We associated singing males to the closest nest box in the vicinity. During the chick-rearing phase, those males were caught and described again in terms of plumage characteristics and ring combination. In most years (except 2005 and 2012), we also collected data on "bachelors," that is, males still singing 1 week after the first eggs were found. These latter males were captured, identified and blood sampled and a few became breeding birds later in the season.

Apart from this more detailed dataset on individual arrivals (henceforth "observed arrival dataset"), we also had a second dataset from the Vogelwerkgroep Arnhem, a bird observation group that collected data on arrival dates of male pied flycatchers from 1980 to 2015, allowing the analyses of much longer term temporal shifts. This data collection occurred around 10 km from our study area and there was a high correlation (Pearson correlation coefficient = 0.83, 95% CI [0.45, 0.95], n = 11 years; Figure S1) between their mean arrival data and the mean arrival dates of the observed arrival dataset. We are confident that this is a reliable and representative dataset for longer term trends in the studied pied flycatcher population; however, because the intercept was larger than 0 and the slope not equal 1 (slope: 0.52 ± 0.12; intercept: 6.73 ± 2.87; $p < .01$, Figure S1), we used a calculated arrival date based on the Arnhem dataset (henceforth "calculated arrival dataset"). We estimated the arrival dates of the males in the Hoge Veluwe National Park for the years we do not have data (before 2005) using the slope and intercept obtained in the relation between Arnhem and Hoge Veluwe arrival dates as follows: Calculated arrival = Intercept + Slope × Arnhem arrival. This calculated arrival date was then used in subsequent statistical analyses.

Female individual arrival date was not obtained directly as in the males' case. Instead, we used data from the start of nest building as a proxy, following the same procedure of Visser et al.(2015). Female pied flycatcher nest building reflects well their arrival dates as shown in Visser et al.(2015) since they choose a male and start nest building shortly after arriving (Dale, Rinden, & Slagsvold, 1992; Dale & Slagsvold, 1995). Nest building of individual pied flycatcher females was collected in our study area from 1980 to 2015, allowing the analysis of potential long-term shifts in annual timing of arrival of females.

2.2.3 | Timing of moult

From 2005 to 2015, we had information on whether birds were moulting or not when they were caught for identification (when they had 7-day-old chicks). From 2009 to 2015, we also had information on moult score, that is, which feather was dropped and how much

its replacement feather had grown. Finally, from 2013 to 2015, we had the actual date when the first feather was dropped for most of the breeding birds (Tomotani et al., submitted). We could, thus, use the latter to define the accuracy of each type of measurement. We only used male data for this, since for most years we only had data on one or two moulting females. In 2007 and 2012, no information on moult was collected, and thus, we could not use these years in our analysis.

We used the R "moult" package (Erni, Bonnevie, Oschadleus, Altwegg, & Underhill, 2013) to calculate the population average moult onset based on two analyses: (1) using presence/absence data (moulting/nonmoulting individuals), we calculated the annual average starting date with a "probit model," a generalized linear model with a binomial distribution and probit link function (Erni et al., 2013). (2) Using the moult scores of different individuals (based on which feather was missing or re-growing and how much it had grown) converted to a value of new feather mass grown (Dawson & Newton, 2004; Erni et al., 2013) and regressing a line through the values of all individual new feather mass grown to obtain the population moult onset per year (with feather mass as response and date as explanatory variable). When we compared these values with the averages of the actual observed individual moult onsets, we noticed that the first presence/absence model provided a better estimate of moult onset than the feather mass regression (2013: observed = 76.93 ± 1.22, presence/absence model = 73.09 ± 0.05, feather mass regression = 59.22 ± 3.69; 2014: observed = 71.70 ± 1.15, presence/absence model = 66.65 ± 0.04, feather mass regression = 61.81 ± 2.30; 2015: observed = 74.42 ± 1.02, presence/absence model = 71.14 ± 0.17, feather mass regression = 62.81 ± 4.39). This was probably due to the fact that moult scores were mostly collected early in the season, with very few individuals with large moult scores, making the linear regression less reliable. It is also important to mention that we could use this "probit model" because we have experimental data showing that, within a year, the male moult onset is independent of the termination of breeding. Thus, in a given year, most individuals moult more or less on the same calendar day (Tomotani et al., submitted.). Therefore, it is not so problematic that we have to use mid- to late breeding birds to calculate the populational moult onset in the present paper as the majority of early breeders would not be moulting when captured at the standardized chick-day 7. We, thus, used the 9 years of moult onset based on data of presence/absence of moulting birds; even when we had the exact onsets, in order to have comparable data over years.

2.2.4 | Departure dates and arrival at African wintering grounds

From 2013 to 2015, a subsample of the males (38 in 2013, 30 in 2014 and 30 in 2015) was equipped with light-level geolocators (Intigeo-W50, Migrate Technology Ltd, Cambridge, UK) using a leg loop harness built with an 0.7-mm elastane cord and adjusted to each bird with a knot in the posterior mounting tube, between the device's mounting loops.

