

Shifts in vegetation phenology along flyways entail varying risks of mistiming in a migratory songbird

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Abstract. Long-term shifts in vegetation phenology generally follow the pattern of global warming. Yet, topographical complexity and biome diversity cause uneven spatial trends in the phenological response of vegetation to climate change. If phenology changes similarly along migration routes, individuals may adequately respond by shifting the whole migration schedule to still time life history with local phenological events. On the contrary, phenological shifts that differ in direction or magnitude between sites can enhance the risk of mistiming, resulting in reduced survival and reproductive success and eventually population declines. We identified the direction and magnitude of long-term shifts in vegetation phenology along avian migration routes, using remotely sensed vegetation data over 29 yr (1982–2010) to estimate the risk of mistiming for different sets of assumptions concerning cues and adaptability of migration timing. For this study, we used individual series of non-breeding, spring stopover and breeding sites (determined by light-level geolocation) of three European populations of *Luscinia megarhynchos* (Common Nightingale), an insectivorous Palearctic long-distance migrant. The breeding populations in France, Italy, and Bulgaria are representatives for populations migrating on the western, central, and eastern flyway toward sub-Saharan Africa. The direction and magnitude of phenological shifts differed between migration stages and across flyways and under most sets of assumptions, the resulting risk of mistiming was higher in the Western compared to Central and Eastern flyway. We emphasize that estimates for the risk of mistiming as resulting from phenological shifts highly depend on the cues that migrants use to time migratory progression and on the adaptive potential of the particular migratory species to react to phenological shifts.

Key words: bird migration; climate change; geolocation; green-up; normalized difference vegetation index; seasonality; vegetation phenology.

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INTRODUCTION

The timing of life-history activities, particularly migration and breeding, strongly influence the

demographic parameters of migratory animals (Gordo et al. 2013, Clark et al. 2014, Johansson et al. 2015). If migrants stay at sites when local resources peak (van Wijk et al. 2012), they can

swiftly replenish body reserves and move on to subsequent sites (Schaub et al. 2008). In contrast, arriving outside the optimal time at a site can lead to diminished fuelling rates (Cohen et al. 2015), tardy arrival at subsequent sites and reduced survival (Baker et al. 2004). If this late arrival concerns the breeding site, this may delay the onset of reproduction, resulting in reduced reproductive output, because the offspring's energy needs and the availability of high quality food are mistimed (van Asch and Visser 2007, Burger et al. 2012).

The current climate changes have influenced the phenology of many biotic processes worldwide (Parmesan and Yohe 2003, Stocker et al. 2013). Although rising temperatures often lead to advances in seasonal processes (Menzel et al. 2006), shifts in phenology vary across regions, continents, biomes, and trophic levels (Walther et al. 2002, Badeck et al. 2004, Zhang et al. 2014, Fontaine et al. 2015). Such variable shifts in phenology may pose particular challenges to migratory animals as they typically use several distant sites in their annual cycles (Cresswell 2014).

To assess the risk of mistiming that migrants may be facing, it is thus an important first step to know local phenology on sites used by migrants and their recent changes. If, for instance, phenology changes similarly at all sites visited, it would be sufficient if migrants simply shifted the whole migratory schedule to retain the desired match between migrant staging and local phenology. However, if trends differ geographically—be it their direction and/or magnitude—this may entail a considerable risk of mistiming and possibly reduce survival or reproductive success.

Over the past decades, the population sizes of many migratory animals have been decreasing (Inger et al. 2015) with long-distance migrants being apparently at a higher risk than short-distance migrants (Sanderson et al. 2006, Vickery et al. 2014). There are many underlying reasons for these declines but uneven phenological shifts are among the prime (causal) factors (Jones and Cresswell 2010). Comparing trends in vegetation phenology between sites migrants use throughout the year would allow us identifying whether species and populations on particular flyways are at risk (of mistiming).

