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Resident bird species track inter-annual variation in spring phenology better than long-distance migrants in a subalpine habitat

Jørgen Skavdal Søraker[a,*], Bård Gunnar Stokke[b], Oddmund Kleven[b], Arne Moksnes[c], Geir Rudolfsen[d], Gine Roll Skjærvø[c], Henriette Vaagland[c], Eivin Røskaft[c], Peter Sjolte Ranke[a]

[a] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, NO-7491 Trondheim, Norway
[b] Norwegian Institute for Nature Research (NINA), Høgskoleringen 9, NO-7034 Trondheim, Norway
[c] Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, NO-7491 Trondheim, Norway
[d] UiT The Arctic University of Norway, Tromsø, Norway

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ABSTRACT

The ability to track variation in climate is important for species to persist in a given environment. Lack of responses to both long-term changes and inter-annual variation in climate parameters can result in reduced fitness and population decline. Furthermore, migration strategy can influence the ability to track climatic variation due to the potential to use reliable environmental cues. Here, we studied the temporal relationship between birch leafing and onset of breeding for three bird species with contrasting migration strategies over a 20-year period in a subalpine habitat in Central Norway. We found no temporal change in birch leafing date or breeding onset for the three bird species over the study period. However, we found a statistically significant difference in the ability to track inter-annual variation in birch leafing date between the resident and two long-distance migratory species. The resident great tit *Parus major* was more capable of initiating egg laying in closer association to variation in birch leafing in early springs, than the long-distance migratory European pied flycatcher *Ficedula hypoleuca* and common redstart *Phoenicurus phoenicurus*. Long-distance migrants seem to have been constrained by arrival date or time from arrival to entering the breeding areas, in contrast to resident birds, which might be better able track early initiation of spring in breeding areas by adjusting egg laying date. Our findings highlight the importance of not solely studying directional long-term climatic change, but also pay attention to inter-annual variation.

1. Introduction

Climate change has in general increased the global temperature over the past decades [1], and as a consequence, the onset of spring in the Northern Hemisphere has advanced [2]. These changes may potentially affect whole biological ecosystems, and hence, it is crucial to understand the effect of such changes both within and among species. Phenology, defined as the annual timing of life-cycle events in organisms [3], has shown to be affected by the current temperature increase in a variety of species [4–6]. According to the match-mismatch hypothesis, species should change their phenology to match that of the resources they depend on [7,8]. In lack of this phenological response, the timing of life-cycle events can be moved away from the optimum, potentially causing reduced individual fitness [9] and population decline [8,10]. Change in breeding phenology is one of the events that has received most attention [10,11]. Advancing breeding onset in response to shift in phenology of important food sources is crucial in order to optimize breeding success [8], a relationship which is documented for several bird species over the last decades [5,10,12,13].

The degree of advanced breeding onset is, however, potentially constrained by arrival date for migratory birds [14]. Several studies have investigated how the arrival date has changed over the last decades, generally showing that migrating birds adjust their arrival dates as a response to climate change both in Europe [15,16,17] and North America [18]. Furthermore, Møller et al. [17] reported population declines in species that responded less to climatic change compared to species with a stronger response. Specifically, long-distance migrant species responded less to climate change than short-distance migrants and residents, which has also been supported by other studies (e.g., Newson et al. [19]). Nevertheless, even resident birds may mistime the onset of breeding according to food availability, due to inappropriate cues [9,20]. Individual differences in arrival date within migrating species may also impact breeding success. Populations of pied flycatcher *Ficedula hypoleuca* in the Netherlands that showed a weak response to temperature increase

* Corresponding author.
E-mail addresses: jorgsso@stud.ntnu.no (J.S. Søraker), bard.stokke@nina.no (B.G. Stokke), arne.moksnes@ntnu.no (A. Moksnes), geir.rudolfsen@uit.no (G. Rudolfsen), gine.skjarvo@ntnu.no (G.R. Skjærvø), henriette.vaagland@ntnu.no (H. Vaagland), eivin.roskaft@ntnu.no (E. Røskaft), peter.s.ranke@ntnu.no (P.S. Ranke).

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experienced up to 90% decline in population size, while populations displaying stronger advancement experienced no change [10].

Despite thorough documentation of advanced arrival date on an inter-specific level [17], advanced breeding onset has mostly been investigated for residents [12,21] or long-distance migrants [10,22], separately. Thus, few studies have investigated differences in breeding onset advancement of both residents and long-distance migrants within the same habitat over several decades and compared their ability to track spring phenology. To predict the effects of advanced spring onset across different migration strategies, it is important to test the ability to respond to the change, and to which extent, across different habitats, as habitat may influence the match-mismatch relationship [23,24]. Studies focusing on the relationship between spring advancement and breeding phenology have used a variety of environmental variables that potentially act as cues for onset of spring, such as temperature in pre-breeding periods [24,25,26] and birch leafing date [27,28].