Geolocators were recovered in the subsequent years (2014–2016) when birds returned for breeding and 26 tracks (out of 98, 26%) could be analysed (12 from 2013, seven from 2014 and seven from 2015). Data were processed similarly to Åkesson, Klaassen, Holmgren, Fox, and Hedenström (2012), but due to the imprecision of latitude data, we only used the information collected for longitude (inferred from local solar noon/midnight). Twilight transitions were determined using TransEdit (British Antarctic Survey, Cambridge) with a single threshold value of five, minimum daylight periods of 1 hr and minimum night period of 4 hr. Positions were obtained using the software BirdTracker, which gave us two positions per day (noon and midnight). Data were then visually inspected to detect large changes from the study area longitude, indicating a departure from breeding grounds and then arrival at the wintering grounds, since pied flycatchers move to the west, following the African coast during autumn migration (Ouwehand et al., 2016).

If the logger was still working upon recapture and a full track could be downloaded, we used the data corrected for clock drift; otherwise, clock drift effects on longitude were tested as described in (Ouwehand et al., 2016). There was no noticeable clock drift effect (always <1 min).

2.2.5 | Temperatures

Daily temperature values were collected from the Dutch meteorological institute database (KNMI—https://www.knmi.nl/nederland-nu/klimatologie/, accessed February 2016) for the Dutch temperatures and from the US National Oceanic and Atmospheric Administration database (NOAA—ftp://ftp.ncdc.noaa.gov/pub/data/gsod/, accessed February 2016) for African temperatures. Temperatures from the NOAA database were converted from Fahrenheit to Celsius to match the KNMI database.

For the Dutch weather variables, we used data from the Deelen weather station which is directly adjacent to the study area. For African temperature data, we used information on the pied flycatchers' wintering location using the data from the geolocators that we deployed and also from the literature (Ouwehand et al., 2016) to identify the closest weather station from their wintering grounds. Pied flycatchers from the Netherlands winter in the Ivory Coast, where Daloa (6°27′W 6°53′N) is the closest weather station with a reasonable amount of data. Because the dataset still had large gaps, we also used information from two other nearby locations (Gagnoa, 5°56′W 6°08′N, and Yamoussoukro, 5°17′W 6°49′N). We still ended up with a few gaps in the data, which we interpolated using the average of data at the boundaries of the gap. This was seen as a minimal issue due to the way these data are used in the statistical analysis (see section "causes of variation in timing"). We obtained complete data from 1980 until 2015 for Dutch temperatures.

We also obtained data on photoperiodic variation of the Netherlands from the NOAA. We considered the civil twilight as the boundary of the effective light phase important for the birds (Gwinner, 1989). Because photoperiodic variation of the breeding and wintering grounds has a high correlation and varies in the same

direction, it was not necessary to obtain and model day length data for Africa separately.

2.2.6 | Adult survival

We used two datasets with data on individual capture histories; one with 11 years for which we had data on the average interval between breeding and moult for each year (2005–2015, 1,252 individuals) and a second one with 35 years for which we had data on the average interval between arrival and breeding for each year (1980–2015, 3,887 individuals). Individuals were not included in the analyses when nestlings, but only when breeding for the first time. Thus, we did not include the nestling survival in this analysis. We used these datasets to estimate adult survival and recapture probability and whether the change in the two intervals (arrival breeding and breeding moult) had an effect on adult survival, while taking into account effects of sex, capture occasion (two categories: first or later), and age at first capture (three categories: (1) second calendar year birds (hereafter **SY**), ringed as nestling in the previous year; (2) after second calendar year birds (**ASY**), ringed as nestling two or more years prior to the capture; and (3) unknown age (**Unknown**), for the birds that were not ringed as nestlings and consequently their age (SY or ASY) could not be reliably determined.

2.3 | Data analysis

All analyses were performed in R version 3.2.1 (R Core Team, 2015) and focused on the annual means of each annual cycle stage. To define the minimal models, we always used backwards model selection, dropping nonsignificant terms in each step. Survival analyses were performed with program MARK (White & Burnham, 1999).

2.3.1 | Shifts in timing

We used simple and multiple regressions fitting year as linear and quadratic terms to test for shifts of the annual average value of each annual cycle component across years (including both longer-calculated and shorter-observed datasets for male arrival dates). Then to test whether there has been any change in the amount of days available between arrival, breeding and moult, we calculated the differences between arrival and breeding dates (arrival date of males and females and egg-laying dates) and between chick fledging date and moult onset. Predicted chick fledging was calculated from egg-laying dates by adding 6 days of egg laying, 12 days of incubation and 15 days of chick care until fledging. In all analyses involving timing of moult, we used the standard errors of the estimates as weights (weight = $1/SE$) in weighted analysis to account for the prediction error of the moult dates.

We also tested whether the different slopes that we obtained from the separate regressions were significantly different from each other. We used multiple regression analyses with date as the response variable and the interaction of annual cycle stage (arrival, moult, egg-laying and hatching dates) and year (linear and quadratic) as the explanatory variables. We ran two separate analyses, one including all stages, starting in 1980 but with missing values for some stages in earlier years, and a second one only including those stages that we had complete data since 1980 (calculated arrival, egg-laying and hatching dates).