As a first step toward this goal, we identified direction and magnitude of shifts in

vegetation phenology along spring migration flyways of an insectivorous Palearctic long-distance migrant bird, the Common Nightingale (*Luscinia megarhynchos*). To this end, we analyzed normalized difference vegetation index (NDVI)-derived measures for the local phenology of non-breeding, stopover, and breeding sites of Nightingales from three European populations (see Emmenegger et al. 2014; Hahn et al. 2014). We quantified changes in these measures over a 29-yr period for each site and compared direction and magnitude of changes along flyways to estimate the risk of mistiming. We assumed that there is a higher risk of mistiming if phenology changes into different directions within an ensemble of sites and similarly, that a greater magnitude of changes also increases the risk of mistiming. Since it is not known in detail which cues trigger the timing of migration in nightingales and their capability of adapting to a certain rate of phenological change, we apply complementary sets of assumptions to estimate risks of mistiming. If, for instance, photoperiod is the only cue for birds to start migration, local phenology will have no influence on migration schedules. In contrast, if migratory departures are triggered by a specific stage of vegetation development, shifts in phenology on any site will change the timing of migratory steps. Therefore, we considered either only the direction (D) or both direction and magnitude (M) of phenological shifts (1) only at the breeding sites; (2) at both breeding and non-breeding sites, and (3) at all sites, i.e., non-breeding, stopover and breeding sites, resulting in six complementary sets of assumptions.

Since ecological mismatches not only impact individual fitness but also translate into population trends, we expect that we will find a higher risk of mistiming within the flyways of declining populations than within those of stable or increasing populations. Long-term data from monitoring schemes indicate a general decline in the western European populations, whereas central and eastern European populations were found to be stable or even increasing (Burfield et al. 2004, PECBMS 2013). Thus, we expect to find higher risks of mistiming in western European populations, like the one in France, compared to central and eastern European populations, like Italy and Bulgaria.

METHODS

Study populations and geolocators

We considered non-breeding, stopover and breeding sites of *Luscinia megarhynchos* (Common Nightingale) from three European populations—a western (France, $n = 4$), a central (Italy, $n = 1$), and an eastern population (Bulgaria, $n = 4$)—identified by light-level geolocation in earlier work (Emmenegger et al. 2014, Hahn et al. 2014). All three populations spend the non-breeding period in sub-Saharan Africa from the West African coast to eastern Sudan. Individuals departed from the non-breeding sites on average on 23 March. The three populations used relatively distinct flyways between nonbreeding and breeding sites: a western flyway via the Strait of Gibraltar, a central along

Italy and an eastern around the Levantine Sea. Intermediate stopovers were spread across the whole Mediterranean region, with individual sites in Spain, southern France, Corsica, northern Algeria, Tunisia, and Libya. Individuals arrived on these stopover site on average on 31 March, stayed for approx. 13 d and reached the breeding sites on average on 19 April (Fig. 1; for individual routes and timing, see Emmenegger et al. 2014; Hahn et al. 2014).

Vegetation phenology

For each non-breeding, stopover, and breeding site, we characterized vegetation phenology for the whole year. To this end, we acquired remotely sensed NDVI data from the Global Inventory Modelling and Mapping Studies (GIMMS) dataset (Box et al. 1989, Tucker et al.

