

“The influence of climatic and intraspecific factors on the migration timing of two *Sylvia* species: the Garden Warbler and the Eurasian Blackcap across the southern Baltic coast”

Agata Pinszke, M.Sc.

Many bird species migrate twice a year between their breeding and wintering grounds, relying on stopover sites to feed and rebuild energy reserves on their way (Newton 2008). The environmental conditions along these routes influence the progress and timing of their migration (Gordo 2007). Climate change in Europe and Africa affects the timing of bird migrations within the Palearctic-African migration system (Jenni and Kéry 2003; Lehikoinen et al. 2019). Although the timing of bird migrations is genetically determined, it can be modified by temperatures at wintering grounds and along migration routes, which act directly by altering birds' thermoregulatory costs and indirectly by shaping the availability of their food base (Newton 2008). Besides temperatures at subsequent locations visited by birds, their migration is influenced by atmospheric circulation patterns that shape temperatures, precipitation, and winds over large areas (Saji and Vinayachandran 1999; Hurrell et al. 2003). Large-scale climate indices, such as the North Atlantic Oscillation (NAO), Scandinavian Index (SCI), Mediterranean Oscillation Index (MOI), and Indian Ocean Dipole (IOD), which reflect circulation patterns within large areas of Europe and Africa, are related to bird migration timing (Stenseth et al. 2002; Jonzén et al. 2007). Because regional climate changes continuously, the responses of bird populations to weather might shift over the decades (Jonzén et al. 2006; Romano et al. 2023).

One of the effects of climate warming on bird migration is their generally earlier spring passage and therefore earlier arrival at their breeding grounds in the Northern Hemisphere (Forchhammer et al. 2002). While the advancement of spring migration is well documented, especially in Europe, autumn migration has received less attention, so less is known about how these changes have affected the phenology of post-breeding southward migration (Gallinat et al. 2015). Autumn migration in different passerine species has adjusted to climate change in varied ways, ranging from an advance to a delay of passage (Jenni and Kéry 2003). Studies showing how weather that one generation of migrants encounters during their spring migration to the breeding grounds might affect autumn migration of their offspring are few (Jenni and Kéry 2003; Tomotani et al. 2018). Warm springs might promote early arrival of adults at the breeding grounds and early nesting, leading to early hatching and departure of immatures to the south (Halupka et al. 2017). Most studies have focused on interspecific differences in phenological shifts, while intraspecific variation, including possible sex differences, remains

poorly understood (Nakazawa et al. 2023). In many migrant passerines, protandry, which is an earlier arrival of males than females at the breeding grounds, occurs already at stopover sites during spring migration (Morbey and Ydenberg 2001; Rubolini et al. 2004). The main mechanism explaining protandry is the mate opportunity hypothesis, where earlier arrival allows males to secure high-quality territories, increasing their chances of attracting females and improving reproductive success (Kokko 1999; Møller 2004). The earlier arrival of males at stopover and breeding sites may also result from spatial sex segregation during the non-breeding season, when males and females use different wintering grounds or migration routes (Catry et al. 2006). These differences in migration timing are also linked to the varied energy management strategies of the sexes, because females must maintain fat and protein reserves for egg production and avoid too early arrival at the breeding grounds during harsh springs, which could deplete these resources (Francis and Cooke 1986; Schmaljohann et al. 2016). In contrast, sperm production is less demanding, allowing males to risk exposure to adverse weather to secure the best territories and mates (Péczeley 2017). Thus, in spring, males often act as time minimisers, prioritising migration speed over energy saving, whereas females behave as energy minimisers to preserve good body condition, which is crucial for egg production (Dierschke et al. 2005).

I selected two related species from the genus *Sylvia* that use similar habitats and migrate through the southern Baltic coast to northern breeding grounds, but differ in migration distance and the number of broods per year, as our model species to investigate these complex responses of migrants to changing climate (Cramp and Brooks 1992). The Eurasian Blackcap (*Sylvia atricapilla*) is a sexually dimorphic passerine that can raise multiple broods in a year, overwinters across southern Europe, West and East Africa, and shows remarkable plasticity in adjusting its migrations to climate change by shortening migration distances and establishing new wintering areas increasingly closer to the breeding grounds in recent decades (Pulido and Berthold 2004; Spina et al. 2022). In contrast, the Garden Warbler (*Sylvia borin*) is a monomorphic, single-brooded migrant with an even twice as long migration distance between Fennoscandia and sub-Saharan Africa and central Africa (Maciąg et al. 2017; Spina et al. 2022).