2.3.2 | Causes of variation in timing

We tested whether the variation of each of the annual cycle's components (with the exception of hatching dates, which depend mostly on egg-laying dates) could be explained by variation in temperature cues alone or in interaction with changes in day length. As in other analyses we also used the annual means of each stage here. Following the method described in Gienapp, Hemerik, and Visser (2005), we used proportional hazard models (Cox, 1992) implemented in the R "survival" package (Therneau, 2015) to model the relationship between the climatic event and the occurrence of the event. Proportional hazard models calculate the daily probability of an event to occur. They, therefore, allow including time-dependent variables, that is, variables that change their value during the time an individual is "at risk." Modelling effects of weather variables on annual cycle stages, as arrival date, is biologically more realistic than using fixed time windows over which these variables are averaged (Gienapp et al., 2005). The value of this time-dependent weather variable at day t was calculated as the average over periods of various lengths (5, 10, 15, 20, 25 or 30 days) ending at day t (See Table S3 for more details). For African weather variables, we also used lagged shifting windows of the same length (of 20 days) but ending 20, 40, 60 or 80 days before day t (Table S3). We defined intervals that we deemed biologically significant; thus African temperatures were only tested for arrival dates because it is unlikely that African temperatures would have affected the egg-laying dates and moult onset, as the birds were already in the Netherlands. Therefore, in total, we compared 24 possible combinations for arrival dates, five for egg-laying dates and five for moult (Table S3). Identification of the best period was done by comparing the log-likelihoods of the different models; however, their close values made such selection challenging in some cases (Table S3). After the best window was defined for each stage, we tested what temperatures significantly explained the variation in timing of different stages using different proportional hazard models for each annual cycle stage (compared with likelihood ratio tests). We fitted African temperatures (with and without lag), Dutch temperatures and the interactions of day length and Dutch temperature and day length and lagged African temperature, depending on the stage. The temperatures selected in the best models for each stage were also fitted against year as a trend (linear and quadratic) to test whether these temperatures also changed across years.

2.3.3 | Consequences of variation in timing

We used multiple regressions to test whether the intervals between the arrival and breeding dates and breeding date and moult onset

explained the fitness components. We looked at two components related to breeding success (the annual average clutch size and the annual proportion of fledged chicks that recruited per year) and at adult survival.

We used generalized linear models with binomial (Bernoulli) response and logit link function to test whether the annual proportion of fledged chicks that recruited was explained by either the annual difference of the interval between arrival and breeding or the interval between breeding and moult. For the interval between arrival and breeding, we only used the longer-calculated arrival dataset, since it correlated with the shorter (Hoge Veluwe) dataset, showing a similar pattern, but included many more years. Clutch size was similarly analysed using multiple regressions testing for year and interval effects.

To analyse adult survival, we performed a Cormack–Jolly–Seber (CJS) mark–recapture analysis using the software MARK (White & Burnham, 1999). The CJS model estimates annual local survival probabilities (Φ) based on live recaptures only, while controlling for capture probability (p). In this analysis, we used Akaike's information criterion (AIC_c) for the model selection and goodness of fit was tested using the bootstrap procedure in the MARK software. We first defined the best model including time ("year" as a factor), capture occasion (first or later), sex (male or female) and age at first capture (SY, ASY or unknown), for both survival and recapture probabilities. In the most complex models, birds that were in their SY or of unknown age at their first capture moved to the ASY age class in the following year and remained in this age class for the rest of the years. Birds first caught in their ASY never moved to another age class in subsequent captures. We could not use plumage characters as ageing criteria because they were not deemed as precise enough and also not always recorded for all captured individuals. However, in the simplified models that did not include the age at first capture, the capture occasion variable only explained differences between the first or later captures of the same individual independent on their age. We first fitted the model with the interaction between time, capture occasion and the interaction between sex and age at first capture and then used backwards comparison to define the best model. After the best model was defined, we replaced the time variable by the interval between arrival and breeding (longer dataset) or breeding and moult (shorter dataset) and compared these new models with the best model to investigate specifically whether variation in survival among years could, in fact, be explained by variation in these intervals.

3 | RESULTS

3.1 | Shifts in timing

Annual means of male and female arrival (nest building) date, egg-laying date and date of moult onset shifted at different rates, as shown by the significant interaction between stage and year both when all stages were considered ($F_{5,152} = 6.74$, $p < .01$; Table S1) and also when we only included stages for which we had data since 1980 ($F_{3,136} = 8.12$, $p < .01$; Table S1). There were no significant advancements for male arrival (calculated arrival, estimate = -0.03 ± 0.03 Table S1, linear slope not significant in post hoc test, Table S2) and male moult onset advanced faster than the other stages (estimate = -1.11 ± 0.29; significant slope $F_{1,7} = 12.90$, $p = .01$, Tables 1, S1 and S2), both in the long- and short-term dataset. The rates of advancements for (observed) arrival dates of the males, arrival date of the females, egg-laying dates and hatching dates were strikingly similar (observed male arrival = -0.32 ± 0.28, no significant slope; arrival females = -0.30 ± 0.05, egg-laying = -0.30 ± 0.05, hatching = -0.30 ± 0.05, significant slopes $F_{1,34} = 29.55$, $F_{1,34} = 48.8$, $F_{1,34} = 29{,}72$, respectively, $p < .01$, Tables 1 and S2).

