

REVIEW

Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis

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Abstract

The alteration of the timing of biological events is one of the best documented effects of climate change, with overwhelming evidence across taxa. Many studies have investigated the phenology of consumers, especially birds. However, most of these studies have focused on specific phenophases, whereas a global analysis of avian phenological trends during recent climate change across different phases of the circannual cycle is still lacking. Here, we performed a comprehensive meta-analytic synthesis of the phenological responses (temporal shifts in days year⁻¹) of birds across different phenophases (prebreeding migration, breeding, and postbreeding migration) by summarizing more than 5500 time series from 684 species from five continents during 1811–2018. Our results confirm that avian taxa have advanced prebreeding migration and breeding by ~2–3 days per decade, whereas no significant temporal changes in the timing of postbreeding migration were documented. Advancement in the timing of prebreeding migration and breeding strongly depended on migratory behavior, with the advance being the weakest for long-distance migrants and the strongest for resident species. Diet generalists and primary consumers tended to advance prebreeding migration timing more than species with different dietary specializations. Increasing body size resulted in a larger advancement in the onset (but not in the mean date) of prebreeding migration and breeding, whereas phenological advances were larger in the northern than in the southern hemisphere. Our synthesis, covering most of the world, highlighted previously unappreciated patterns in avian phenological shifts over time, suggesting that specific life-history or ecological traits may drive different responses to climate change.

KEYWORDS

adaptive response, arrival date, birds, breeding date, climate change, global warming, meta-analysis, migration, phenology

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INTRODUCTION

Over the past century, global temperatures have increased unprecedentedly, mainly due to anthropic activities, and are predicted to increase at an even steeper rate in the next decades (Collins et al., 2013). Such dramatic global warming has already impacted biodiversity at all levels of organization (Cohen et al., 2018; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Thackeray et al., 2010, 2016; Walther et al., 2002). Organisms can display adaptive phenotypic responses to cope with the ongoing climate change, for example by changing their distribution according to the spatial variation in their temperature optima (e.g., Burrows et al., 2011), or by means of phenotypically plastic or micro-evolutionary changes in life-history traits in response to concomitant changes in biotic and abiotic conditions (e.g., Charmantier & Gienapp, 2014; McLean et al., 2022; Pulido & Berthold, 2004). However, the rate of phenotypic/micro-evolutionary change might be insufficient to keep up with climate change in most instances (Radchuk et al., 2019). Consequently, the populations of many organisms have suffered substantial demographic declines (Both et al., 2006; Møller et al., 2008), and climate change is expected to surpass habitat destruction as the greatest global threat to biodiversity over the next decades (Thomas et al., 2004; Urban, 2015).

Change in the timing of biological events is one of the most widespread and well documented biotic impacts of climate change (Cohen et al., 2018; Parmesan & Yohe, 2003; Radchuk et al., 2019; Root et al., 2003; Walther et al., 2002). Increase in global temperatures has generally led to an advanced onset of spring events in seasonal environments, such as earlier flowering and leafing of plants (Fitter & Fitter, 2002; Thackeray et al., 2016), emergence of insects (Bale et al., 2002; Forister & Shapiro, 2003; Thackeray et al., 2016), and migration and breeding of higher-level consumers (Cohen et al., 2018; Jonzén et al., 2006; Knudsen et al., 2011; Li et al., 2013; McLean et al., 2022; Thackeray et al., 2016; Usui et al., 2017), especially in regions outside the tropics (Cohen et al., 2018; Thackeray et al., 2016). Because most species of seasonal environments have strictly defined periods of the year during which they perform specific activities, such as reproduction and migration, the timing of circannual events is crucial to determine their fitness. Such a general advancement in different activities over time across different taxa is therefore considered an adaptive response to climate warming, because it allows organisms to adjust the timing of their annual events to match changes in the timing of abiotic conditions that are relevant to their activities, as well as climate-driven shifts in

the phenology of the populations to which they are ecologically linked, as observed in predator–prey, consumer–primary producer and host–parasite relationships (e.g., Both, Van Turnhout, et al., 2009; Cohen et al., 2018; Kharouba et al., 2018; Møller et al., 2011; Parmesan, 2006). However, these advances are not always adaptive (Radchuk et al., 2019), and often they are not sufficient to keep up with phenological shifts at lower trophic levels, resulting in mismatches of ecological interactions (e.g., Both, Van Asch, et al., 2009; Thackeray et al., 2010; Visser & Gienapp, 2019). Under this scenario, the phenology of reproduction in seasonally reproducing organisms is crucial because of its obvious importance in determining fitness. However, the severe repercussions that events at one stage of the annual life cycle of an organism have on those at subsequent stages (carry-over effects; see e.g., Ambrosini et al., 2019; Saino et al., 2017) emphasize the importance of focusing on the entire annual life cycle to fully understand the impact of climate change on populations.

Among animals, avian species are considered important bioindicators of ecological effects of climate change because they are one of the most widely and intensively studied taxa. There is compelling evidence that avian populations have been affected by recent climate change across the world (e.g., Dunn & Møller, 2019; Knudsen et al., 2011; Parmesan & Yohe, 2003; Root et al., 2003; Usui et al., 2017). The effects of climate change on birds have been summarized by comparative studies and meta-analyses, and include shifts in geographical distribution, earlier breeding, changes in migration schedule and in reproductive performance, as well as variation in population size (e.g., Chen et al., 2011; Dunn & Møller, 2014, 2019; Møller et al., 2008; Radchuk et al., 2019; Usui et al., 2017). In particular, temporal trends in the phenology of avian circannual activities in response to global warming have been extensively documented over broad spatial and temporal scales (Bitterlin & Van Buskirk, 2014; Dunn & Møller, 2014, 2019; Hällfors et al., 2020; Horton et al., 2020; Lehikoinen et al., 2019; Usui et al., 2017), showing a general advancement in prebreeding migration and breeding dates in recent years and with increasing temperatures (Bitterlin & Van Buskirk, 2014; Dunn & Møller, 2014, 2019; Usui et al., 2017). These trends show a large variability among species and regions (e.g., Rubolini et al., 2007; Samplonius et al., 2018).

Some life-history/ecological features that make particular groups of birds more susceptible to climate change have been identified. Migration over long, inter-continental distances has been suggested to predispose species to demographic decline (Both et al., 2006;

Møller et al., 2008; Saino et al., 2011). Indeed, residents and partial migrants should rely on more (and more reliable) information than migratory species, especially long-distance migrants, regarding the ecological conditions that are expected to occur in the breeding areas (Knudsen et al., 2011). Therefore, these species are expected to be more flexible in adjusting their migration and breeding schedules to avoid mismatches with the phenology of resources/prey to which they are ecologically linked than species migrating over longer distances, whose circannual activities are more dependent on photoperiod and on constraints in crossing ecological barriers (Both et al., 2006; Lehikoinen et al., 2019; Møller et al., 2008; Saino et al., 2011; Samplonius et al., 2018; Usui et al., 2017). Trophic level has also been shown to predict negative effects due to climatic alterations at the local scale, with consumers at higher trophic levels being more negatively affected (Both, Van Asch, et al., 2009; Parmesan, 2006). Primary consumers may indeed respond more strongly to environmental changes because they can exploit earlier vegetation phenology without being constrained by cascading effects on the phenology of organisms belonging to higher trophic levels (Both, Van Asch, et al., 2009; Thackeray et al., 2010, 2016). In addition, diet generalists should be more able to easily find appropriate food during migration and upon arrival on the breeding areas, and thus they might be able to better respond to climate change compared with diet specialists (Klueen et al., 2017; Vegvari et al., 2010). Other life-history traits, such as body mass and nest type, have been associated with variation in phenological changes, but the strength and the direction of their effects showed large variability among studies and locations (Dunn & Møller, 2014; Klueen et al., 2017; Stevenson & Bryant, 2000; Vegvari et al., 2010). Finally, latitudinal variation in response to climate change has been observed among populations of some bird species (e.g., Both et al., 2004; Both & te Marvelde, 2007; Sanz, 2003), the effects of earlier spring phenological events being more pronounced in seasonal high-latitude environments (e.g., Both, Van Turnhout, et al., 2009).