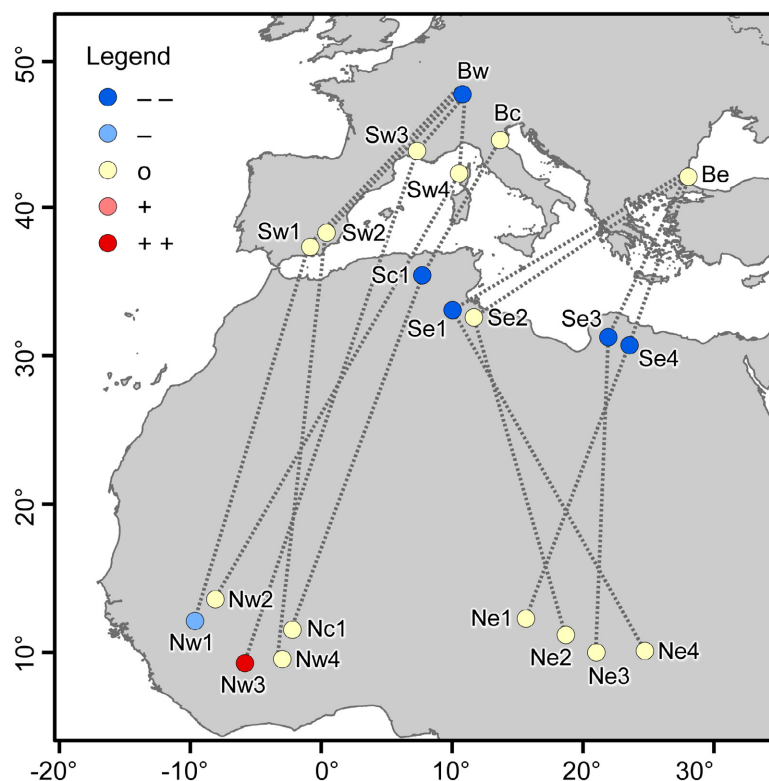


Fig. 1. The direction and magnitude of the shift in green-up dates from 1982 to 2010 at the non-breeding sites, stopover sites, and breeding sites varying from severe advancement (---, dark blue) through no significant change (o, light yellow) up to severe delay (++, dark red). Capital letters in the site-coding stand for the phase of the annual cycle (N, non-breeding; S, stopover; and B, breeding), lower case letters stand for the geographic course of the flyway (w, west; c, central; and e, east) and the numerals continuously number the sites from west to east. The combinations of sites used by individuals of the study populations are connected with dotted lines.

2004). For each site, we determined the 90% isopleths (i.e., the contour line that connects points of equal density) of a kernel density estimation on raw positions, extracted NDVI values for this polygon from January 1982 to December 2010 and averaged pixel-based weekly NDVI values within the polygon area. NDVI values theoretically range from -100 to 1,000, where values <0 indicate snow, bare areas or very sparse vegetation/low primary production and high values indicate dense vegetation/high primary production (Box et al. 1989).

We characterized NDVI dynamics (see Appendix S1: Tables S1–S3) at a particular site by fitting a logistic regression to the weekly unitless NDVI values over time (Pettorelli et al. 2005):

$$\text{NDVI}(\text{time}) = \frac{\text{Asym}}{1 + \exp\left(\frac{\text{xmid} - \text{time}}{\text{scal}}\right)}$$

where Asym (unitless as the NDVI) represents the maximum NDVI values, scal (unitless) the slope of change in NDVI values, and xmid (week of the year) the inflection point of the logistic regression, i.e., the time when NDVI-values increase most steeply (see exemplary regression plots in Appendix S1: Fig. S1). We define this latter measure (converted to day of the year; DOY) as the local green-up and thus, as a measure for the onset of spring.

Subsequently, we quantified shifts in local green-up date by applying a linear regression to yearly green-up dates over the period 1982–2010. If there was a shift in green-up dates, we expected a slope significantly different from zero in this regression; a positive slope indicating a shift towards later green-up dates (“delayed springs”) and a negative slope indicating advanced springs. In addition to these directions of changes, the absolute value of the slope quantifies the magnitude of the change, i.e., how many days per year the green-up date had been shifting.

Risk of mistiming

We estimated the risk of mistiming for sets of non-breeding, stopover and breeding sites. If there were more than one non-breeding or stopover site within a flyway, we calculated the risk of mistiming for all possible

combinations of non-breeding and stopover sites (see Appendix S2). This assumes that the non-breeding and stopover sites we identified are a representative sample of sites within the three flyways. Although long-term tracking studies for nightingales are lacking to date, individuals of a closely related species (*Luscinia luscinia* Thrush Nightingale) repeatedly used the same stopover sites in subsequent migrations (Csörgő and Lövei 1995).

Inferring the risk of mistiming from local phenological shifts requires us to make assumptions about the (local) factors that trigger migratory departures. As it is notoriously difficult to identify the cues for migratory decisions, we consider three assumptions of how the timing of migration is linked to the phenology of specific sites. In the first (1), we assume the timing of migratory progression to be independent of phenology on any site (e.g., only resulting from internal clock or photoperiod-driven) but the timing of arrival in the breeding sites/onset of breeding has fitness-consequences, e.g., on reproductive success. In the second (2), we additionally assume that the timing of departure from the non-breeding grounds involves local phenological cues (and that conditions on stop-over sites are irrelevant to migratory progression). Finally, in the third (3), we assume that timing of migration is modulated by local phenology on all sites.

Moreover, we considered either only the direction (D) of changes or also their magnitude (M; see Appendix S2: Tables S1 and S2 for detailed description of the risk estimation process). We assume that nightingales are limited in their capacity to adapt to changing phenology. Since no studies have targetly quantified such a limit yet, we estimated an attainable rate of change from a meta-analysis (Table 2 in Gienapp et al. 2007). Consequently we assumed that nightingales are able to cope with changes in phenology up to 0.4 d/yr, which is the 10% quantile of the phenotypic rates of change in avian migration time found for long-distance migrants in the meta-analysis mentioned above. Accordingly, when vegetation phenology changed more than 0.4 d/yr—regardless of whether advancement or delay—this was considered a severe change and changes between -0.4 and +0.4 d/yr were considered slight changes.