The aim of this study was to test the relation between spring phenology measured as birch leafing day, and the onset of breeding (measured as first laying date) for the great tit *Parus major*, pied flycatcher and common redstart *Phoenicurus phoenicurus*, in a high-altitude habitat in mid-Norway over more than two decades. Birch leafing has been found to be dependent on spring temperature [29] and occurrence of caterpillars, an important factor for the nestlings [30]. The great tit mostly acts as a resident species in Norway, although it occasionally can act as a short-distance migrant [31]. However, this partial migratory behavior is mostly restricted to other parts of Norway [32]. Therefore, we will mainly refer to it as a resident species. Both the European pied flycatcher and common redstart are regarded as long-distance migrants, as they winter in sub-Saharan Africa [33]. Moreover, both species arrive at high latitude in Norway mostly at the same time [34]. All the three study species are cavity-nesters frequently occupying nest-boxes. In addition, it has been suggested that all are dependent on insect phenology for successful breeding [35]. Because of the potentially greater ability to track the local environment for resident species [36], we predicted a more adaptive response to spring phenology change for the resident great tit, than for the two long-distance migrants. We also assumed that the strength of tracking would be strongest early in the breeding season, thus, a proportional effect of spring date.

2. Material and methods

2.1. Study site

The study was conducted in the valley Hådalen, Røros municipality in Central Norway (62° 28′ N, 11° 39′E) during the period 1999–2020. Here, nest-boxes have been mounted gradually on 169 locations over the study period (Supplementary material Table S1). The habitat is characterized by a mixture of pine and birch forest approximately 660 m above sea level, just below the area's treeline. For additional details about the study site, see Kleven et al. [37]. Here, the snow is usually melting around mid-May and the breeding season is delayed compared to more costal and lowland areas of Norway. The three study species counted for more than 95% of all the nest-box breeding attempts (for details, see Supplementary material Table S2).

2.2. Data collection

The fieldwork was conducted from the last week of May to the first weeks of July, but we adjusted the timing of visits depending on the snow-conditions reported from the locals in order to more accurately record breeding phenology. At least three visits were made to every nest-box, spacing visits by three-week intervals during the breeding season. Species identity, the number of eggs and estimated age of nestlings were recorded. Based on the number of eggs between visits and/or on estimated chick age, we assumed 14 days incubation period for all species to estimate first laying date [35] (see, "Estimation category" in Table 1).

Table 1
Model output from a linear mixed-effects model using log laying day of first egg as response, and the log date for birch leafing (log spring day) and species as fixed effects, with May 11th as intercept and great tit as reference. We accounted for the effect of "estimation category" (whether estimated egg laying was based on egg laying or from nestling age; reference = egg stage). Year was added with random intercept. We present untransformed parameter estimates with 95% confidence intervals. Confidence intervals not overlapping zero are regarded statistically significant and highlighted with bold font.

Predictors	Estimates	95% CI
Intercept	2.80	[2.69, 2.92]
Common redstart	0.20	**[0.09, 0.31]**
Pied flycatcher	0.37	**[0.27, 0.46]**
log(spring day)	0.17	**[0.13, 0.22]**
Estimation category	0.04	**[0.00, 0.07]**
Common redstart × log(spring day)	−0.06	**[−0.10, −0.01]**
Pied flycatcher × log(spring day)	−0.07	**[−0.11, −0.04]**

The median for first laying date was used as a measure for population level onset of breeding. Environmental data was extracted from the Norwegian Centre for Climate Services (www.klimaservicesenter.no) as source for climatic measurements. We used the weather station at Røros (62°34′ N 11°22′ E) for the years 1999–2003 and Røros Airport (62°34′ N 11°21′ E) from 2004 to 2020 due to incomplete data series, however, the weather stations are located on the same site (1.7 km apart) and are thus located between 7 and 31 km from our nest-boxes. We used the daily mean of hourly temperature to calculate the growing degree days (GDD) starting from April 1st using a baseline of zero degrees Celsius [29]. When mean was not available, the mean of daily minimum and maximum temperature was used. Then we used the cumulative GDD [38] in order to estimate the leafing of birch. Using a subset of breeding seasons (n = 7) with known birch bud break dates and following GDD for the study area, provided a mean of 181.01 ± 20.06 GDD for bud burst. Therefore, we could use 180 GDD as a reliable threshold to estimate when birch leafing occurs (a leave-one-out test showed a mean error of 1.86 days, and an error range of [−2,2]).