Aims and hypotheses

This dissertation aims to determine the influence of selected external factors (regional temperatures and large-scale climate patterns) and an intra-population factor (sex) on the timing of spring and autumn migration of two *Sylvia* species across the southern coast of the Baltic

Sea, using the unique long-term bird ringing dataset of the Operation Baltic project collected since 1961.

Firstly, I examined long-term changes in the timing of migration: the spring migration phenology of male and female Eurasian Blackcaps (1982–2025), and the autumn migration timing of Garden Warblers (1967–2018). Earlier studies showed that spring migration of blackcaps advanced during the late 20th century. Therefore, I expected further advancement of spring migration in both sexes. Given advances in autumn migration timing of Garden Warblers in other locations, I expected a shift to earlier autumn passage of this species on the Baltic coast of Poland over 1967–2018.

Secondly, I aimed to determine relationships between migration timing and external environmental conditions for both species. For Garden Warblers, I determined relationships between the timing of autumn migration and temperatures on the breeding grounds and along spring and autumn migration routes. Shifts in autumn migration timing have been previously attributed to breeding biology and migration distance of a species, but rarely linked to temperatures encountered by adults during spring migration to the breeding grounds. Therefore, I hypothesised that the timing of immature Garden Warblers' autumn migration would be related not only to the temperatures they experienced at the breeding grounds and during autumn migration, but also to temperatures the adults had encountered earlier, during their spring migration. For Eurasian Blackcaps, I aimed to determine relationships between spring migration timing and large-scale climate indices (NAO, SCI, MOI, and IOD), as well as winter and spring regional temperatures across Europe and Africa. I expected that these large-scale climate indices and regional temperatures influence spring migration timing of blackcaps on the southern Baltic coast.

Thirdly, I aimed to test if the degree of protandry has changed over 1982–2025 in Eurasian Blackcaps, and to determine sex-specific responses to the environmental conditions. I expected an increase in protandry over the study period, considering more rapid recent climate change and temperature increases. Furthermore, I expected that males and females might respond differently to these environmental conditions.

Fourthly, I divided the long-term dataset of male and female Eurasian Blackcaps into two periods (1982–2004 and 2005–2025) to test if multi-year trends, the degree of protandry, and sex-specific responses to regional temperatures differed between past and recent decades.

Because in the previous paper I revealed that blackcaps constantly advanced their migration over 44 years, I tested a hypothesis that the multi-year trends would not differ between the two periods, expecting a continuous advancement of spring migration. I also expected that winter and spring regional temperatures across Europe and Africa would influence migration timing in both periods. Thus, I aimed to determine these relationships, and test whether they changed between the two periods, considering the species' plasticity.

Materials and methods

Research presented in this thesis was based on long-term data collected during daily standardised mist-netting from dawn to dusk at the Bukowo-Kopań bird ringing station on the Polish Baltic Sea coast, following the standard methods of the Operation Baltic research project (Busse and Meissner 2015). The analysed dataset included the ringing records (first capture) during autumn migration (14 August–15 October) for Garden Warblers (1967–2018) and during spring migration (26 March–16 May) for Eurasian Blackcaps (1982–2025). Garden Warblers are infrequent on spring passage at Bukowo-Kopań, which impeded direct comparison of spring migration patterns between these two species. To identify the regions visited by the studied populations across their annual cycle, the ringing recoveries of individuals of these two species captured at all Operation Baltic stations on the Polish coast, including Bukowo-Kopań, were mapped and compared with literature data. I obtained daily mean temperatures and large-scale climate indices (NAO, SCI, MOI, IOD) for geographic regions I distinguished within the species' ranges, from the European Climate Assessment and Dataset (ECA&D), NOAA climate databases, and KNMI Climate Explorer.