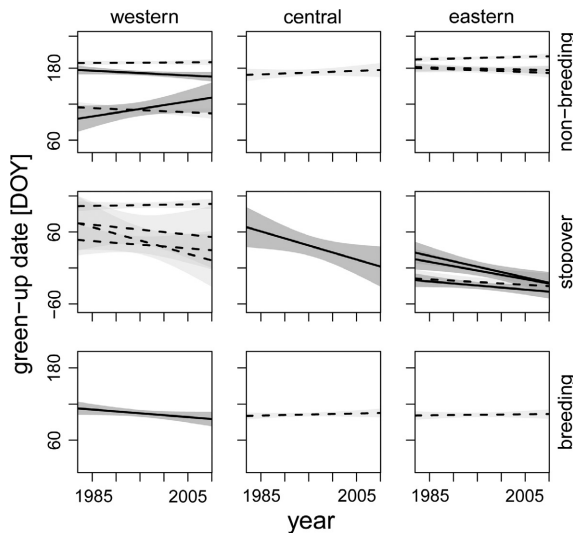


Fig. 2. Green-up date (day of year [DOY]) from 1982 to 2010 at all sites used by individuals on the three flyways. Significant linear shifts are presented as solid regression lines with 95% confidence intervals (dim gray areas). Dashed lines indicate there was no significant long-term shift in green-up date (confidence intervals are given in pale gray). Because DOY is a circular unit and green-up date can also shift over the turn of the year, we were forced to use values below 0.

By combining the three assumptions on use of the cues with either only the direction or both direction and magnitude of shifts in vegetation phenology, we ended up with six sets of complementary assumptions (D1–M3), which enable us to link our shifts in NDVI phenology with a risk assessment for the related bird populations.

Maps were prepared in ArcGIS (ESRI 2011) and all other analyses performed in R (R Development Core Team 2012).

RESULTS

Shifts in vegetation phenology

Direction and magnitude of shifts in green-up dates varied between sites and flyways (Figs. 1 and 2): Green-up dates did not significantly shift at the non-breeding sites in Central Africa and three of five sites in West Africa (all $P > 0.1$). However, at one west-African site, green-up tended to advance by 0.4 d/yr (Nw1: $r^2 = 0.123$, $P = 0.086$) and tended to delay by 1.3 d/yr at another (Nw3: $r^2 = 0.128$, $P = 0.086$). At two

of five stopover sites at the North African coast, green-up dates have advanced (Se3: -1.5 d/yr, $r^2 = 0.253$, $P = 0.009$, Se4: -1.8 d/yr, $r^2 = 0.313$, $P = 0.003$) and at two sites there was a tendency toward advancement (Se1: -0.7 d/yr, $r^2 = 0.153$, $P = 0.053$; Sc1: -2.4 d/yr, $r^2 = 0.128$, $P = 0.086$). Neither of the four stopover sites at the north Mediterranean coast showed significant shifts in vegetation phenology (all $P > 0.1$). Similarly, there was no significant shift in green-up dates for the eastern and central European breeding sites but green-up dates have advanced at the western breeding site (Bw: -0.6 d/yr, $r^2 = 0.129$, $P = 0.078$; at an alpha level of 0.1; see Fig. 2 and Appendix S3: Tables S1–S3).

Risk of mistiming

Depending on the set of assumptions applied, the risk of mistiming—which was estimated based on three assumptions concerning cues triggering migration timing, combined with either only the direction (advancement, no change, or delay) or both the direction and magnitude (severe or non-severe/slight changes) of the shift in phenology—varied considerably between flyways (Fig. 3).