Because arrival date, egg-laying dates and moult dates shifted unequally, we calculated the interval between each stage and tested whether they changed across years. As expected from the previous analyses, the intervals between male arrival and breeding and between breeding and male moult changed across years. In contrast, the interval between female arrival (nest building) and egg-laying dates did not significantly change since 1980 (Table S2, Figure 1e). The interval between male (calculated) arrival and egg-laying date changed nonlinearly: it became shorter until around 2008 and then started to increase again (estimate for the quadratic term = 0.01 ± 0.01, $F_{1,33} = 7.86$, $p < .01$; Table S2). A post hoc broken stick analysis suggested that two separate regressions, one before 2008 and one after 2008, had a better fit than the quadratic model (adjusted R^2 for quadratic term = .53, adjusted R^2 for two regressions before and after 2008 = .59). Dividing the dataset before and after this year and testing separately we found that these two regressions were significant with distinct slopes (First: slope = -0.42 ± 0.07, $F_{1,26} = 37.11$, $p < .01$. Second: slope = 0.60 ± 0.20, $F_{1,6} = 9.08$, $p = .02$; Figure 1e). Finally, the interval between calculated fledging date (termination of breeding) and date of male moult onset significantly decreased across years. As a consequence, there was a larger overlap between moult and breeding in recent years (slope = -1.38 ± 0.26, $F_{1,7} = 27.87$, $p < .01$; Table S2, Figure 1e).

Annual average departure dates from the breeding grounds varied between the 7th and 11th of August (with a significant advancement across years using a weak test that included the 3 years with available data; see Figure 1, Table S2) and annual mean arrival dates in Africa varied between the 6th and 19th September. Average wintering longitude was $-7.46°$ (range: -9.71 to -4.86, 26 loggers), suggesting that this pied flycatcher population winters in Ivory Coast similarly to what was reported for other Dutch populations (Ouwehand et al., 2016).

3.2 | Causes of variation in timing

Variation in annual male arrival date was not explained by temperatures; moreover, these temperatures also did not significantly change since 1980 (Tables S4 and S5, Figure S2).

Variation in annual female arrival (nest building) and egg-laying dates, however, were significantly explained by Dutch temperatures (arrival: coefficient = 0.23 ± 0.07, $\chi^2 = 10.26$, $p = .01$; egg-laying:

TABLE 1 Direction of the effects of Dutch and African temperatures on the annual cycle stages of pied flycatchers (red: negative, blue: positive). The values correspond to the coefficients obtained with a Cox-proportional hazards model (see Table S4 for the full results), and thus high positive values indicate the earlier occurrence of the event with higher temperatures (a higher hazard for the event to occur)

Annual-cycle stage	Sex	Years	Average date	Linear trend	Day length: Temp. NL	Temp. NL	Day length: Temp. Africa (lag)	Temp. Africa (lag)	Temp. Africa (no lag)	Window size (no lag)/Window place (lag Africa)
Arrival (observed)	M	2005–2015	19 Apr	−0.32 (±0.20) n.s.	0.01 (±0.02) n.s.	0.16 (±0.11) n.s.	−0.01 (±0.01) n.s.	−0.77 (±0.50) n.s.	0.9 (±0.49) n.s.	5 days/10 Mar
Arrival (calculated)	M	1980–2015	20 Apr	−0.03 (±0.05) n.s.	0.004 (±0.02) n.s.	0.25 (±0.10)	−0.001 (±0.01) n.s.	0.21 (±0.29) n.s.	0.76 (±0.50) n.s.	15 days/11 Mar
Arrival	F	1980–2015	01 May	−0.30 (±0.06)	−0.01 (±0.01) n.s.	0.23 (±0.07)	0.004 (±0.01) n.s.	0.33 (±0.22) n.s.	−0.18 (±0.38) n.s.	15 days/22 Mar
Egg laying	F	1959–2015	11 May	−0.30 (±0.04)	0.001 (±0.01) n.s.	0.58 (±0.12)				25 days
Moult	M	2005–2015	13 Jun	−1.11 (±0.29)	−0.08 (±0.06) n.s.	−0.26 (±0.31) n.s.				30 days

coefficient = 0.58 ± 0.12, χ^2 = 25.89, p < .01; Tables 1 and S4), with higher temperatures being related to earlier arrival and egg-laying. However, while the temperatures important for egg-laying significantly changed across years (estimate = 0.05 ± 0.07, $F_{1,34}$ = 4.41, p = .04), this was not the case for those important for arrival (Table S5, Figure S2). A post hoc test for the egg-laying date data, in which we included year and temperature in the same model to correct for the trends of temperature and year in the same direction, resulted in both temperature and year as significant.