The timing of migration was quantified using the dates when 10%, 50%, and 90% of the birds were captured each season, expressed as Julian days. This was calculated for immature Garden Warblers in autumn (Paper 1), and separately for male and female Blackcaps in spring (Papers 2, 3). Additionally, to assess overall passage shifts for Garden Warblers, I calculated an Annual Anomaly (AA) for each autumn as the departure of the daily cumulative curve for each year from the many-year average daily cumulative curve (Paper 1). I applied linear regression to estimate multi-year trends in these parameters of passage. For Blackcaps, I estimated multi-year trends separately for males and females. Furthermore, spring migration data on Blackcaps were divided into two sub-periods (1982–2004 and 2005–2025) to test differences in multi-year trends between them, using linear regression models with year, sex, study period, and their interactions as explanatory variables (Paper 3).

To determine the effects of climate factors on migration timing, I built multiple linear regression models. In these models, the response variables were the dates when 10%, 50%, and 90% of the birds were captured, and additionally AA for Garden Warblers. The explanatory variables consisted of the year number and the selected climate factors relevant for each species. To test the effects of regional temperatures (Papers 1, 3), the explanatory variables were bi-monthly averages of spring, summer, and autumn temperatures at the breeding grounds and along the migration routes for Garden Warblers (Paper 1), and tri-monthly averages of winter and spring regional temperatures across Europe and Africa for Blackcaps (Paper 3). To assess the influence of large-scale climate indices on Blackcaps (Paper 2), the explanatory variables were the tri-monthly averages of winter and spring large-scale climate indices. All explanatory variables were standardised, as they were on different scales. Because the explanatory variables representing climate factors were too many to include in one model, I first ran partial models for each season separately (spring, summer, and autumn for Garden Warblers; winter and spring for Blackcaps). Then, the variables from the best seasonal models were integrated into final combined models. I then interpreted these best combined models. Finally, to investigate whether the relationships between migration timing and temperatures changed between the periods for Blackcaps, I formulated period-comparison models. These period-comparison models included the combinations of temperature variables selected by the best combined "winter and spring" models, testing the interaction between the study period and these variables (Paper 3). To determine differences between sexes in the effect of these climate factors on Blackcap spring migration, I included interactions between the climate factors and sex in the respective models (Papers 2, 3). To check for protandry and test whether its degree changed over the years, I ran multiple linear regression models including sex, year (as the year number since 1982), and their interaction (Papers 2, 3), and tested for differences in protandry between the two sub-periods by including the study period in the models (Paper 3). All multiple linear regression models used in this dissertation were built using the "all-subsets approach", and models were ranked by the Akaike Information Criterion corrected for small sample sizes (AICc). The best model was the one with the lowest AICc. All statistical analyses were conducted in R software (versions 4.1.2, 4.4.2, and 4.6.1).

Results and discussion

Paper no. 1:

In the Garden Warbler, the overall autumn passage (AA) of immatures advanced by 7 days, and the dates of the 50% and 90% of passage advanced by 6–11 days over 1967–2018, which led to a shorter migration period. This likely reflects a condensed breeding season, in which this single-brooded species adjusts egg-laying timing to match the peak of food resources, which also shifted earlier, in response to increasing temperatures (Halupka et al. 2017). The overall passage (AA) and the dates of 10%, 50% and 90% of autumn passage at the Baltic coast were early with higher spring temperatures on the spring migration route in Italy, or late with low temperatures in Italy, as these relationships work both ways. This relationship suggests a trans-generational carry-over effect, as warm springs encourage fast migration, and thus early arrival and nesting of returning adults, leading to earlier hatching and faster growth of juveniles (Tomotani et al. 2018). Furthermore, warm summers at the breeding grounds in southern Sweden and Norway were related to an earlier autumn passage. Warm summers support early maturity, allowing immatures to grow faster and depart earlier from their breeding grounds than after cold summers (Sparks and Crick 1999). However, high summer temperatures in Finland delayed the median and the overall autumn passage at Bukowo-Kopań. I suggest that favourable feeding conditions during warm summers at these breeding grounds and stopover sites delayed the passage because these inexperienced young birds took advantage of the conditions to accumulate fuel before migrating south (Ożarowska 2015).