The analysis of the consequences of climate change for bird populations and communities has been tackled using diverse approaches and methods, which hamper the possibility to generalize the results. Although the evidence for climate change effects is unambiguous, our understanding on how bird populations respond to climate change in different ecological contexts is incomplete, and impairs our ability to project the future of avian biodiversity under different climatic scenarios (Knudsen et al., 2011; Pereira et al., 2010). For instance, in spite of the vast literature published on phenological shifts, including

meta-analyses (Bitterlin & Van Buskirk, 2014; Dunn & Møller, 2014; Usui et al., 2017), current evidence has focused on a specific phenophase (e.g., Dunn & Møller, 2014; Hällfors et al., 2020; Usui et al., 2017), is limited in time and space (e.g., Bitterlin & Van Buskirk, 2014; Hällfors et al., 2020; Klueen et al., 2017; Vegvari et al., 2010), and/or is restricted to a single or a few species only (e.g., Samplonius et al., 2018; Tomotani et al., 2018). In the present study, we performed a comprehensive meta-analytic synthesis of the effects of climate change on the phenology of different phases of the circannual cycle of birds (i.e., prebreeding migration, breeding, and postbreeding migration) at the worldwide scale, while accounting for phylogenetic relationships of species. We made an extensive literature search combined with a collection of unpublished data that allowed us to compile a database containing more than 5500 effect sizes for phenological changes from 684 species. Our main aim was to compare the temporal change in the phenology of different phases of the avian circannual cycle (i.e., the slope of the linear regression between the date of prebreeding migration/breeding/postbreeding migration and year; see also Usui et al., 2017) among groups of birds with different life-history and ecological traits from different regions of the globe. As predictors, we included traits that have been suggested to affect the strength of phenological response of birds to climate change at a local/continental scale (e.g., migratory behavior, body mass, clutch size, trophic level, nest type) and/or to be linked to behavioral plasticity potentially favoring phenological shifts in response to changing climate (e.g., diet diversity, latitudinal variation in the range of distribution). As climate change has accelerated over the last few decades, we also examined whether the effect was stronger (i.e., steeper slopes) in more recent time series.

MATERIALS AND METHODS

Literature search and data selection

We performed an extensive literature search to find relevant papers according to the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA; Appendix S1: Figure S1) guidelines (<http://www.prisma-statement.org>). We first collected possible suitable studies (including any associated supplementary results) on Scopus, ISI Web of Science, and Google Scholar by combining the keywords “bird/avian” with “timing of migration/breeding,” “arrival/breeding/departure date” or “migration/breeding phenology” and “climate.”

We also carefully screened the references in each paper to obtain the broadest possible coverage of the

literature. In addition, we used all the published information that was included in previous meta-analyses (e.g., Dunn & Møller, 2014; Rubolini et al., 2007; Usui et al., 2017). We extracted data from studies reporting changes in prebreeding migration, breeding, and postbreeding migration phenology over time. In particular, we used data from studies reporting the slope from simple linear regressions between the timing of the aforementioned phenophases and year (days year^{-1}), which is considered a good proxy to estimate the (linear) response of organisms to climate change (see e.g., Cohen et al., 2018; Jonzén et al., 2006; Usui et al., 2017). For studies in which suitable information was reported in graphics, datapoints were extracted with WebPlotDigitizer v3.12 (Rohatgi, 2015) and then re-analyzed using linear regression. We also included studies that reported annual dates of phenological events but did not estimate a trend over time, which was then calculated by linear regression. Whenever we analyzed raw data, we removed the years representing clear outliers (Grubb's tests) and annual data when the phenological variable was estimated using a very small sample size ($n < 4$ individuals/observations). We also included slopes reported in datasets associated with previous meta-analyses (e.g., Dunn & Møller, 2014; Usui et al., 2017). Furthermore, some studies did not report a slope for a given phenophase against year, but a difference in phenology between two or more distinct timespans (e.g., 1950–1970 vs. 1971–2000). If, upon contact, the authors did not reply or did not supply us with the original data, which happened in very few cases, we calculated the slopes using the available information ($n = 76$).

Whenever a study did not report either the value of the slope between phenology and year nor sufficient information to extract it (e.g., nonstatistically significant trends), we contacted the authors to obtain this information or raw data. In some cases, authors also provided us with unpublished datasets, which were converted into slopes and included in our database. Importantly, we also contacted authors who investigated bird phenological variation across time without explicitly analyzing the temporal trend in a given phenophase (e.g., authors analyzing variation in a given phenophase according to variation in temperature, or other climatic factors, across time; e.g., Chausson et al., 2014). Several authors ($n = 29$) kindly provided us with their original data. Although some of these data ($n = 5$) were discarded for the reasons explained below, this procedure allowed us to include in the present meta-analysis a large number of phenological series that were not published in previous studies ($n = 1190$ slope estimates).

The literature survey and data collection were completed on 31 December 2019. Our final database thus includes some papers formally published in 2020, which

were however already available online by the end of 2019. We assume that inclusion of newer datasets (published in 2020 and 2021) would not bias the results presented below, whereas we also infer that the omission of the most recent relevant studies did not raise any power issue given the large sample size we already achieve here.

Similarly to previous studies (Bitterlin & Van Buskirk, 2014; Cohen et al., 2018; Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2002), we discarded phenological time series spanning < 10 years, and including < 5 years of data. In addition, we focused only on time series ending after 1989 in order to capture the most recent trends (Appendix S1: Figure S1).

Most of the studies provided information of entire bird populations, including birds of both sexes. Considering that in many species males and females migrate during different periods and at different speeds (see e.g., Morbey & Ydenberg, 2001; Rubolini et al., 2004 for studies on protandry) and in order to avoid generating a bias in the data, we refrained from including data from studies reporting migration data of one sex only (Appendix S1: Figure S1). Conversely, information on reproduction on one sex only was used because, for example, “male courtship song” and “female laying date” are good proxies of breeding onset of both sexes. Moreover, from the selected papers, we excluded those using different methods to collect recent versus, past phenological information (e.g., Newson et al., 2016), those collecting data on a very small sample size (e.g., Wellicome et al., 2013), and those reporting only significant slopes (e.g., Crick et al., 1997) to avoid generating biases in the data (Appendix S1: Figure S1). Finally, we also excluded papers reporting phenological trends at a continental scale (e.g., Dunn & Winkler, 1999), because it was difficult to associate precise geographical coordinates to these data (Appendix S1: Figure S1).

To avoid “duplication of study” effects (Wood, 2008), a single slope between year and a particular phenophase (e.g., early breeding; see *Definition of circannual phenophases* for details of phenophase identification) in the same species and in the same timespan was included per location by adopting the following criteria. If a given study reported multiple similar measures (e.g., laying date and hatching date; first laying date and laying date of the first 5% of the population), we chose the information which was more common in the database (i.e., laying date and first laying date, respectively). In addition, when a study reported phenological information on both adult and yearling individuals, we used the information about the former only, because we expected it to be more representative of the whole population (Appendix S1: Figure S1).

In some cases, different studies reported information on the same phenophase for the same species and location. Whenever the timespans of different studies did not fully overlap, we included in the database both pieces of information (e.g., Burthe et al., 2012; Frederiksen et al., 2004). Whenever the time series fully overlapped, we selected the longest one. However, in a single case, when the difference in length between the two timespans was very large (Askeyev et al., 2009 reporting the slopes in two different periods: 1811–2008 and 1979–2008) both datapoints were used. In a few additional cases, the same research group published different studies including the same phenological information of the same species in the same location, but in different years (e.g., Bosch et al., 2015; Martínez et al., 2006). Under such circumstances, whenever possible, we integrated all the information and calculated a single slope (Appendix S1: Figure S1).

At the end of these procedures, our database included 5589 slopes for 684 species from 407 studies (both published and unpublished; mean slopes per study: 13.73; range: 1–339). All sources used in the meta-analysis are listed in Appendix S2. Time series spanned over 200 years, with initial year spanning from 1811 to 2007, but the vast majority focused on migration trends starting at least in the second half of the 20th century ($n = 4941$). Considering that the largest effects of climate change are expected to have occurred in the last decades (Masson-Delmotte et al., 2021), all the analyses below were re-run on the subsample of time series starting since 1970 ($n = 3149$). All the results were qualitatively similar to those reported in the “Results” (see below).

Definition of circannual phenophases

We included studies reporting temporal changes in dates of prebreeding migration (i.e., the migration from the nonbreeding to the breeding grounds), breeding, and postbreeding migration (i.e., the migration from the breeding to the nonbreeding grounds). Different studies used a large variety of measures to collect phenological data. As proxies for breeding dates, we used dates of courtship (including emission of courtship songs), mating, nesting, laying, and hatching. As proxies for pre/postbreeding migration, we used dates of departure from nonbreeding/breeding grounds, dates of passage during migration, and dates of arrival in the breeding/nonbreeding ground. We pooled arrival and passage dates even though each reflects a different phenomenon (Gordo, 2007), because it is rarely possible to distinguish transient migrants from newly arriving individuals that will subsequently breed in the area of data collection (but see Usui et al., 2017), especially at high latitudes of

the northern hemisphere where most of the data were collected. To be consistent with this choice and because they represent a very small fraction of pre/postbreeding migration data in our database (~4%, and only 1% for the prebreeding migration), we decided also to include departure dates in the same analyses. In such cases, departure dates from breeding and nonbreeding grounds were included in the analyses of postbreeding and prebreeding migration, respectively. However, analyses performed without departure dates were qualitatively similar to those shown in the “Results” section (details not shown).