2.3. Statistical analysis

2.3.1. Spring phenology

To test for a directional change in spring phenology due to changes in climate over the study period, we used linear models to investigate the relationship between birch leafing date and year. A negative relationship is expected if climate change has caused advances in spring onset.

2.3.2. Onset of breeding

First, we calculated the annual median date for onset of breeding for each species. Second, we examined whether there has been a directional change in annual median date for onset of breeding using linear models. If spring onset has changed towards earlier in spring, the bird species are expected to change their breeding onset in the same direction. This test was assigned for each species separately, allowing them to respond differently.

2.3.3. Response to spring phenology inter-annually

Finally, we examined variation in annual onset of breeding with a linear mixed-effects model, using log day number after May 1stwhen the first egg was laid as a response, and as fixed effects; the species, log birch leafing day number after May 11th (earliest leafing day recorded with the study period was May 12th), with an interaction species × log leafing day, and year as random intercepts. The model was fitted using '*glmmTMB*' [39]. We used R version 3.6.3 [40] in all statistical analyses and model fit were assessed with '*DHARMa*' [41].

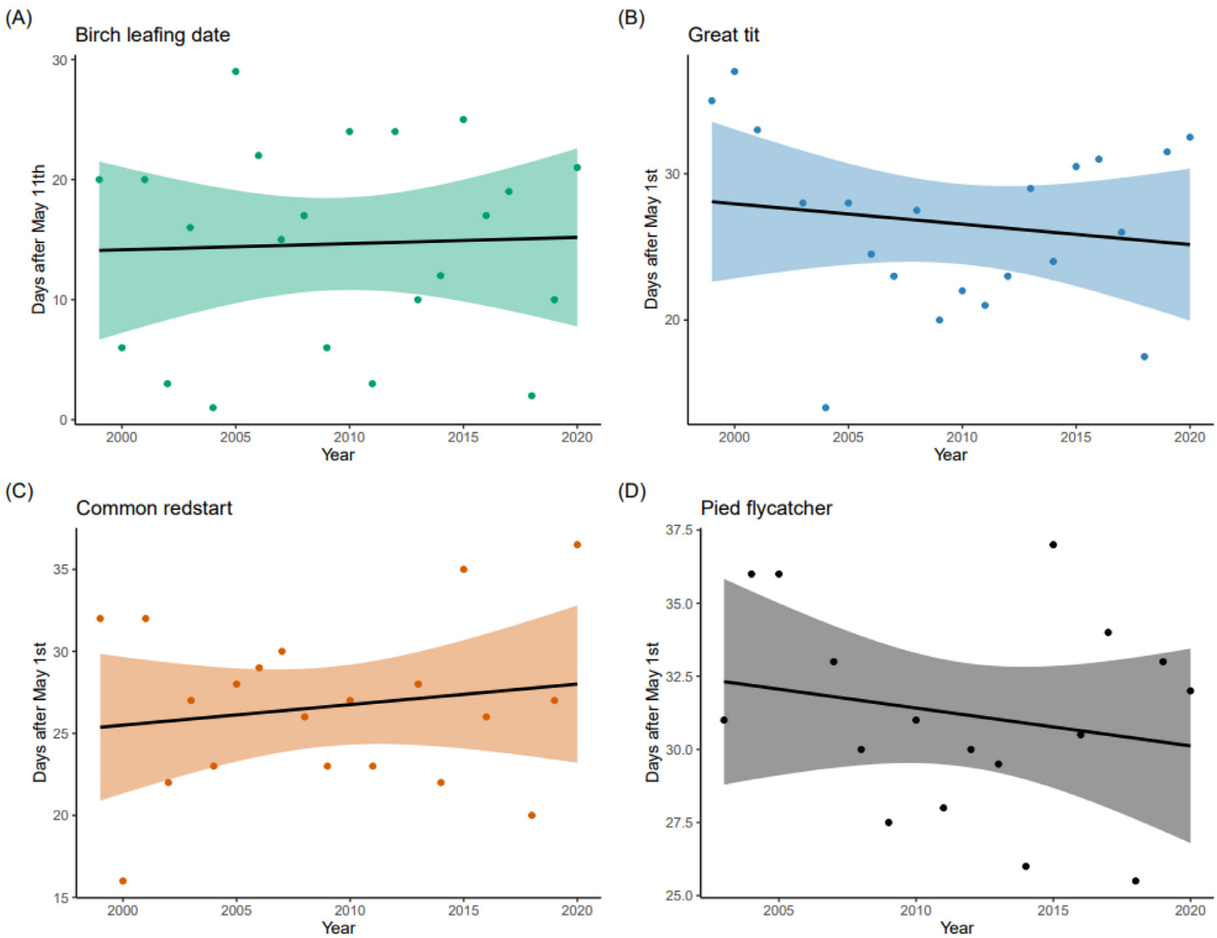

Fig. 1. Linear predictions for birch leafing day (A) and breeding onset for great tit (B), common redstart (C) and pied flycatcher (D) as a function of year.