Paper no. 2:

In Blackcaps, both males and females advanced the first (10%) and median (50%) phases of spring passage by 7–9 days during 1982–2025. Similar advancements of both sexes suggest that earlier spring passage benefits both sexes equally, enabling males to maximise mating opportunities and females to extend the breeding season for potential second broods (Fontaine and Martin 2006). Because both sexes shifted their timing at the same rate, the degree of protandry remained stable, with males migrating about 2.2 days earlier than females. This stable degree of protandry supports the mate opportunity hypothesis, indicating that selective pressures preserve the timing differences between sexes regardless of the interannual variation in weather conditions (Tøttrup and Thorup 2008). Males and females showed uniform responses to the large-scale climate indices, suggesting that broad weather conditions influence migration timing of both sexes similarly, even if they adopt different strategies of energy allocation during migration or overwinter in slightly different areas. Positive winter and spring NAO and spring SCI, reflecting warm and wet winters and springs in Europe, were related to early 10% and 50% of passage, while positive winter IOD was associated with a delayed 90%

of passage. This indicates that successive migrating cohorts arrive from areas under different climatic influences, adjusting their migration pace to different broad atmospheric patterns across Europe and Africa, similarly in both sexes.

Paper no. 3:

Comparing spring migration timing between two sub-periods (1982–2004, 2005–2025) revealed that the 2.2-day protandry in Blackcaps at the first phase of passage (10%) remained stable across both time periods, but did not manifest in the median (50%) of passage. The stable protandry among the first migrants is likely maintained by the increased mating opportunities of males arriving early, regardless of continuous warming. The lack of protandry at the median and late (90%) phases of passage probably reflects the energy-minimising strategy of inexperienced young birds, which dominate on the coastal stopover sites, such as Bukowo-Kopań (Neate-Clegg and Tingley 2023). The median (50%) of passage of both sexes shifted earlier by 10 days during 1982–2004, but stabilised during 2005–2025. The first (10%) and median (50%) phases of passage were early with warm springs in Central Europe and Eastern Africa. I suggest that these early migrants dynamically adapt to environmental cues by escaping drying environments in Africa and utilising favourable spring conditions to speed up their passage across Europe (Aloni et al. 2019). Notably, the influence of Central European spring temperatures on the median of passage weakened during the second period (2005–2025), even though warming in this region continued. This weaker response and the recent stabilisation of the median of passage indicate that parts of the migrating population reached a biological threshold of advancing spring passage. Since the advancement of the food peak at the breeding grounds is ultimately constrained by photoperiod (Tougeron et al. 2019), this stabilisation prevents birds from arriving too early, thereby avoiding a severe ecological mismatch between breeding and food availability, despite continuous climate warming (Romano et al. 2023). In contrast, the late phase (90%) was delayed with high winter temperatures in the Western Mediterranean. Warm winters in the Western Mediterranean region frequently cause vegetation to develop early (Solakis-Tena et al. 2025), shifting the peak abundance of insects too early for the late migrants, which struggle to refuel and have to make longer stopovers in this region (Mayor et al. 2017; Maggini et al. 2020), hence their delayed passage at the Baltic coast.

Conclusions

This dissertation demonstrated the influence of climatic and intraspecific factors on the migration phenology of two species of *Sylvia* warblers passing in spring or autumn through the southern Baltic Sea coast. Analysing long-term data series on bird migration timing against the climate data revealed how these related species respond to global climate change. In the Garden Warbler, the autumn migration timing of immatures is shaped directly by environmental conditions at the breeding grounds and indirectly by the influence of spring temperatures on spring migration of their parents, through a trans-generational carry-over effect. For the Eurasian Blackcap, the two-day protandry at the beginning of spring passage remained stable over 44 years of study, and across both sub-periods. This is in line with the mate opportunity hypothesis, showing that selective pressures preserve differences in spring phenology between sexes, regardless of continuous climate warming. Furthermore, despite their different energy allocation strategies during migration, both male and female Blackcaps responded uniformly to regional temperatures and large-scale climate indices. However, while shifting migration is a universal population response to changing regional climates, this adaptability seems to be restricted by ecological limits and lower foraging efficiency of inexperienced young birds, which prevail during migration along the coast. This was evident in Blackcaps, where the spring migration timing for the majority of the population advanced during 1982–2004 but stabilised during 2005–2025. This recent stabilisation indicates that migrants have reached a biological threshold in their phenological flexibility, which likely prevents ecological mismatches with their peak food availability on stopovers and breeding grounds.