Finally, variation in annual male moult onset was not related to Dutch temperatures (Tables 1 and S4); thus, the advancement observed for the moult onset cannot be related to any recent increase in Dutch temperatures.

3.3 | Consequences of variation in timing

There was no effect of the interval between arrival and breeding and breeding and moult on clutch size. Clutch size, however, changed across years since 1980 in a nonlinear way, increasing until around 2003 and later on decreasing again (quadratic estimate = −0.001 ± 0.0005, $F_{1,33}$ = 9.50, p < .01; Table S6). A post hoc broken stick analysis suggests that two regressions before and after 2008 have a better fit than the model with the quadratic term (adjusted R^2 for quadratic term = .40, adjusted R^2 for two regressions before and after 2008 = .48). Dividing the dataset before and after this year and testing them separately, we found that the first regression was significant (slope = 0.03 ± 0.01, $F_{1,26}$ = 17.43, p < .01), but the second was not (n.s. slope = −1.03 ± 0.05, $F_{1,6}$ = 4.90, p= .07; Figure 2a).

The proportion of fledged chicks that recruited also changed nonlinearly across years (quadratic estimate = −0.001 ± 0.0002, χ^2 = 10.49, p< .01; Figure 2b, Table S6), but it was also significantly related to the interval between arrival and breeding, even when year as a continuous term was included in the same model (Table S6). A higher proportion of chicks fledged when this interval was shorter (slope = −0.04 ± 0.01, χ^2 = 6.99, p = .01; Figure 2c, Table S6). A shorter interval is also related to earlier egg-laying dates of the females, and earlier laying was significantly related to a higher proportion of fledged chicks that recruited (slope = −0.03 ± 0.02, χ^2 = 4.04, p = .04; Figure 2d, Table S6). Thus, the improved chick recruitment may be related to the earlier breeding.

Finally, the proportion of fledged chicks was affected by the interval between breeding and moult, but the relation was nonlinear (quadratic estimate = −0.02 ± 0.01, χ^2 = 5.40, p = .02; Table S6).

We did not observe a trend in adult survival across years and neither the interval between arrival and breeding nor breeding and moult explained the variation in adult survival. When analysing adult survival probability (Φ), none of the models including the interval between arrival and breeding and almost none containing the interval between breeding and moult was among the best models (delta AIC_c always larger than 2; Table 2). Even those models containing the breeding/moult interval, with a delta AIC_c smaller than 2,