When we only considered phenological shifts in the breeding areas (assumption 1), only the Western population would be at a risk for mistiming—regardless of whether we only consider direction (D1) or both, direction and magnitude (M1). When we considered the direction of phenological shifts in both non-breeding and breeding sites (assumption 2), the Western flyway still has a higher risk of mistiming compared to the Central and Eastern flyways and this difference is even pronounced when additionally considering the magnitude of changes (M2) compared to the direction of change (D2) only. However, when we consider phenological shifts at non-breeding, stopover, and breeding sites (assumption 3), the differences in risk of mistiming between the flyways level out at moderate levels. While the Western and Eastern flyways reached the same intermediate risks of mistiming when only considering the direction of changes (D3), it was slightly higher on the Central flyway. This overall pattern slightly changed when direction and magnitude of the phenological shifts were considered (M3) with the Eastern flyway featuring a slightly higher

shift assumptions →	direction only (D)			direction & magnitude (M)		
	west	central	east	west	central	east
↓ cue assumptions	n=4	n=1	n=4	n=4	n=1	n=4
breeding site only (1)	Red	Green	Green	Red	Green	Green
non-breeding & breeding site (2)	Orange	Green	Green	Orange	Green	Green
all stationary sites (3)	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow

Fig. 3. The risk of mistiming estimated based on the shifts of vegetation phenology (see Fig. 1) and under the premises of the six sets of assumptions (D1–M3). Assumptions 1–3 delineate the cues triggering migration timing. Assumptions D and M describe whether only the direction or both direction and magnitude of the shift in vegetation phenology was used. The color gradient differentiates risk of mistiming from the highest possible risk shown in red over intermediate risk shown in yellow to no risk of mistiming shown in dark green. For visualization of the procedure of risk estimation, see Appendix S2: Tables S1 and S2.

risk of mistiming than the Western flyway (for details on resulting risks of mistiming, see Appendix S2: Table S2).

DISCUSSION

We identified shifts in local vegetation phenology that varied in both direction and magnitude between three flyways of a long-distance migrant, which is clearly in line with earlier studies (Fontaine et al. 2015). We hypothesized that these uneven phenological shifts result in risks of mistiming. But whether, indeed, these shifts incur a risk of mistiming, depends on both the cues that determine the timing of migration and the costs of matching or mismatching local phenology (Both et al. 2010).

Shifts in vegetation phenology

Both in terms of direction and magnitude, earlier studies have found similar trends in phenology, e.g., Zhang et al. (2014) reported moderate, but mostly non-significant shifts of green-up dates (−0.77 to +0.93 d/yr for central to northern Africa; −0.68 to 0.21 d/yr in Europe). While the annual rates of change match the ranges we found for the African (−2.4 to +1.3)

and European (−0.6 to 0 d/yr) sites, we found more distinct and significantly advancing trends in some stopover sites in the Mediterranean and one of the breeding sites. The disagreement might be caused by methodological differences, because Zhang et al. (2014) averaged phenological trends across larger areas at the scale of biomes.

Our results are also in accordance with trends identified in basic meteorological variables (Walther et al. 2002). However, these can only be compared to shifts in NDVI-derived measures if it is known which of those variables are driving vegetation phenology in a region, e.g., mainly spring temperatures in Europe but precipitation in much of Africa and the Mediterranean. The trends in precipitation varied regionally ranging from slightly increasing to slightly decreasing for western Africa and no changes for central Africa—which is in accordance with the heterogeneous shifts we found for our non-breeding sites. All stopover sites as well as the breeding sites of the central (Adriatic coast) and eastern (Black Sea coast) population are dominated by Mediterranean climate. For this climate region, Walther et al. (2002) reported a slight increase in temperature and a decrease in precipitation over

the past 50 yr. As we only found advancing or no shifts for these sites, plant growth seems to be limited by temperature rather than by rainfall. North-western and north-eastern Europe experienced the strongest increases in temperatures, with up to 1°C per decade, which supports the very clear advancing shift at the breeding site of the western population in France.

Risk of mistiming

Depending on the combinations of non-breeding, stopover, and breeding sites, shifts in phenology over entire flyways ranged from no shift at any site (the routes from Nc1 to Bc as well as from Ne1-4 to Be) to shifts into opposing directions, i.e., with delay at the non-breeding site and advancement at the breeding site (the route from Nw4 to Bw). In how far these opposing shifts incur a risk of mistiming depends on the determinants of migration timing (“cues”) and the costs of matching or mismatching local phenology. Consequently, the risks of mistiming varied also in dependence of how we think birds time migration and which environmental information they supposedly use for migration decisions. Unfortunately, the cues used for migration timing are unknown for many species or specific migration steps—typically photoperiod is involved (Studds and Marra 2012) but also biotic variables, e.g., vegetation phenology can be included (Bauer et al. 2011).