3. Results

3.1. Spring phenology

We found no evidence for a directional trend in birch leafing date following year (slope=0.0519, SE= ± 0.289, $t = 0.179$, $p = 0.860$) indicating no shift in spring onset across a 20-year period (Fig. 1A). The mean birch leafing date during the study period was May 26th (range=May 12th- June 9th, SD=8 days). Due minor violations of model assumptions (Fig. S1), we performed an additional set of non-parametric test corroborating these results, see Supplementary materials Tables S3.

3.2. Breeding onset

Further, we found no evidence of an association between median onset of first egg-laying date and year for neither great tit (slope=−0.139, SE ± 0.208, t=−0.669, $p = 0.512$) (Fig. 1B), common redstart (slope=0.125, SE ± 0.179, $t = 0.699$, $p = 0.494$) (Fig. 1C), or pied flycatcher (slope=−0.129, SE ± 0.161, t=−0.800, $p = 0.436$) (Fig. 1D), indicating no significant change in onset of breeding across the study period. Some smaller violations of the models were present (Fig. S2–4), but use of Spearman rank correlations gave similar results (Supplementary materials Table S3).

3.3. Effect of spring phenology on breeding onset

When examining the relationship between breeding onset and spring phenology, we found a strong positive association for great tit, while pied flycatcher and common redstart responded significantly less to advances in spring phenology (Table 1,Fig. 2, see model fit and back-transformed plot in Supplementary material Fig. S5 and S6, respectively). With one percent increase in spring day number after May 11th would lead to 0.17 percent days later egg laying in great tit, but only 0.11 and 0.10 percent later in common redstart and pied flycatcher, respectively (Table 1; Table S4). Thus, the great tit, a resident species, was able to initiate egg laying early in the season when birch leafing occurred early, in contrast to pied flycatcher and common redstart (Table 1), where egg laying was less affected by an early spring.

4. Discussion

In this study, we investigated the relationship between spring phenology and breeding onset among the resident great tit, and the migratory pied flycatcher and common redstart over a 20- year period in a subalpine nest-box population. We found no statistically significant pattern in temporal change in birch leafing dates over the study period (Fig. 1). Similarly, we found no evidence of a temporal change in median onset of breeding across the study period. However, a change in breeding onset is not expected in absence of a change in spring phenology [8].

Despite no evidence of long-term temporal change in breeding onset across the study period, the three species investigated diverged in their ability to track inter-annual variation in spring phenology (Table 1). Both long-distance migrants showed less ability to adjust breeding onset compared with the resident great tit. Although the different species may feed on different prey species, the leafing dates should be a reliable proxy of spring phenology, important for many prey species [42].