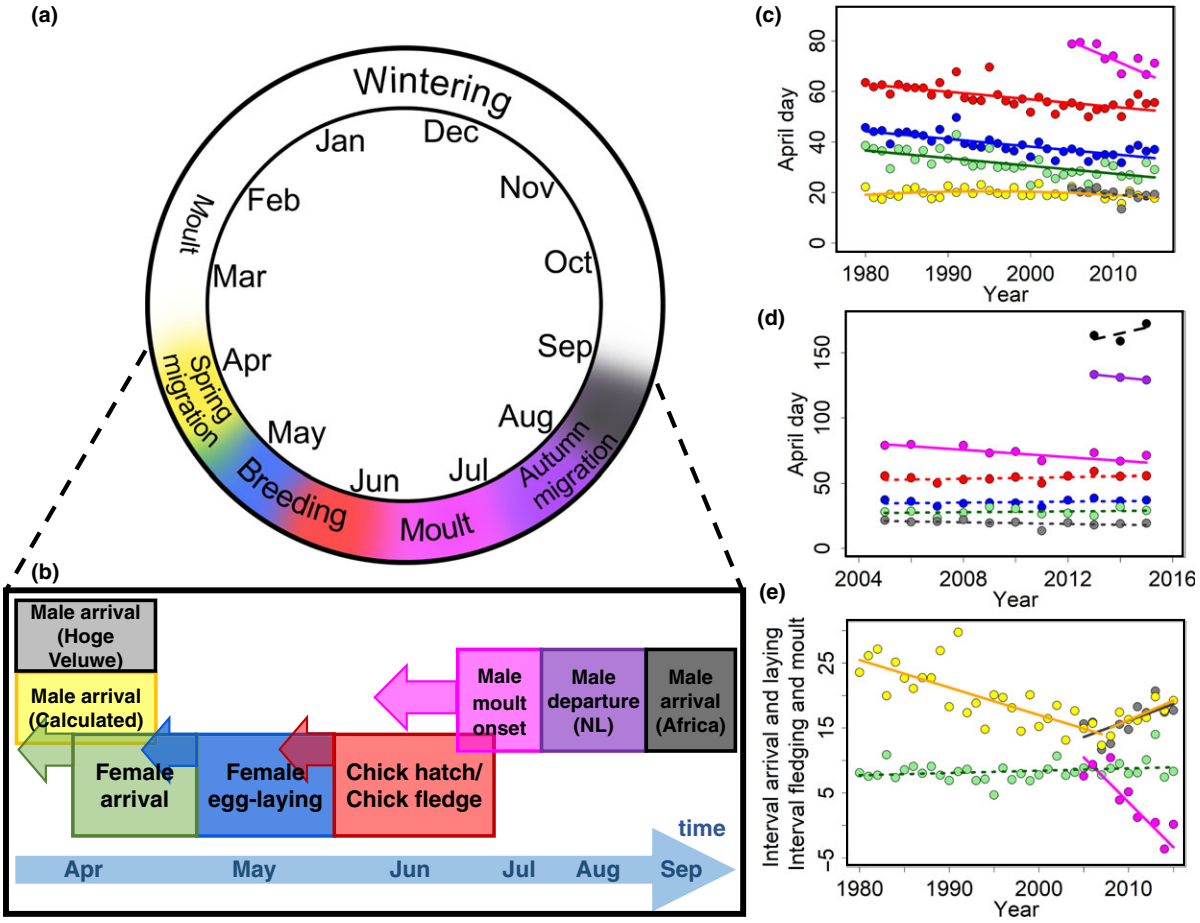


FIGURE 1 Long-term trends in annual cycle stages of pied flycatchers. (a) Schematic illustration of the pied flycatcher annual cycle. (b) Schematic illustration summarizing the observed shifts in timing of annual cycle stages across years. (c) Year to year variation in the timing of different annual cycle stages of pied flycatchers from 1980 until 2015 (without autumn migration) and (d) 2005 until 2015 (including departure from the Netherlands and arrival at the African wintering grounds). Each point represents the yearly average date (in April days) of the occurrence of the event and each colour represents one stage (grey: observed arrival date of males; yellow: calculated arrival dates of males; green: arrival date of females; blue: laying dates; red: hatching dates; pink: moult onset; purple: departure dates; black: arrival dates at the wintering grounds). (e) Interval (in days) between arrival and laying dates (grey: observed dataset; yellow: calculated dataset; green: females) or between the calculated chick fledgling date and male moult onset (pink) in relation to year. Solid lines represent significant linear or quadratic trends; the thin yellow line represents the significant regression using a broken stick analysis on the interval between arrival and breeding in the calculated arrival dataset

however, had negligible effects of this interval (beta estimate in the model only including that interval = 0.0001 ± 0.0008).

4 | DISCUSSION

Our results show that climate change affected the annual cycle stages of the European pied flycatcher, making them shift at different rates from one another. This was probably due to the different changes in the various temperatures that correlate with the phenology of these annual cycle stages. Although timing of moult advanced rapidly, we could not detect a correlating temperature period to explain this shift. Our results also suggest that the advancement of breeding allows more time for events such as fledgling development, which could explain at least, in part, the increase in the proportion of fledged chicks that recruited when the breeding–moult interval got longer. The shortening of the interval between arrival and breeding and the larger moult/breeding overlap would be expected to incur fitness costs, but we did not detect effects on adult survival. Therefore, at least for the aspects studied so far, climate change has actually led to an improvement in breeding conditions for this species, potentially by allowing more time for fledgling development (Tomotani, Gienapp, Beersma, & Visser, 2016).

4.1 | Other consequences of unequal shifts

While costs of shortening the intervals between stages could not be detected in terms of adult survival, it is still possible that costs are present in other aspects we have not investigated. Females, for instance, may suffer costs that are much more subtle. For example,

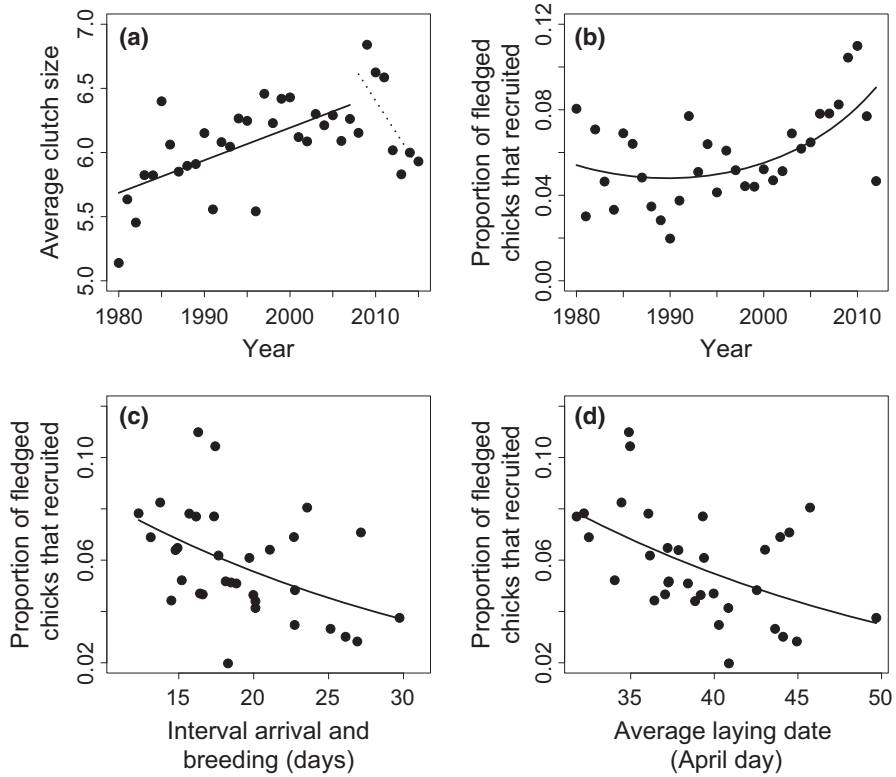


FIGURE 2 Trends across years in fitness components: (a) Clutch size and (b) proportion of fledged chicks that recruited in relation to year. Solid lines represent model predictions (logistic in b). Proportion of fledged chicks that recruited in relation to (c) the interval between calculated male arrival and breeding and (d) the average laying date. Solid lines represent logistic model predictions