Our data were divided into different subsets, depending on whether the time series referred to the phenology of the precocious part of a given population (e.g., the date of the first-arriving individual) or its central value (e.g., the mean arrival date), which represent the two most commonly used measures of timing of migration/arrival/breeding in bird studies (Dunn & Møller, 2014; Lehikoinen et al., 2004, 2019; Rubolini et al., 2007; Sparks et al., 2005; Usui et al., 2017). In the “early” subset we included the data on the phenological variation concerning up to the first 10% of individuals (but mostly the very first individual migrating, arriving or breeding), whereas the “central” subset was composed of data on indicators of the central tendency value of a given phenophase in a given location (e.g., mean, median) or to the peak of the data. These two data types are usually, although weakly, positively correlated (see e.g., Forchhammer et al., 2002; Lehikoinen et al., 2019; Møller & Merilä, 2004; Sparks et al., 2005; but see Goodenough et al., 2015), but they generally reflect two different phenomena. On the one hand, the “central” data are generally considered more robust estimates of the response of a whole population (Goodenough et al., 2015; Lehikoinen et al., 2004), but the very large sampling effort needed to collect reliable “central” data usually limits the number of represented species. On the other hand, the “early” data have been proven to be affected by different potential biases, such as anomalous behaviors (e.g., phenodeviants), sampling effort and population size (Lehikoinen et al., 2004; Sparks et al., 2001, 2005). In addition, they show a strong dependence on short-term meteorological fluctuations. However, temporal trends estimated on “early” data are generally steeper than those observed using “central” data (Lehikoinen et al., 2004). Moreover, these data are easier to collect, including by nonspecialists (e.g., citizen science data), and are therefore more abundant. As there are pros and cons in the analysis of both data types, which may reflect different biological phenomena, and given that pooling all the data would have resulted in pseudoduplication (e.g., because many studies reported both the information on the “early” and “central” value for the same species, phenophase, time period, and geographical location), we performed separate analyses on “early”

and “central” data. This procedure also allowed us to investigate whether not only species characterized by different life-history/ecological features, but also if different groups of individuals within their populations (i.e., those with an “early” or a “central” phenology) are responding differently to climate change in different phenophases. We note that quantile data (i.e., date of migration and breeding of the first of 5%–10% individuals of a given population) are more robust than simple observations of the first individual migrating, arriving or breeding, because the former stems from standardized migration/breeding counts. Thus, these data do not suffer from the issues mentioned above. However, these data (which make up a small fraction of all the data included in the “early” categories) were included in the “early” categories because they nevertheless belong to the leftmost tail of the seasonal phenological distribution.

Furthermore, considering that for postbreeding migration many of the available data reflect changes in the date of the latest part of a given population (e.g., the departure date of the last individual[s]; see also Bitterlin & Van Buskirk, 2014), a third subset (“late”) was defined for the analyses of this phenophase only. This “late” category included all the data concerning the phenological trends calculated up to the last 10% of individuals.

In summary, we considered seven different phenophases in our analyses (Appendix S1: Tables S1 and S2): timing of prebreeding migration of precocious individuals (hereafter “early prebreeding migration,” sample size: $n = 2632$), timing of prebreeding migration of the average individual in the population (“central prebreeding migration,” $n = 1144$), breeding time of precocious individuals (“early breeding,” $n = 449$), breeding time of the average individual in the population (“central breeding,” $n = 526$), timing of postbreeding migration of precocious individuals (“early postbreeding migration,” $n = 120$), timing of postbreeding migration of the average individual in the population (“central postbreeding migration,” $n = 446$), and timing of postbreeding migration of late individuals (“late postbreeding migration,” $n = 272$).

Information on study location and species

Each slope was associated with information about time and location of data collection, as well as with data on the ecological and life-history traits of a given species. In particular, for each study, we recorded the geographical coordinates (latitude and longitude, expressed in decimal degrees, WGS84 ellipsoid), country and continent of the study site (Appendix S1: Tables S1 and S2). Whenever coordinates were reported using other coordinate systems, they were converted to geographical coordinates. When data were collected on a regional scale

(including studies conducted on a country scale), the coordinates of the centroid of the region were used. We also recorded the years of the beginning and end, as well as the number of years of available data, of each time series.

A major aim of the present study was to highlight differences in phenological variation among species displaying different life-history/ecological features. For each species, we therefore collected ecological and life-history traits that have been previously suggested to affect the strength of avian phenological response of at least one of the phenophases included in our analyses and/or to promote behavioral plasticity, thus potentially favoring phenological shifts in response to changing climate. Migratory behavior was coded as a four-level factor, as follows: (1) species spending the nonbreeding period in the same area where they breed were classified as “resident” (these species were included in the analyses on breeding phenology only); (2) partial migrants, that is, species including both (short-distance) migratory and nonmigratory populations, as well as irruptive, altitudinal, nomadic and vagrant species (i.e., species performing irregular or weather-related movements), were globally coded as “partial migrants”; (3) species spending the nonbreeding and breeding periods in geographically distinct areas but within the same biogeographical region (including marine species spending the nonbreeding season in pelagic sea waters) were classified as “short-distance migrants”; (4) species spending nonbreeding and breeding periods in different biogeographical regions were classified as “long-distance migrants.” When different studies reported a different classification of migratory behavior of the same species, we assigned to that species the category that was most represented in the papers included in the dataset. For example, if a species was coded as “short-distance migrant” by four studies and as “long-distance migrant” by eight studies, that species was defined as “long-distance migrant.” However, to account for intraspecific differences in migration, we also re-ran the analyses using a classification that differed from the previous one in two cases: (1) populations of species that are generally migratory were re-coded as “resident” if a given paper declared that the study population was resident in the study area; (2) populations of migratory species breeding in very isolated areas (e.g., Iceland) were re-coded as “long-distance migrants.” Results of the analyses using this alternative coding for migration were always qualitatively very similar to those reported in the “Results” section (details not shown). Conversely, we preferred not to re-categorize migratory behavior at the population level according to the information reported in each paper (see e.g., Usui et al., 2017) because of the different criteria used by different studies (e.g., in many cases the same species was coded as a short- or long-distance

migrant in nearby locations). We also note that in many circumstances the study did not report any categorization of the migration for the studied species, thus making it necessary to use the general criteria described above. However, we note that, although this categorization represents a compromise between species-specific variation in migration strategies and sample size for each category, it does not catch the entire spectrum of variability in movements observed among and within species. This is especially the case for partial migrants, whose migration strategies may vary in space and time, with different populations showing highly variable migration patterns (see e.g., Chapman et al., 2011). In addition, migration strategies may change over time according to actual climatic conditions, with many populations becoming sedentary in the last decades (see Ambrosini et al., 2019). Interpretation of the results about migratory behavior should therefore consider this caveat.

We also coded each species according to whether it typically breeds in cavities (both primary and secondary cavity nesters) or not (i.e., open nesters, weavers and brood parasites). Such a distinction was made because data on cavity nesters may be more readily available and because these species may be more constrained to advance their circannual activities because of competition for nesting sites (see Samplonius et al., 2018; Vegvari et al., 2010).

Data on diet were obtained from Del Hoyo et al. (2017). Food sources considered were: (1) terrestrial invertebrates, (2) aquatic invertebrates, (3) terrestrial vertebrates, (4) aquatic vertebrates, (5) fruits and berries, (6) sedges and seeds, (7) other plant materials (e.g., nectar, grass or aquatic plants). From this information, we recorded the number of food sources representing a substantial contribution to a species' diet to obtain an estimate of diet diversity. In order to generate broad categories including a sufficient number of species to perform more robust statistical analyses, the above-mentioned diet categories were then summarized into a three-level code indicating: (1) specialist species (i.e., species consuming one or two food sources); (2) species consuming an "intermediate" range of food sources (i.e., three or four food sources); (3) generalist species (i.e., species consuming five or more different food sources). Information on the main diet was also used to define the trophic level of each species into a three-level category, including: (1) species mostly eating vegetable matter were coded as primary consumers; (2) species mostly consuming invertebrates (either aquatic or terrestrial ones) were coded as secondary consumers; (3) species mostly relying on vertebrate prey as food were coded as tertiary consumers. We did not include an additional category indicating top predators (i.e., species mostly eating tertiary consumers and generally not being predated by other species) because of the small number of species matching these criteria. A few very generalist

species (e.g., corvids, larids or cranes) can rely on a wide spectrum of food sources, spanning from plants to vertebrates. Because there is no general criterion to define the trophic level of these species and to avoid creating a specific category for them, which almost coincided with the diet diversity information, they were coded as tertiary consumers because they often prey on vertebrates. However, because these generalist species can easily rely on plants as food when necessary, and their phenology is not necessarily linked to the phenology of primary and secondary consumers, we re-ran the analyses while coding these species as primary consumers. These analyses, however, returned similar results to those presented in the "Results" section (details not shown).

Information on mean body mass (g) and average clutch size for each species was extracted from BirdLife International (2015). In the few cases when these data were not available, we searched for missing information on other sources (e.g., Del Hoyo et al., 2017). We also collected the information on latitudinal spread of the breeding range (i.e., the difference between the maximum and the minimum breeding latitude) of each species as a proxy for habitat generalism (see Belliure et al., 2000) from the breeding map reported in BirdLife International (2015).

We discarded some other variables potentially affecting bird phenology, such as diversity of exploited habitats and generation time, because they were highly and positively correlated with at least one of the aforementioned variables (e.g., in our sample the Pearson's correlation between body mass and generation time was 0.77).