Ultimately, comparing these two *Sylvia* species highlights how their differences in migration distance and the number of broods shape their responses to climate change. The Eurasian Blackcap, which migrates over shorter distances and can raise even two broods a year, exhibits remarkable plasticity. This plasticity enabled Blackcaps to significantly advance their spring passage over the past decades, to maximise reproductive success. In contrast, the single-brooded, long-distance Garden Warbler operates under a tight annual schedule of subsequent life stages. With such time constraints, its adaptation to changing environmental conditions manifested as a shortened period of autumn passage, likely due to the condensed breeding season. Together, these findings emphasise that while migratory birds are affected by climate warming, their phenological adaptations are limited by their breeding biology and migration distance. Understanding how these biological constraints shape species-specific responses to climate change is essential for predicting their vulnerability and developing effective conservation strategies for migratory birds.

References

- Aloni I, Markman S, Ziv Y (2019) Autumn temperatures at African wintering grounds affect body condition of two passerine species during spring migration. PLoS ONE 14: e0217619. <https://doi.org/10.1371/journal.pone.0217619>
- Busse P, Meissner W (2015) Bird Ringing Station Manual. De Gruyter Open, Warsaw, Poland; Berlin, Germany. <https://doi.org/10.2478/9788376560533>
- Catry P, Phillips RA, Croxall JP (2006) Sexual segregation in birds: Patterns, processes and implications for conservation. In: Ruckstuhl K, Neuhaus P (eds) Sexual Segregation in Vertebrates: Ecology of the Two Sexes. pp. 351–378. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511525629.019>
- Cramp S, Brooks DJ (eds) (1992) The Birds of the Western Palearctic. Warblers. Oxford University Press, Oxford
- Dierschke V, Mendel B, Schmaljohann H (2005) Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behav Ecol Sociobiol 57:470–480. <https://doi.org/10.1007/s00265-004-0872-8>
- Fontaine JJ, Martin TE (2006) Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428–434. <https://doi.org/10.1111/j.1461-0248.2006.00892.x>
- Forchhammer MC, Post E, Stenseth NChr (2002) North Atlantic Oscillation timing of long- and short-distance migration. Journal of Animal Ecology 71:1002–1014. <https://doi.org/10.1046/j.1365-2656.2002.00664.x>
- Francis CM, Cooke F (1986) Differential Timing of Spring Migration in Wood Warblers (*Parulinae*). The Auk 103:548–556
- Gallinat AS, Primack RB, Wagner DL (2015) Autumn, the neglected season in climate change research. Trends in Ecology & Evolution 30:169–176. <https://doi.org/10.1016/j.tree.2015.01.004>

Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* 35:37–58. <https://doi.org/10.3354/cr00713>

Halupka L, Wierucka K, Sztwiertnia H, Klimczuk E (2017) Conditions at autumn stopover sites affect survival of a migratory passerine. *Journal of Ornithology* 158:979–988. <https://doi.org/10.1007/s10336-017-1472-5>

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) An overview of the North Atlantic Oscillation. *Geophysical Monograph Series* 134:1–35. <https://doi.org/10.1029/134GM01>

Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences* 270:1467–1471. <https://doi.org/10.1098/rspb.2003.2394>

Jonzén N, Ergon T, Lindén A, Stenseth NC (2007) Bird migration and climate: The general picture and beyond. *Climate Research* 35:177–180. <https://doi.org/10.3354/cr00724>

Jonzén N, Lindén A, Ergon T, et al (2006) Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science* 312:1959–1961. <https://doi.org/10.1126/science.1126119>

Kokko H (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68:940–950. <https://doi.org/10.1046/j.1365-2656.1999.00343.x>

Lehikoinen A, Lindén A, Karlsson M, et al (2019) Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators* 101:985–991. <https://doi.org/10.1016/j.ecolind.2019.01.083>