TABLE 2 The top five best models obtained from the mark–recapture analysis that analysed adult survival in relation to the interval between arrival and breeding and breeding and moult, for both the long and short datasets. In all cases, the best models included the six groups for the recapture component but just sex for the survival component. In both cases, the bootstraps values for c-hat were slightly larger than 1 and deviance and AIC_c values were adjusted accordingly

	Delta AiC_c	Number of parameters	Deviance
Model name (dataset 1980–2015), c-hat = 1.11			
(Capture occasion × Sex + Time), P(capture occasion × Time × (Sex × Age first capture))	0.00	261	1,127.24
(Sex × Arrival + Capture occasion × Sex), P(capture occasion × Time × (Sex × Age first capture))	8.71	234	1,194.99
(Capture occasion × Sex + Capture occasion × Arrival + Sex × Arrival), P(capture occasion × Time × (Sex × Age First capture))	10.71	235	1,194.81
(Capture occasion × Sex × Arrival), P(capture occasion × Time × (Sex × Age first capture))	14.99	237	1,194.75
(Capture occasion × Sex + Time × Sex), P(capture occasion × Time × (Sex × Age first capture))	16.92	287	1,086.75
Model name (dataset 2005–2015), c-hat = 1.07			
(Capture occasion × Sex), P(capture occasion × Time × (Sex × Age first capture))	0.00	65	305.24
(Capture occasion × sex × moult), P(capture occasion × Time × (Sex × Age first capture))	1.64	67	302.56
(Capture occasion), P(capture occasion × Time × (Sex × Age first capture))	1.84	63	311.40
(Capture occasion × Sex + Moult), P(capture occasion × Time × (Sex × Age first capture))	2.16	66	305.24
(Moult), P(capture occasion × Time × (Sex × Age first capture))	2.50	63	312.06

a decrease in the number of days between arrival and breeding may also mean that females need to be much faster in choosing a male (Dale & Slagsvold, 1995; Dale et al., 1992), building the nest and initiate egg-laying. Indeed, in recent years, male and female arrivals are happening almost at the same dates, so when the first females arrive, a good number of males are not settled and territories are still being claimed. This could, for example, result in a reduced time to assess male quality (Alatalo et al., 1984) and increase the probability of a female to pair with a male that already has another female. Polygyny is costly for females since the number of unfertilized eggs and chick mortality are higher when a male has more than one female (Lubjuhn, Winkel, Epplen, & Brün, 2000). This could be problematic for late-arriving females, as they would supposedly be even more constrained by the increased competition with other females late in the season (Dale et al., 1992). This shorter time span could also decrease the females' body condition and in the long run be detrimental to their breeding success, since egg laying is particularly costly (Visser & Lessells, 2001). This may have been reflected in the previously increasing clutch size trend, which changed in recent years (although there was no significant decline detected by the broken stick analysis; Figure 2a).

The shifts observed in the timing of moult in males may also result in a shortening of the total time available for breeding, similarly to what was reported by Moyes et al. (2011). Males advanced their moult onset at a higher rate than the breeding dates, which suggests that they are regressing their gonads earlier as well. Experimental studies in captive starlings (*Sturnus vulgaris*) show that onset of moult is related to the gonadal regression in males (Dawson, 2006); moreover, both gonadal regression and moult advanced in great tits (*Parus major*) experimentally exposed to higher spring temperatures in captivity (Visser et al., 2011). In the present study, there was no effect of temperatures on moult onset, but regardless of the factor that is causing advancements in the timing of moult, an uncoupling between onset and termination of breeding is possible.

4.2 | Underlying causes of unequal shifts

A curious outcome of our analysis is the faster advancement of moult in relation to breeding. Moult onset in males seems to be determined earlier in the season and not by the termination of breeding (Tomotani et al., submitted). If moult is not connected to timing of breeding, it could advance independently. Another possibility is that moult is set when the individual is born. It is known, for example, that the photoperiod when the animal is born can modify the timing of events later in life (Coppack & Pulido, 2009; Coppack, Pulido, & Berthold, 2001; Lee & Zucker, 1988). In particular, it has been proposed that advancements in birth date (as laying dates advance) could modify the timing of migration at the population level (Both, 2010; Gill et al., 2014). If the timing of moult is set when the birds are born, this may explain the observed change in moult onset at the population level (but see Larsson, 1996).