Statistical analyses

The analyses were performed with a mixed effects phylogenetic meta-analytic approach using the slope between phenology and year (days year^{-1}) as a dependent variable. This method allows the inclusion of multiple fixed and random effects in a single model (Hadfield & Nakagawa, 2010; Nakagawa & Santos, 2012). Analyses were implemented in a Bayesian setting using the R (R Core Team, 2019) package *MCMCglmm* (Hadfield, 2010). Each datum was weighed (using the *mev* argument) by the reciprocal of the square root of the number of years used to calculate the slope. This procedure thus ensured that slopes estimated over larger timespans were given more weight in the models, but also that the mean estimates of the models were not biased by the slopes estimated over extremely large timespans. Species, study identity and country where the data were collected were included in all the models as random effects.

We extracted 100 phylogenetic trees from a pseudoposterior distribution of species-level bird

phylogenies (Jetz et al., 2012) from www.birdtree.org. The Hackett et al. (2008) backbone was used for this purpose. The phylogenetic information was included in the models as an inverse matrix of the phylogenetic correlation among all the species included in each tree, using the *ginverse* procedure (J. Hadfield, personal communication).

As the phenological data used in the analyses originated from studies performed with different procedures (citizen scientist observations, national monitoring programs, nonstandardized field studies, observatory observations, ornithological club reports, standardized capture and ringing at observatories, standardized field studies; see Usui et al., 2017), we controlled for variance in the quality of data by allowing for heterogeneity of residual variance across these data types with the *rcov* statement of the *MCMCglmm* procedure.

For each of the aforementioned phenophases, we fitted three different models: (1) a *null model*, aiming at estimating the global mean change in phenology over time; (2) a *life-history model*, including life-history features of the species, such as migratory behavior, nest type, clutch size and (log-transformed) body mass, as fixed effects; and (3) an *ecological model*, including ecological features of the species, such as diet diversity, trophic level and latitudinal breeding range as fixed effects. We refrained from fitting models including all the predictors together because of the unbalanced sample size of different levels of each categorical factor. Indeed, the combination of the three categorical predictors we aimed at investigating (migratory behavior, diet diversity and trophic level) always resulted in some combination of categories with no data. For example, in the analysis of central prebreeding migration, primary consumer generalists occurred only among short-distance migrants, and no data were available on partial and long-distance migratory species. In addition, in the same analysis, no species was simultaneously a secondary consumer, a generalist, and a partial migrant. Similarly, tertiary consumer and partial migratory species were always generalists in our dataset. On the one hand, these imbalances in the dataset would clearly impair model estimations. On the other hand, such uneven data distribution among levels of categorical predictors included in life-history and ecological models (Appendix S1: Table S3) could influence result interpretation, and the possible implications are discussed below.

All the models included the same random factors described above and the inverse matrix of the phylogenetic correlation among the species. In order to account for spatial and temporal change in the data, the life-history and the ecological models also included hemisphere, the absolute value of latitude of each study site,

their interaction, and the median year of each phenological series as fixed effects. However, we did not include also the effect of continent in the models both because spatial information was already included (i.e., hemisphere and latitude) and because these predictors were obviously highly collinear, causing large variance inflation and model instability (details not shown). In addition, we note that for the continents located in both hemispheres the phenological slopes might be different in either side of the equator. Importantly, each fixed effect was centered to its mean value (i.e., we subtracted the mean from each value). This procedure was applied also to categorical predictors (e.g., diet diversity) by first converting each of them into a set of dichotomous variables and then centering each dichotomous variable. This procedure was used because it allows comparing the different levels of each categorical variable, after accounting for the concomitant effects of all the other variables.

MCMCglmm models were run for 150,000 iterations on each of the 100 trees, discarding the first 50,000 iterations as burn-in, and sampling every 500 iterations. In order to ensure appropriate sampling of the posterior distribution, these parameters were set after preliminary analyses of autocorrelation across iterations, and after the inspection of trace plots for fixed and random effects. An inverse Wishart prior with $V = 1$ and $\nu = 0.02$ was specified for random effects (Gelman & Hill, 2007).

The results reported below are the combination of the posterior distribution for fixed and random effects of the analyses repeated across 100 trees. We note that the *MCMCglmm* procedure produced 200 estimates of the coefficients for each phylogenetic tree, thus generating 20,000 estimated values of the coefficients over all the phylogenetic trees. Because we are not aware of a reliable procedure to assess the overall significance of categorical factors in *MCMCglmm* models (i.e., a procedure analog to a *F*-test or a likelihood ratio test; J. Hadfield, personal communication), we devised the following procedure to examine the differences among the levels of categorical factors (e.g., between different categories of diet diversity). First, we extracted from the *MCMCglmm* model the 20,000 estimates of all the coefficients of the model and calculated the corresponding 20,000 marginal mean values for that level of the factor. Second, we performed comparisons between each pair of levels of the factor under investigation by calculating the difference between the marginal mean values, thus obtaining a distribution of 20,000 differences for each pair of levels of a factor. Third, we calculated the proportion of differences that were above or below zero and used twice this proportion as the *p*-value for the difference between these levels of the factor under scrutiny. Fourth, we accounted for multiple statistical tests in all the pairwise comparisons

among the levels of a factor by applying the false discovery rate (FDR) procedure of Benjamini–Hochberg (Benjamini & Hochberg, 1995) to these p -values. Factors showing FDR-corrected statistically significant differences ($P_{\text{FDR}} < 0.05$) in at least one pair of their levels were considered significant predictors.

RESULTS

Geographic and taxonomic coverage of the data

Time series spanned >200 years, from 1811 to 2018 (start years between 1811 and 2007, end years between 1989 and 2018), with the vast majority of studies focusing on migration trends in the past 50 years (see above). Time series length ranged from 10 to 198 years, with a mean length of 38.92 years (± 19.30 SD). The number of years in a time series spanned between 5 and 131, with a mean of 32.14 years (± 15.34 SD). Over the 684 species representing 100 families and 25 orders, Passerines comprised 69.0% of the species (Appendix S1: Table S1). From a geographical point of view, most data were collected in Europe (50.05%) and North America (33.65%) (Appendix S1: Table S2). Markedly, no time series was available for South and Central America (Appendix S1: Table S2).

Null models

Overall, birds significantly advanced their prebreeding migration and breeding by 2–3 days per decade depending on the phenophase. Conversely, the postbreeding migration has not changed significantly over time (Appendix S1: Table S4; Figure 1). Results were similar when the analyses were limited to time series collected since 1970, with slopes of prebreeding migration and breeding being generally smaller than those obtained from the analysis of the full dataset (Appendix S1: Table S4).

Life-history models

Temporal change in early prebreeding migration significantly differed among species with different migratory behavior (Figure 2; Table 1; Appendix S1: Table S5), with long-distance migratory species advancing less than short-distance and partial migrants (partial vs. long: -0.133 ± 0.061 SE, $P_{\text{FDR}} = 0.05$; short vs. long: -0.126 ± 0.021 SE, $P_{\text{FDR}} < 0.001$; a negative coefficient indicates a larger advancement in the former group

compared with the latter one), which in turn did not differ (partial vs. short: -0.007 ± 0.071 SE, $p = 0.91$). In addition, early prebreeding migration advanced more in recent years (effect of median year of phenological series: -0.0025 , 95% CI: -0.0048 to -0.0003) and in species with larger body size (effect: -0.0910 , 95% CI: -0.1339 to -0.0474 ; Table 1; Appendix S1: Table S5).

Temporal advancement in central prebreeding migration did not differ significantly among species with different migratory behavior ($P_{\text{FDR}} \geq 0.075$), despite showing a clear trend of more pronounced advancement in phenology with decreasing migration distance (Figure 2; Table 1; Appendix S1: Table S5). However, the differences between partial migrants and the other categories were marginally nonsignificant after controlling for FDR (partial vs. long: -0.207 ± 0.099 SE, $P_{\text{FDR}} = 0.075$; partial vs. short: -0.165 ± 0.097 SE, $P_{\text{FDR}} = 0.10$), whereas the difference between short- and long-distance migratory species was nonsignificant (-0.042 ± 0.035 ; $p = 0.23$).

Advancement in early breeding date was larger in species with larger body size (effect: -0.244 , 95% CI: -0.416 to -0.072), whereas no other fixed effect predicted temporal change in this phenophase (Figure 2; Table 1; Appendix S1: Table S5).

Temporal change in central breeding date showed a trend according to migratory behavior, with resident species significantly advancing their phenology, whereas this was not the case for the other categories (Figure 2; Table 1; Appendix S1: Table S5). However, differences between resident species and the other categories were not significant after controlling for FDR (all $P_{\text{FDR}} \geq 0.23$).

Temporal change in postbreeding migration was not predicted by any geographical or life-history variable (Appendix S1: Table S5). Short-distance migrants delayed late postbreeding migration slightly more than long-distance ones, but the difference was marginally nonsignificant after controlling for FDR (0.197 ± 0.085 SE, $P_{\text{FDR}} = 0.070$).

All models also showed a large variation in phenological shifts between the hemispheres, with the northern one showing a significant advancement in early (effect: -0.209 , 95% CI: -0.298 to -0.124) and central (effect: -0.193 , 95% CI: -0.353 to -0.038) prebreeding migration as well as in central breeding date (effect: -0.194 , 95% CI: -0.329 to -0.073), whereas the trend was not significant for the southern one (Table 1; Appendix S1: Table S5). Central breeding and late postbreeding migration dates advanced more with increasing latitude in the southern hemisphere (Table 1; Appendix S1: Table S5).