If departure decisions are fully independent of local phenology, e.g., if photoperiod is the only cue, phenological shifts will not change the timing of migration. In this case, which corresponds to our cue assumption 1, our results suggest that only the Western flyway would experience a risk of mistiming. Also the food niche breadth of a migrant affects the costs of a shift in the schedule and thus the risk of mistiming (Both et al. 2010). The Nightingale, as a more opportunistic insectivorous generalist, might be both better able to adapt to phenological changes and shifts in the breeding schedule might be less costly compared to a food specialist (Emmenegger et al. 2014).

If other, phenology-related, variables are considered for the timing of migration, migrants might be better able to respond to phenological changes, e.g., pink-footed geese that advanced migration with an advanced vegetation

phenology (Duriez et al. 2009). This is reflected in the overall risk of mistiming that is lower for assumption 2 compared to assumption 1. However, the risk of mistiming is then again higher in the third scenario, in which shifts in all sites had been considered. This scenario assumed that migrants fine-tune migration timing considering vegetation phenology on all sites and that they are able to respond to advancements or delays in phenology by de- or accelerating migration en route (Both 2010). Remarkably, the risks of mistiming resulting from this set of assumptions were generally higher than the ones from the other two sets of assumptions and much more equal between the three flyways. The differences in estimated risks of mistiming were much higher between the assumptions on which cues are involved in timing migration than between the assumptions on the role of direction and magnitude of shifts. This suggests that the investigation of cues triggering migration timing might play a much more important role in the risk assessment, than the investigation of a potential threshold in the migrants’ ability to adapt to a certain rate of change.

Including phenological shifts at stopover sites is risky, because it is unknown, whether any shift in these shallow vegetation phenologies (i.e., when NDVI is only fluctuating very little on a low level over the year, like in the stopover sites of the central and eastern flyway; see NDVImax/min in Appendix S1: Tables S1–S3) is able to affect timing of migrating birds. Moreover, we know that these birds stopped-over only relatively briefly (Emmenegger et al. 2014) so that we can assume that stopover sites just have to provide some food for refueling, but that no particular food peak has to be matched.

Thus, the most important finding of our study is probably that the risks of mistiming from climate-induced phenological shifts highly depend on the degree to which migrants use local information along their migration routes. Although it is generally assumed that incorporating environmental information in migratory decisions would improve the migrants’ capacity to cope with environmental changes, it might actually be better to “sometimes” ignore this information: For instance, the nightingales in our study would be facing a higher risk of mistiming if they incorporated the phenology of all sites

visited into their migratory decisions as compared to incorporating the phenology of selected site(s) only.

If phenological shifts have already led to mistimed migrations with concurrent consequences for fitness, we expect the estimated risks of mistiming to also match population trends among the flyways. Although there are no detailed data available to tackle this hypothesis explicitly, existing data from long-term monitoring schemes (Burfield et al. 2004, PECBMS 2013) indicate stable population sizes in the East and decreasing population sizes in the West—a pattern that is consistent with our findings.

We acknowledge that our findings and their interpretations rest on several assumptions. In how far these apply to nightingales or other migratory species remains to be shown in future studies. However, our study emphasizes that for estimating the risk of mistiming in migratory animals it is crucial to be explicit about direction and magnitude of phenological shifts and the cues that underlie migratory decisions.

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LITERATURE CITED

- Badeck, F.-W., A. Bondeau, K. Bottcher, D. Doktor, W. Lucht, J. Schaber, and S. Sitch. 2004. Responses of spring phenology to climate change. *New Phytologist* 162:295–309.
- Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society B* 271:875–882.
- Bauer, S., B. A. Nolet, J. Giske, J. W. Chapman, S. Åkesson, A. Hedenström, and J. M. Fryxell. 2011. Cues and decision rules in animal migration. Pages 68–87 in E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. *Animal migration: a synthesis*. Oxford University Press, Oxford, UK.
- Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology* 20:243–248.
- Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B* 277:1259–1266.
- Box, E. O., B. N. Holben, and V. Kalb. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary production and net CO₂ flux. *Vegetatio* 80:71–89.
- Burfield, I., F. Van Bommel, U. Gallo-Orsi, S. Nagy, C. Orhun, R. G. Pople, R. van Zoest, and D. Callaghan. 2004. *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Cambridge, UK.
- Burger, C., et al. 2012. Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. *Journal of Animal Ecology* 81:926–936.
- Clark, R. G., H. Pöysä, P. Runko, and A. Paasivaara. 2014. Spring phenology and timing of breeding in short-distance migrant birds: phenotypic responses and offspring recruitment patterns in common goldeneyes. *Journal of Avian Biology* 45:457–465.
- Cohen, E. B., Z. Németh, T. J. Zenzal Jr., K. L. Paxton, R. Diehl, E. H. Paxton, and F. R. Moore. 2015. Spring resource phenology and timing of songbird migration across the Gulf of Mexico. Pages 63–82 in E. M. Wood and J. L. Kellermann, editors. *Phenological synchrony and bird migration: changing climate and seasonal resources in North America*. *Studies in Avian Biology* 47. CRC Press, Boca Raton, Florida, USA.
- Cresswell, W. 2014. Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis* 156:493–510.
- Csörgő, T., and G. Lövei. 1995. Autumn migration and recurrence of the Thrush Nightingale *Luscinia luscinia* at a stopover site in central Hungary. *Ardeola* 42:57–68.
- Duriez, O., S. Bauer, A. Destin, J. Madsen, B. A. Nolet, R. A. Stillman, and M. Klaassen. 2009. What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behavioral Ecology* 20:560–569.
- Emmenegger, T., S. Hahn, and S. Bauer. 2014. Individual migration timing of common nightingales