If the dates when birds are born affect both their arrival and moult, we should also observe an advancement in arrival dates, but it was not the case in our study population. Other migratory species, however, have been reported to advance their arrival dates (Usui, Butchart, & Phillimore, 2016) and also other populations of pied flycatcher (Ahola et al., 2004; Both et al., 2016; Valtonen et al., 2016). Arrival dates, in comparison to the onset of moult, are much more susceptible to modulations by environmental conditions, such as weather, body condition and wind patterns (Ahola et al., 2004; Bauer, Gienapp, & Madsen, 2008; Both et al., 2016; Eikenaar & Schmaljohann, 2014; Erni, Liechti, & Bruderer, 2005; Sinelschikova, Kosarev, Panov, & Baushev, 2007; Teitelbaum et al., 2016). Moreover, arrival dates can usually only be assigned to individuals that survived the migration and thus there might be a bias if early arrival increases mortality (Brown & Brown, 2000). In comparison to arrival, moult is a relatively cleaner expression of the individuals (endogenous) timing (i.e. more directly assessed; Gwinner, 1996), thus potential changes related to birth effects are supposedly more detectable in timing of moult than timing of arrival.

None of the temperatures important for timing of stages directionally and significantly changed over the past years, with the exception of those explaining the variation in egg-laying dates (Figure S2). We would expect that the temperatures important for female arrival (nest building) would also have changed since the stage advanced at the same rate as egg-laying dates. However, while the Dutch temperatures that are important for female arrival (nest building) and breeding are almost the same and partly overlap (Table 1), the window size of the temperature important for laying date is 10 days larger. One possibility is that the temperatures important for female arrival (nest building) and egg laying are nearly the same and trends are not detected for the arrival temperatures due to a larger variation in temperatures in the prelaying period especially in recent years (Figure S2).

In this study, while we included multiple annual cycle stages, we were limited to the stages that occur on the breeding grounds—for which we have long-term data available. Even so, there was one stage at the breeding ground that we could not include: the timing of autumn migration. Date of departure in late summer seems to be correlated with the timing of egg-laying, but not so much with the timing of chick hatching (Tomotani et al., submitted). Departure dates also seem to be variable across years. Thus, it is possible that, together with the advancement of breeding and moult, the birds are now also departing earlier. However, if there is no change in timing of migration, males have more time to moult. It has been reported that conditions late in the season may improve for some birds, such as for some short-distance migrants (Jenni & Kery, 2003). For now we can only speculate how climate change has affected the timing of autumn migration in our population.

Another aspect that we are unable to assess is the timing of stages at the wintering grounds in Africa. It is unknown if birds remain time constrained at their wintering grounds or if the wintering grounds serve as "time buffers." Early arrival at the wintering grounds may, for example, be important to secure resources, which could result in improved body reserves that carry-over to the next season (e.g. in terms of earlier arrival and/or improved individual

quality). This is the case for American redstarts (*Setophaga ruticilla*; Marra, Hobson, & Holmes, 1998; Marra, Studds et al., 2015; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004). In pied flycatchers, an experimental delay of hatching dates imposed a larger moult-breeding overlap and made males from this group winter at a different location than controls and advanced males (Tomotani et al., submitted). This suggests that the selection of wintering territory also depends on what birds experience at the breeding grounds, but whether wintering will later impact breeding remains unknown (Ouwehand & Both, 2017).

4.3 | Final remarks

Climate change unequally affects the annual cycle stages of bird (Eichhorn et al., 2010; Valtonen et al., 2016; Van der Jeugd et al., 2009) and mammal species (Moyes et al., 2011; Ozgul et al., 2010). Such shifts may lead to positive fitness consequences in some cases, for example, in marmots' offspring that now have more time. But it may also have negative consequences, in the case of the red deer in which not only a mismatch between male and female timing happened but also a shortening in their breeding window. In this study, there were also positive and negative fitness consequences of unequal shifts, but they depended on the sex or life stage of the animal. In pied flycatchers, climate change seems to benefit males and offspring, which have more time available due to the advancement of breeding, but it can also be costly for the females. The impacts of climate change, thus, are not only different for distinct trophic levels (Parmesan, 2006) but also for stages (e.g. breeding, moult) sex and life stages (e.g. males, females, offspring) within the same species. It is very possible that such patterns are widespread, especially among organisms with complex annual cycles, meriting a careful look as new and more complete datasets covering the full annual cycle become available for other populations and species.

For a broader understanding of the ecological consequences of climate change, different stages of the annual cycle should be considered (Crozier et al., 2008; Yang & Rudolf, 2010), in particular for organisms with complex cycles, such as migratory birds (Marra, Cohen, Loss, Rutter, & Tonra, 2015; Small-Lorenz, Culp, Ryder, Will, & Marra, 2013). Our knowledge on climate change impacts on organisms will, thus, greatly benefit from continued standardized data collection that includes more than one stage.

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ORCID

Barbara M. Tomotani http://orcid.org/0000-0002-8855-4803
Phillip Gienapp http://orcid.org/0000-0002-9368-8769
Marcel E. Visser http://orcid.org/0000-0002-1456-1939

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