Clutch size and nest type did not significantly predict temporal change in any of the phenophases analyzed here (Table 1; Appendix S1: Table S5).

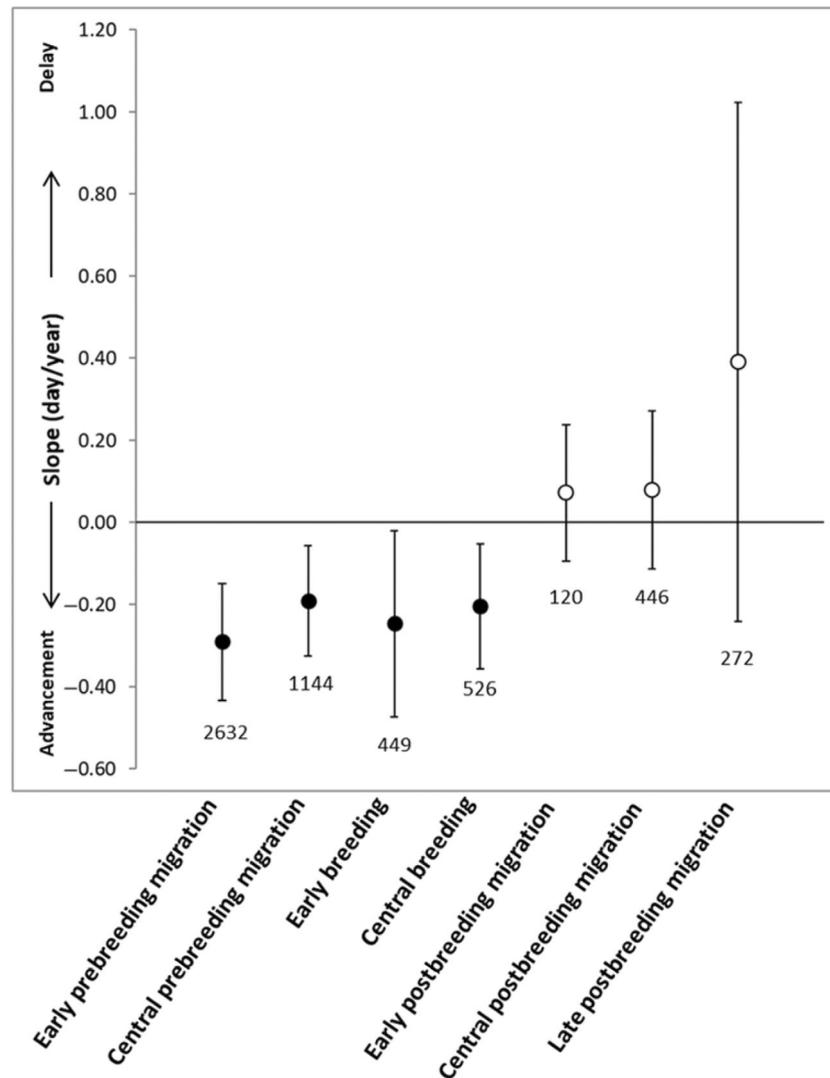


FIGURE 1 Global temporal shifts in phenology (days year⁻¹) of different phenophases across the annual cycle. Error bars indicate the 95% credible interval. Full dots denote estimates that differ significantly from zero (i.e., the 95% credible interval of the estimate does not overlap zero). Estimates are the combination of the posterior distribution of the *MCMCglmm* analyses, that produced 200 estimates of the coefficients for each phylogenetic tree, repeated across 100 phylogenetic trees (i.e., an average value of 20,000 estimated values of the coefficients over all the phylogenetic trees). Negative values indicate an advance in phenology over time. “Early,” “central,” and “late” indicate whether the estimate refers to the onset (i.e., up to the earliest 10% of the population), the mean/median/modal/peak, or the last (i.e., up to the latest 10% of the population) value of a given phenophase. The number of time series is reported close to each corresponding datapoint.

Finally, all results were qualitatively similar when the analyses were performed on time series beginning after 1970 (Appendix S1: Table S5). However, these analyses also showed that the delay in central postbreeding migration was larger in species with larger body size (Appendix S1: Table S5).

Ecological models

Diet diversity and trophic level were significantly associated with changes in early prebreeding migration timing

(Figures 3 and 4; Table 1; Appendix S1: Table S6). Specifically, diet generalist species advanced more than those relying on an intermediate number of food sources (-0.119 ± 0.041 SE, $P_{\text{FDR}} = 0.006$) and diet specialists (-0.163 ± 0.042 SE, $P_{\text{FDR}} = 0.006$). In addition, intermediate feeders advanced more than diet specialists (-0.045 ± 0.021 SE, $P_{\text{FDR}} = 0.0375$). Moreover, secondary consumers advanced less than both herbivores (0.173 ± 0.043 SE, $P_{\text{FDR}} < 0.001$) and tertiary consumers (0.120 ± 0.042 SE, $P_{\text{FDR}} = 0.008$). However, no significant difference was observed between these latter two groups (-0.054 ± 0.056 SE, $p = 0.34$). The analysis also

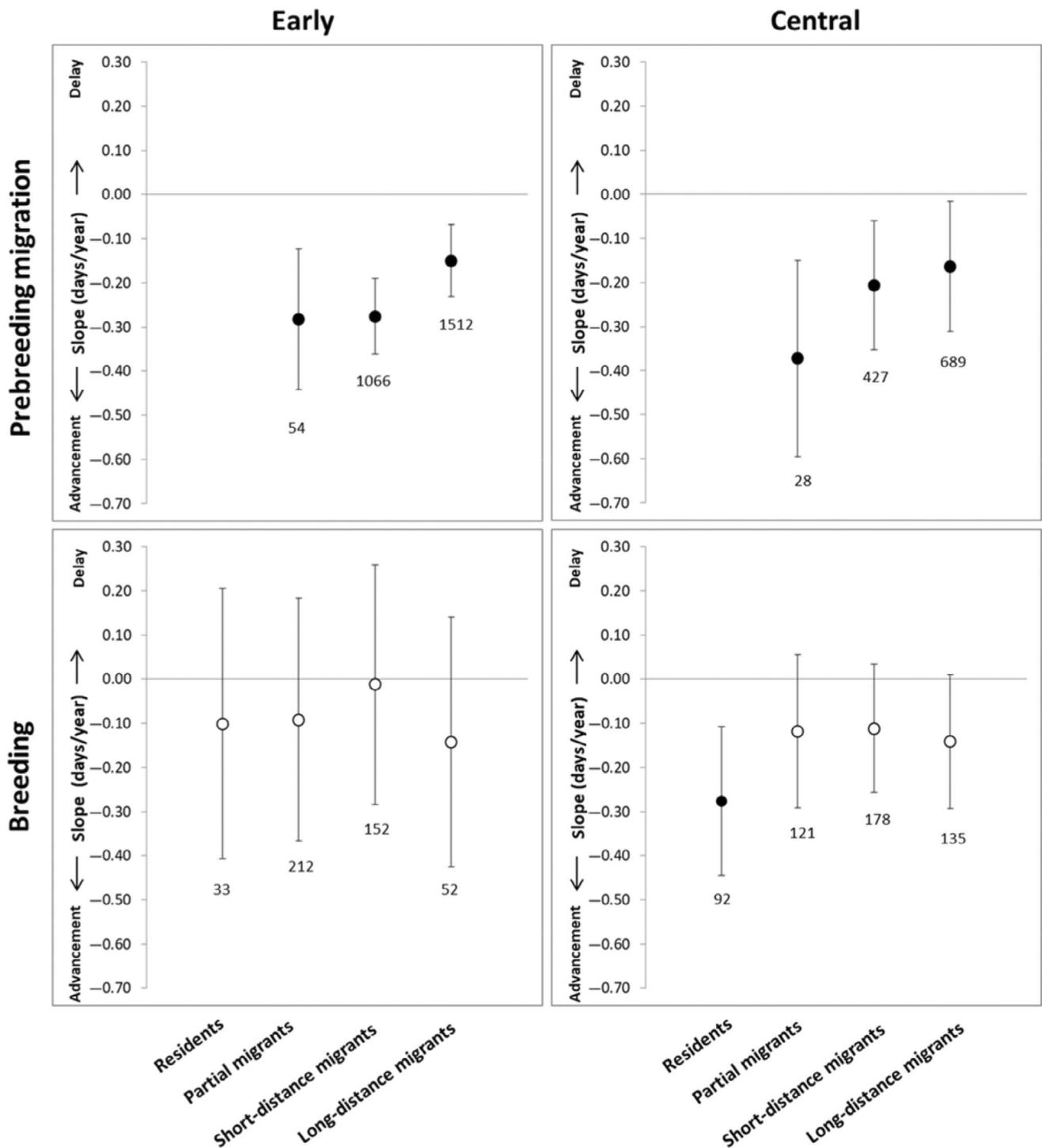


FIGURE 2 Temporal shifts in the phenology (days year⁻¹) of prebreeding migration and breeding according to migratory behavior. Error bars indicate the 95% credible interval. Full dots denote estimates that differ significantly from zero (i.e., the 95% credible interval of the estimate does not overlap zero). Estimates are the combination of the posterior distribution of the *MCMCglmm* analyses, that produced 200 estimates of the coefficients for each phylogenetic tree, repeated across 100 phylogenetic trees (i.e., an average value of 20,000 estimated values of the coefficients over all the phylogenetic trees). Negative values indicate an advance in phenology over time. “Early” and “central” indicate whether the graph refers to the onset (i.e., up to the earliest 10% of the population) or the mean/median/modal/peak value of a given phenophase. The number of time series is reported close to each corresponding datapoint.

confirmed the life-history model result that early prebreeding migration advanced more in recent years (Table 1; Appendix S1: Table S6).