Maciąg T, Nowakowski JK, Redlisiak M, et al (2017) Website of the Bird Migration Research Station. Maps of ringing recoveries. <https://en-sbwp.ug.edu.pl/badania/monitoringwyniki/maps-of-ringing-recoveries/>. Accessed 15 July 2025

Maggini I, Cardinale M, Sundberg JH, et al (2020) Recent phenological shifts of migratory birds at a Mediterranean spring stopover site: Species wintering in the Sahel advance passage more than tropical winterers. *PLoS ONE* 15:e0239489. <https://doi.org/10.1371/journal.pone.0239489>

Mayor SJ, Guralnick RP, Tingley MW, et al (2017) Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Sci Rep* 7:1902. <https://doi.org/10.1038/s41598-017-02045-z>

Møller AP (2004) Protandry, sexual selection and climate change. *Global Change Biology* 10:2028–2035. <https://doi.org/10.1111/j.1365-2486.2004.00874.x>

Morbey YE, Ydenberg RC (2001) Protandrous arrival timing to breeding areas. *Ecology Letters* 4:663–673

Nakazawa T, Hsu YH, Chen IC (2023) Why sex matters in phenological research. *Oikos* 2023:1–14. <https://doi.org/10.1111/oik.09808>

Neate-Clegg MHC, Tingley MW (2023) Adult male birds advance spring migratory phenology faster than females and juveniles across North America. *Global Change Biology* 29:341–354. <https://doi.org/10.1111/gcb.16492>

Newton I (2008) *The Migration Ecology of Birds*. Academic Press, London, UK

Ożarowska A (2015) Contrasting fattening strategies in related migratory species: The blackcap, garden warbler, common whitethroat and lesser whitethroat. *Annales Zoologici Fennici* 52:115–127. <https://doi.org/10.5735/086.052.0210>

Péczely P (2017) *The Eco-Physiology of Avian Reproduction*. Agroinform Publishing and Printing House Ltd., Budapest, Hungary.

Pulido F, Berthold P (2004) Microevolutionary Response to Climatic Change. *Advances in Ecological Research* 35:151–183. [https://doi.org/10.1016/S0065-2504\(04\)35008-7](https://doi.org/10.1016/S0065-2504(04)35008-7)

Romano A, Garamszegi LZ, Rubolini D, Ambrosini R (2023) Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. *Ecological Monographs* 93:e1552. <https://doi.org/10.1002/ecm.1552>

Rubolini D, Spina F, Saino N (2004) Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology* 15:592–601. <https://doi.org/10.1093/beheco/arh048>

Saji NH, Vinayachandran PN (1999) A dipole mode in the tropical Indian Ocean. *Nature* 401:360–363.

Schmaljohann H, Meier C, Bairlein DAF, et al (2016) Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. *Behavioral Ecology* 27:321–331. <https://doi.org/10.1093/beheco/arv160>

Solakis-Tena A, Casimiro-Soriguer Solanas F, Hidalgo-Triana N (2025) Retrospective phenology in western Mediterranean plants: revealing climate change patterns through herbarium specimens. *AoB PLANTS* 17:plaf064. <https://doi.org/10.1093/aobpla/plaf064>

Sparks T, Crick H (1999) The times they are a-changing? *Bird Conservation International* 9:1–7. <https://doi.org/10.1017/S0959270900003300>

Spina F, Baillie S, Bairlein F, et al (2022) The EURING Atlas of Bird Migration. <https://migrationatlas.org/>. Accessed 10 April 2025

Stenseth NC, Mysterud A, Ottersen G, et al (2002) Ecological Effects of Climate Fluctuations. *Science* 297:1292–1296. <https://doi.org/10.1126/science.1071281>

Tomotani BM, van der Jeugd H, Gienapp P, et al (2018) Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. *Global Change Biology* 24:823–835. <https://doi.org/10.1111/gcb.14006>

Tougeron K, Brodeur J, Le Lann C, van Baaren J (2019) How climate change affects the seasonal ecology of insect parasitoids. *Ecological Entomology* 45:24–37. <https://doi.org/10.1111/een.12792>

Tøttrup AP, Thorup K (2008) Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *J Ornithol* 149:161–167. <https://doi.org/10.1007/s10336-007-0254-x>