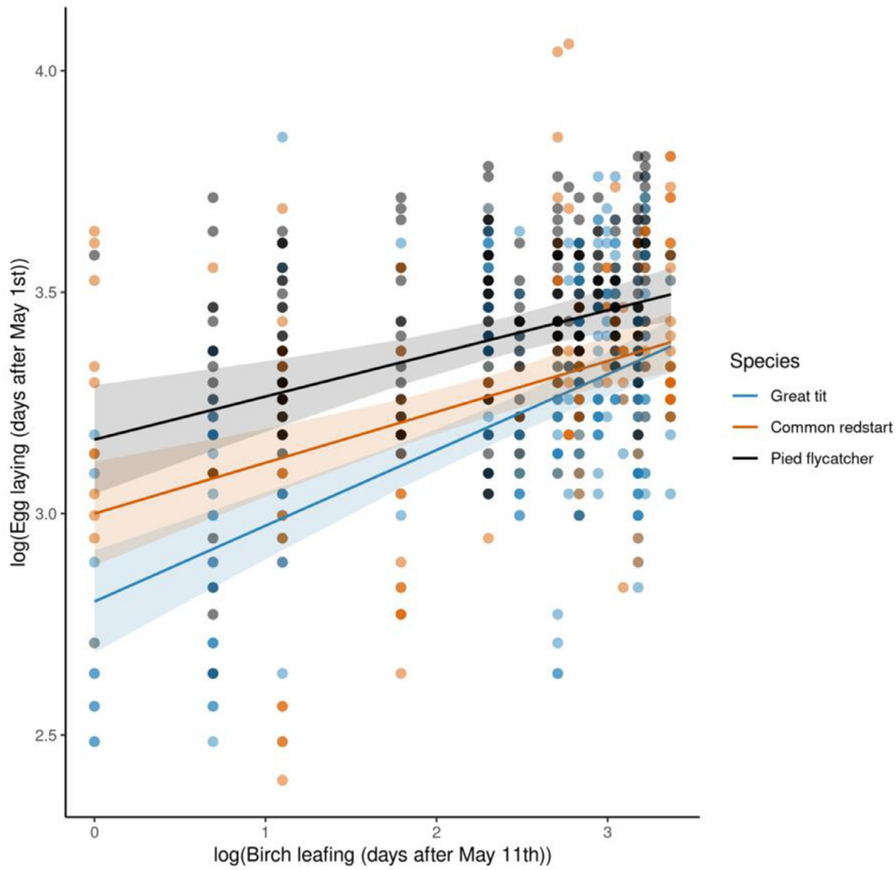

Fig. 2. Initiation of egg laying influenced by birch leafing phenology in Hådalen, Mid-Norway 1999–2020, presented on log-scale. Predictions for each species are based on a linear mixed-effect model using the logarithm of egg laying day after May 1st as response (see all fixed effects and parameter estimates in Table 1). Great tit shows a greater response to early spring phenology, measured as the logarithm of birch leafing day after May 11th (see, Supplementary material Fig. S6 for plot back-transformed to original scale).

This tracking of spring phenology is important for reproductive success, thereby contributing to variation in individual fitness [8,9] and ultimately affecting population size [10,17,43]. Nevertheless, recent studies have highlighted that responses of animals to climate change might be insufficient [11]. Within the range of climatic variation in this study, the investigated species adjusted the breeding onset to changes in spring phenology, but to a varying degree, assuming birch leafing date to be a reliable cue for spring phenology [27,28]. However, without temporal trends in spring phenology, the lack of directional selection pressure could complicate long-term adjustment to spring initiation [20,43]. Moreover, small variation in the timing of the prey's phenology in relation to spring onset [24] might also result in less accurate tracking of spring onset, although some studies imply spring vegetation phenology to be the direct cue to which the birds respond most closely [44]. As we demonstrate in this study, these three species track breeding onset to birch leafing date, which indicate that the birch leafing may act as a reliable cue to the initiation of breeding in this area.

The species difference in tracking of spring phenology presented in this study (Fig. 2) is, even in the absence of long-term climatic change, expected for the long-distance migrants due to its migratory behavior, as breeding onset can be constrained by arrival date [14]. Thus, highlighting that consequences of climate change could be more severe for migratory birds [23]. Indeed, different sensitivity to climate change among residents and short-distance migrants was also the finding of Samplonius et al. [36], when comparing populations of residents and short-distance migrants with long-distance migrants across Europe, relating this to directional change in climate variables. Although these studies have focused on climate change induced long-term trends, the same could be expected in habitats with strong inter-annual variation in spring initiation. Additionally, Both et al. [23] found that the cost of mismatch between breeding onset and food availability was dependent on the width of the food peak in the habitat. Since our study system was characterized by a high-latitude habitat, with strong inter-annual variation in spring phenology, the optimum onset of breeding could shift substantially between years. Moreover, the peak of caterpillar abundance is found to increase with altitude [24]. Despite that the study area is surrounded by lowland habitat, and Shutt et al. [24] demonstrated caterpillar phenology to be delayed considerably with altitude, making them a potential pre-breeding area, the long-distance migrants differed in their ability to track to inter-annual variation in birch leafing compared the resident great tit. Since most of the attention hitherto has been attributed to systems with directional temporal change in spring temperature and breeding onset [9,20,36] the ability of different species to respond to inter-annual variation in spring phenology is less well understood and require further investigation.

More research is needed in order to understand the ability to track climatic variation, not only within, but also between different habitats for species with contrasting migration strategies. In addition, future studies should focus on incorporating breeding success to analyses of tracking climatic variation, and better integrate inter-annual variation in climatic variables.

Data accessibility

All the raw data are available from the Dryad Digital Repository.

Authors' contribution

JSS and PSR conceived the idea, performed the analysis and wrote the paper. All authors conducted the fieldwork, commented and gave feedback on the manuscript.

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Declaration of Competing Interest

We declare we have no competing interests.

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Supplementary materials

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2022.100050.

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