Variation in central prebreeding migration showed similar trends among levels of diet diversity and among trophic levels as those in early prebreeding migration

TABLE 1 Summary of the statistically significant associations of the life-history and ecological variables with avian temporal phenological shifts in prebreeding migration and breeding.

Model	Early prebreeding migration	Central prebreeding migration	Early breeding	Central breeding
<i>Life-history models</i>				
Median year	+			
Hemisphere	×	×		×
Latitude north				
Latitude south				+
Clutch size				
Body mass	+		+	
Migratory behavior	−	(−)		(−)
Nest type				
<i>Ecological models</i>				
Median year	+			
Hemisphere	×	×		×
Latitude north				
Latitude south				+
Diet diversity	+	(+)		
Trophic level	+, −	(+, −)		
Latitudinal range				

Note: For ordinal variables, the symbol “+” indicates that larger values of a given variable resulted in a larger effect size (i.e., steeper negative slope of phenology against time), whereas the opposite is the case for the symbol “−”. The symbol “+, −” indicates that the effect is smaller at the intermediate level of a categorical ordinal factor (i.e., less negative slope at intermediate level). The symbol “×” indicates significant differences between nonordinal factors (e.g., hemispheres). Symbols in parentheses indicate significant effects that disappeared after controlling for false discovery rate. Empty cells indicate no significant effects. For details of the models, the estimates and the 95% credible intervals see text and Appendix S1: Tables S4 and S5.

(Figures 3 and 4; Table 1; Appendix S1: Table S6). Indeed, phenological advancement gradually increased with diet diversity, as well as in primary and tertiary consumers compared with secondary consumers (Figures 3 and 4; Table 1; Appendix S1: Table S6). However, significant differences among levels of diet diversity and among trophic levels disappeared after controlling for FDR (all $P_{FDR} \geq 0.09$).

No fixed factor predicted temporal change in early and central breeding, or in early, central and late postbreeding migration (Appendix S1: Table S6).

Concerning the phenological variation among hemispheres and latitudes, results were very similar to those described above for the life-history models, with a significant advancement in early and central prebreeding migration and mean breeding date in the northern hemisphere (Table 1; Appendix S1: Table S6).

The latitudinal breeding range did not significantly predict temporal change in any of the phenophases analyzed here (Table 1; Appendix S1: Table S6).

Finally, all results were qualitatively similar when the analyses were performed on time series beginning after 1970 (Appendix S1: Table S6).

DISCUSSION

Overall change in phenology over time

Our extensive meta-analytic effort aimed at summarizing temporal shifts in avian phenology in a period of rapid climate change. To our knowledge, this is the only study that investigated in a coherent analytical framework different phenophases covering the entire annual cycle. The results are consistent with previous studies showing a general advancement in the time of prebreeding migration and breeding (Bitterlin & Van Buskirk, 2014; Cohen et al., 2018; Dunn & Møller, 2014; Lehikoinen et al., 2004, 2019; Parmesan & Yohe, 2003; Root et al., 2003; Usui et al., 2017), which varied between 0.19 and 0.29 days per year. These trends were statistically significant and therefore confirmed the substantial global phenological advancement of this taxon. In addition, similarly to previous studies, we did not detect any significant trend in the phenology of the postbreeding migration (see e.g., Bitterlin & Van Buskirk, 2014).

The rate of phenological changes in prebreeding migration and breeding was always large, and generally significant,

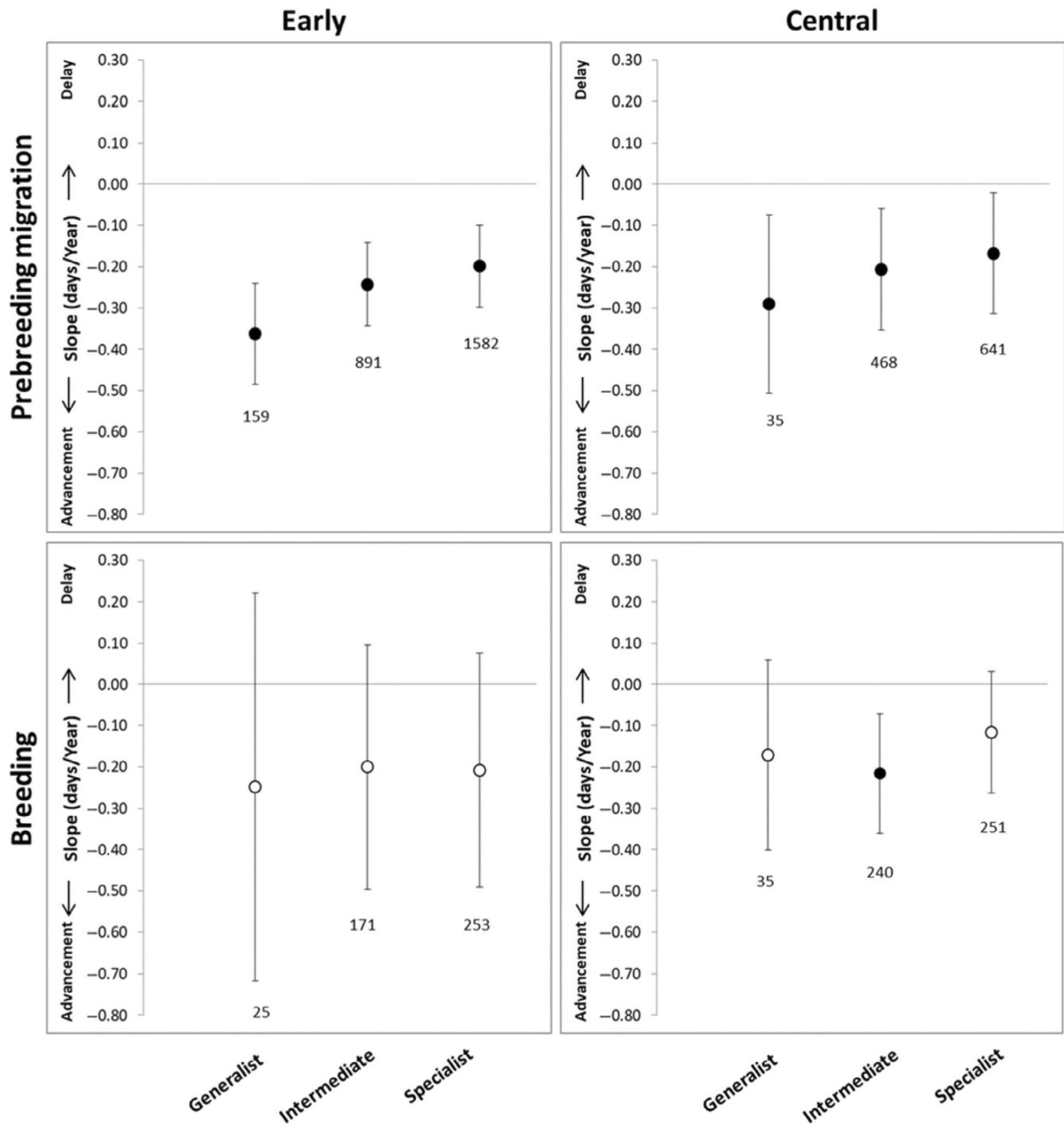


FIGURE 3 Temporal shifts in the phenology (days year⁻¹) of prebreeding migration and breeding according to diet diversity. Error bars indicate the 95% credible interval. Full dots denote estimates that differ significantly from zero (i.e., the 95% credible interval of the estimate does not overlap zero). Estimates are the combination of the posterior distribution of the *MCMCglmm* analyses, that produced 200 estimates of the coefficients for each phylogenetic tree, repeated across 100 phylogenetic trees (i.e., an average value of 20,000 estimated values of the coefficients over all the phylogenetic trees). Negative values indicate an advance in phenology over time. “Early” and “central” indicate whether the graph refers to the onset (i.e., up to the earliest 10% of the population) or the mean/median/modal/peak value of a given phenophase. The number of time series is reported close to each corresponding datapoint.

in the northern hemisphere, but not in the southern one. This result indicates that the phenological shifts are not uniform across the globe and suggests that the effects of climate change have a larger impact in the continents located to the

north of the equator, which is likely to be because the landmasses in the northern hemisphere extend to more polar latitudes than those in the southern hemisphere, and the climate has changed more severely at such subpolar latitudes