- is tuned with vegetation and prey phenology at breeding sites. *BMC Ecology* 14:9.
- ESRI. 2011. ArcGIS desktop. Release 10. Environmental Systems Research Institute, Redlands, California, USA.
- Fontaine, J. J., R. J. Stutzman, and L. Z. Gannes. 2015. Leaps, chains, and climate change for western migratory songbirds. Pages 3–15 in E. M. Wood and J. L. Kellermann, editors. *Phenological synchrony and bird migration: changing climate and seasonal resources in North America*. *Studies in Avian Biology* 47. CRC Press, Boca Raton, Florida, USA.
- Gienapp, P., R. Leimu, and J. Merilä. 2007. Responses to climate change in avian migration time—microevolution versus phenotypic plasticity. *Climate Research* 35:25–35.
- Gordo, O., P. Tryjanowski, J. Z. Kosicki, and M. Fulin. 2013. Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. *Journal of Animal Ecology* 82:1072–1086.
- Hahn, S., T. Emmenegger, S. Lisovski, V. Amrhein, P. Zehndjiev, and F. Liechti. 2014. Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground. *Ecology & Evolution* 4:4150–4160.
- Inger, R., R. Gregory, J. P. Duffy, I. Stott, P. Vorisek, and K. J. Gaston. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters* 18:28–36.
- Johansson, J., J.-Å. Nilsson, and N. Jonzén. 2015. Phenological change and ecological interactions: an introduction. *Oikos* 124:1–3.
- Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology* 79:98–108.
- Menzel, A., et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- PECBMS. 2013. Population trends of common European breeding birds 2013. <http://www.ebcc.info/wpimages/video/Leaflet2013.pdf>
- Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* 20:503–510.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sanderson, F. J., P. F. Donald, D. J. Pain, I. J. Burfield, and F. P. J. van Bommel. 2006. Long-term population declines in Afro-Palaearctic migrant birds. *Biological Conservation* 131:93–105.
- Schaub, M., L. Jenni, and F. Bairlein. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behavioral Ecology* 19:657–666.
- Stocker, T. F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley. 2013. Climate change 2013: the physical science basis. In *Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5)*. Cambridge University Press, New York, New York, USA.
- Studds, C. E., and P. P. Marra. 2012. Reconsidering the role of precipitation and food availability in relation to the effect of photoperiod on spring departure of a migratory bird. *Proceedings of the Royal Society B* 279:17–18.
- Tucker, C. J., J. E. Pinzon, and M. E. Brown. 2004. Global inventory modeling and mapping studies. University of Maryland, College Park, Maryland, USA.
- van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology* 52:37–55.
- van Wijk, R. E., A. Kölzsch, H. Kruckenberg, B. S. Ebbinge, G. J. D. M. Muskens, and B. A. Nolet. 2012. Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos* 121:655–664.
- Vickery, J. A., S. R. Ewing, K. W. Smith, D. J. Pain, F. Bairlein, J. Skorpilov, and R. D. Gregory. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis* 156:1–22.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Zhang, X., B. Tan, and Y. Yu. 2014. Interannual variations and trends in global land surface phenology derived from enhanced vegetation index during 1982–2010. *International Journal of Biometeorology* 58:547–564.

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