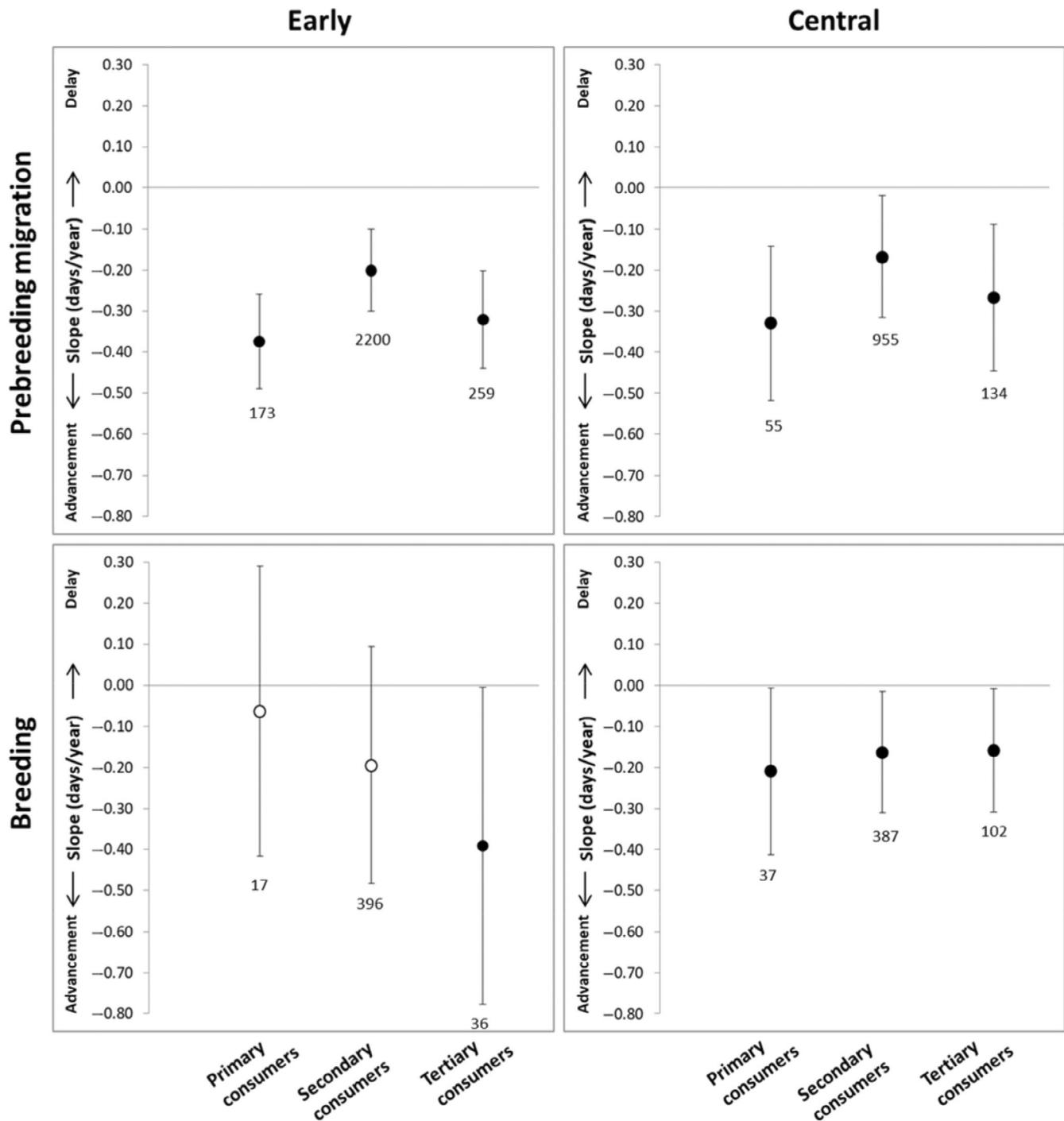


FIGURE 4 Temporal shifts in the phenology (days year⁻¹) of prebreeding migration and breeding of birds according to trophic level. Error bars indicate the 95% credible interval. Full dots denote estimates that differ significantly from zero (i.e., the 95% credible interval of the estimate does not overlap zero). Estimates are the combination of the posterior distribution of the *MCMCglmm* analyses, that produced 200 estimates of the coefficients for each phylogenetic tree, repeated across 100 phylogenetic trees (i.e., an average value of 20,000 estimated values of the coefficients over all the phylogenetic trees). Negative values indicate an advance in phenology over time. “Early” and “central” indicate whether the graph refers to the onset (i.e., up to the earliest 10% of the population) or the mean/median/modal/peak value of a given phenophase. The number of time series is reported close to each corresponding datapoint.

(Masson-Delmotte et al., 2021). However, the continents located to the south of the equator were underrepresented in our database, thus potentially making the estimates for the southern hemisphere less reliable.

Importantly, although a large body of literature has shown that variation in phenology over time is related to the concomitant change in climatic factors, in particular temperatures (see references in the Introduction for

correlative studies; see Verhagen et al., 2020 for an experimental study linking temperature and timing of annual activities), we did not causally link the observed shifts to climate change or climatic-related change in environmental factors. Indeed, many other environmental changes, parallel to but independent of climate change, due to human activity have occurred in the timespan analyzed in the present study (e.g., habitat destruction, urbanization). We cannot therefore exclude that other effects independent of climate change may have contributed to the observed phenological shifts (McLean et al., 2022).

Migratory behavior and phenological shifts

Our study confirms that differences in phenological shifts are linked to differences in migration behavior, with temporal trends becoming steeper with decreasing migration distance. Indeed, resident species advanced timing of breeding much more than migrants, whereas partial and short-distance migratory species advanced the timing of migration more than long-distance migrants. Similar differences have been repeatedly documented by observations at single locations or countries (e.g., Kluehn et al., 2017; Samplonius et al., 2018; Vegvari et al., 2010), as well as by comparative and meta-analytical studies (e.g., Bitterlin & Van Buskirk, 2014; Rubolini et al., 2007; Saino et al., 2011; Usui et al., 2017). Species living in the same location during the entire circannual cycle should be better able to track climatic or other environmental changes at a local scale than those spending breeding and nonbreeding periods in different places (Phillimore et al., 2016). Similarly, birds with breeding and nonbreeding range in a single biogeographic region are subject to the same large-scale climatic variations during the entire year, and thus can rely on a larger amount of reliable information about the ecological and climatic conditions occurring in their breeding sites compared with long-distance migrants (Lehikoinen et al., 2004). Such information can be used to adjust the migration schedule in order to reach the breeding site at a time that avoids mismatches with the phenology of populations or abiotic conditions on which they are dependent. This is not the case for long-distance migrants (Both, 2010), whose migration schedule is more strictly controlled by the photoperiod, which is independent of climate change, and endogenous circannual clocks (Berthold, 1996). Moreover, migration timing is also constrained by different factors, such as the crossing of large ecological barriers (Åkesson & Hedenström, 2000; Tøttrup et al., 2012), and by carry-over effects of previous annual activities (Ambrosini et al., 2019; Saino et al., 2017), such as

plumage molt occurring at the nonbreeding grounds, resulting in a less marked advancement in their phenology.

Trophic ecology and body mass effects on phenological shifts

Another important finding of our study is that the trophic niche might affect phenological responses. Diet generalists and primary consumers, in particular, tended to advance their phenology more than species adopting other diets. These differences were particularly large for prebreeding migration. One possible explanation for the larger advancement with increasing level of diet heterogeneity is that species relying on several sources of food are not as constrained by the phenology of few prey species to which they are ecologically linked as specialist species are, and therefore might be more flexible to adjust the timing of different annual activities (e.g., in response to rising temperatures) while still finding enough resources (i.e., they can use the most readily available food among the many ones they can exploit). Alternatively, we note that diet heterogeneity and migratory behavior are correlated in our dataset, and therefore this correlation may have also contributed to generate the observed pattern (see below for details). This type of link between diet complexity and variation in phenological response to climate change was previously documented only by studies performed at a rather small geographical scale (e.g., Kluehn et al., 2017; Vegvari et al., 2010). Our study confirms that this pattern can be generalized at the global scale.

In addition, herbivores seem to be better able to respond to an advancement of “spring events.” Compared with secondary consumers, these species may more efficiently exploit the earlier phenology of vegetation, which has particularly advanced in the last decades (Ge et al., 2015; Root et al., 2003; Thackeray et al., 2010, 2016; but see Ovaskainen et al., 2013). This result is consistent with previous studies comparing different taxa, from primary producers to secondary consumers (Both, Van Asch, et al., 2009; Thackeray et al., 2010, 2016), or herbivore versus carnivore animals (Cohen et al., 2018), and it provides evidence that such a pattern can be generalized across bird groups and different circannual phases (see also Dunn & Møller, 2014). Why this effect is larger for prebreeding migration compared with breeding is a matter for speculation. A possibility is that, according to the so-called green-wave hypothesis, during migration across seasonal habitats birds exploit the flush of spring growth of forage plants at each stopover site along latitudinal gradients (Marra et al., 2005; Mcgrath et al., 2009; Thorup et al., 2017). Under such circumstances, feeding

rate, particularly of herbivores in the early phase of migration, should be enhanced (Marra et al., 2005; Mcgrath et al., 2009). At temperate latitudes, increasing temperatures are therefore expected to improve conditions for migration by potentially decreasing stopover duration through an increase in food availability at stopover sites, particularly for first-arriving migrants, which can benefit from their early passage in a rich environment (Moore & Yong, 1991; Ottich & Dierschke, 2003). Moreover, primary consumers seem also to delay their postbreeding migration by ~1 day per decade more than other species (but difference among these categories of birds was not significant), thus indicating that the duration of their breeding season considerably increased (see also Hällfors et al., 2020). These findings might indicate that these birds have exhibited a particularly adaptive response to climate change, with the possibility to invest a large amount of energy in reproduction without being constrained by an early start of postbreeding migration.

Furthermore, we observed a significant difference in phenological change between secondary and tertiary consumers for prebreeding migration, but in a direction opposite to expectations. Indeed, tertiary consumers advanced their migration timing more than species relying mainly on invertebrates. This is in contrast with previous studies at specific locations showing that some predators are shifting their phenology at a lower rate than the insectivorous birds they hunt (Both, Van Asch, et al., 2009; Nielsen & Møller, 2006). From our results, and consistently with a previous meta-analysis of timing of breeding (Dunn & Møller, 2014), we therefore cannot conclude that higher trophic levels are providing insufficient responses according to changing phenology of lower levels, and that a mismatch between the timing of predators and prey is systematically occurring because of climate change. As also shown by a recent study investigating the phenological synchrony of interacting species (Kharouba et al., 2018), the direction of shift was not consistent among pairs of species and it appear to depend on the specific conditions occurring in each predator–prey system (e.g., degree of specialization in the interaction). We note that this effect emerged only in the phenology of prebreeding migration and it might be driven, at least partly, by the observation that the advance in migration phenology is more expressed in larger species (which are more likely to be tertiary consumers) than smaller ones. However, it is interesting to note that the effect of body size is significant for the onset of prebreeding migration and breeding, but not for mean dates of both phenophases. This result is consistent with a previous meta-analysis on bird migration (Usui et al., 2017), thus possibly indicating that larger species are better able to advance their annual activities especially in

the earlier, colder, part of a given phenophase, because they have more body reserves to survive the harsh environmental conditions. Conversely, smaller birds might be constrained in their activity by thermoregulation problems or by extreme meteorological events. Alternatively, larger-bodied species, that live longer, may show a larger phenotypic plasticity because they may be better able to adjust their phenology to year-to-year climatic variability based on experience.

Difference in temporal trends between prebreeding migration and breeding

An open question remains as to why ecological and life-history covariates have stronger effects on prebreeding migration phenology shifts than on breeding phenology shifts. The only life-history trait that predicted breeding phenology of birds, although marginally, is migratory behavior, with resident species advancing their breeding times, whereas the other ecological traits were not linked to shifts in breeding phenology. This result is consistent with a previous meta-analysis on European and North American species (Dunn & Møller, 2014). In addition, studies on single well studied populations showed that the same variation in climate can have differential effects on different life stages and that such effects are not causally linked across the circannual cycle (e.g., Tomotani et al., 2018, 2019). A possible explanation of such a discrepancy is that there is a strong selection for early migration and arrival dates due to rapid changes in climatic conditions at the nonbreeding grounds and en route, but once the birds arrive at the breeding grounds, they might be constrained to delay breeding if the environmental conditions are unfavorable. Moreover, given the importance of reproduction in determining annual fitness, most populations/species advanced their reproductive activities, irrespective of their biological and ecological features, in a way that limits the mismatch with the phenology of other organisms, even if this advancement implies that they are reducing the timespan between arrival from prebreeding migration and the onset of breeding (Hällfors et al., 2020). Under such a scenario, birds that are more exposed to the consequence of climate change during migration might pay the costs of an early reproduction because they may not be in an optimal condition when they start reproducing (e.g., because they may have not fully recovered from migration) and therefore suffer a cost in terms of quantity and quality of offspring, as well as in terms of future survival prospects. Alternatively, it is also possible that diet traits play a major role during the first part of the season (i.e., before breeding), and become less important later in the season. However, we cannot exclude the possibility that the different number of species and time series included in

the analyses of these two phenophases might have also affected our results.

Variation in the strength of phenological change over time

Our results indicate that phenological shifts in the early and central prebreeding migration were more pronounced in more recent time series. This is not surprising because global warming has intensified in the last decades (Masson-Delmotte et al., 2021), especially at temperate latitudes, where a large fraction of the analyzed data has been collected. As the increase in temperature, together with the change in other climate-linked and socioeconomic factors, has been faster in more recent decades, this result could be explained by the capacity of birds to respond plastically according to environmental changes. This finding may also suggest that birds are adapting to ongoing rapid climate change, and possibly have the evolutionary potential to adapt further. Obviously, the two interpretations are not mutually exclusive, and the observed pattern might be the consequence of both mechanisms acting together (Charmanier & Gienapp, 2014).

Postbreeding migration

Our analyses did not show any significant trend over time in phenology of the postbreeding migration. In addition, none of the life-history or ecological variables analyzed significantly predicted a change over time in postbreeding migration. These findings might be due to a general larger variation among species in the change over time in the phenology of postbreeding migration—and this clearly emerges for late postbreeding migration—compared with that of the opposite journey, consistently with previous studies (see e.g., Bitterlin & Van Buskirk, 2014; Jenni & Kéry, 2003; Van Buskirk et al., 2009). Indeed, although the timing of postbreeding migration may carry over until the following breeding season (see e.g., Ambrosini et al., 2019; Saino et al., 2017), the fitness consequences of an early departure in postbreeding migration are predicted to be much less intense than for early prebreeding migration, possibly resulting in a weaker selection and more variable phenological shifts. In addition, the departure from breeding grounds is in part constrained by the timing of postbreeding molt (Bitterlin & Van Buskirk, 2014; Van Buskirk et al., 2009), a factor that can considerably vary among species but was not considered in the present study. Finally, the large among- and within-species (e.g., differences between age classes and sexes) variability in the postbreeding migration (and molt)

strategies of the taxa included in our sample, together with the relatively small amount of data available, might have acted together to generate weak temporal shift estimates and perhaps prevented detecting significant effects of ecological and life-history traits.

Biases in the dataset

A large amount of data concerning the temporal shifts in avian phenology was available for this meta-analysis. Due to ecological and historical reasons, most of the information concerns phenological shifts in breeding and prebreeding migration in the northern hemisphere, particularly in North America and Europe (see also e.g., Dunn & Møller, 2014; Lehikoinen et al., 2019; Usui et al., 2017). Further studies from other continents are therefore needed in order to provide a full picture of the responses of birds to climate change at the global scale. This is especially true considering that large differences exist between the migratory systems in different continents, with, for example, most migratory species living in the southern hemisphere mainly migrating within a single continent and rarely across the equator (see e.g., Bussi ere et al., 2015). In addition, information about whether and how tropical species changed their phenology over time (whether or not the changes are due to climate change) is virtually nonexistent. Moreover, there is also a lack of reliable information about some circannual phases concerning even many well studied species, such as the time of departure from the nonbreeding grounds, which is an essential, although rarely collected, information to fully understand the mechanisms underpinning temporal variation in the timing of migration, as well as information on postbreeding migration, which is still scant and mostly collected in only a few well known locations (e.g., bird observatories; Jenni & K ery, 2003). A further limitation of comparative studies investigating phenological shifts is that many bird families and orders are underrepresented (e.g., Bucerotiformes, Psittaciformes), or even absent (e.g., Tinamiformes), in studies of climate change effects on the timing of their circannual activity.

Moreover, it is important to also note that, in some cases, data distribution was uneven among levels of categorical predictors included in life-history and ecological models (see Appendix S1: Table S3), and this may have affected some of our conclusions. For example, in both early and central prebreeding migration datasets, most long-distance migrants are secondary consumers, diet specialists, or both, thus implying that their weak advancement in phenology might be also due to their diet features, and vice versa. Similarly, in the central breeding dataset, most primary consumers are also resident. Thus, we cannot rule out the possibility that the significant

phenological differences observed in some analyses between groups of species with different migratory behavior may be due, at least partly, to differences in their diets. Our results should therefore be interpreted bearing this caveat in mind.

Concluding remarks

Despite these limitations, our synthesis consolidates the growing evidence of the potential effects of rapid climate change on phenological shifts in the most diverse group of terrestrial vertebrates. This study pinpoints previously unidentified generalities in the phenological responses of birds to climate change, showing that the phenology of species with different life-history and ecological features is responding at different rates. We suggest that the strength of phenological adjustment may be predictable based on some traits, including migration, diet and body size. Temporal shifts in phenology are thus not universal across avian taxa, and may be insufficient to track changing climatic conditions for many species (Radchuk et al., 2019). Because climate change is predicted to intensify in the coming decades, these results could improve our knowledge about the sensitivity of different bird groups to global warming, and to help prioritize conservation actions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Romano, 2022) are available in UNIMI Dataverse at https://doi.org/10.13130/RD_UNIMI/JNNSCX.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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