Effects of Variable Responses to Climate Change on the Interactions of Migratory and Resident Birds in Europe

Yuren Cao

Asociación Escuelas Lincoln, B1637 AOS La Lucila, Argentina
E-mail: ycao@lincoln.edu.ar

Abstract. Long-distance migrants and residents may respond to large-scale climate change by advancing egg laying dates. It is expected that variation in changes in avian laying dates among similar species affects their interactions in an ecological community. By analyzing long-term trends of the mean laying dates (MLD) of pied flycatcher Ficedula hypoleuca, collared flycatcher Ficedula albicollis, and great tits Parus major across 25 study sites in Europe from five published studies, the paper uses two-tailed t tests to show that variable adjustments in laying dates in different species have different implications on their interactions across Europe. It is found that pied flycatcher advanced laying dates significantly faster compared to great tits in Central Europe, gaining advantage in their competition for nest holes. Additionally, the study shows that pied flycatcher and collared flycatcher potentially share smaller overlap in laying dates in their sympatric breeding ground in Northern Europe, which may decrease the occurrences of hybridization, whereas the trend reverses in Central Europe. The results highlight that geographical variations in phenological responses to climate change have complicated effects on interspecific interaction, a novel research field that lacks empirical results. The conclusions of this study provide potential directions for empirical studies of climate change in the future.

1. Introduction
Birds have responded to large-scale climate change through changes in avian life-history events (phenology), particularly in the timing of migration and egg laying [1], although the extent of such adjustments may differ significantly within distinct geographical areas for a particular species [2]. The migratory pied flycatcher Ficedula hypoleuca has been reported to advance their arrival dates at breeding grounds in Europe in order to track the warming temperature [3, 4], yet limited adaptive ability to advance their phenology sufficiently causes a mismatch with local conditions such as food availability and may have profound consequences on interspecific interactions within biological communities, leading to declines in population sizes [5, 6]. Therefore, understanding variation between similar species in their responses to a changing environment is critical if we are to understand how climate change impacts the structure of biological communities that include both migratory birds and residents. Although shifts in spring phenology of long-distance migrants such as the pied flycatcher have been well studied [7], it remains an open question as to how different responses between migrants and residents affect their interactions [8]. Recent evidence has indicated that resident birds have higher phenological sensibility than migratory birds among European cavity breeders, yet it is still unclear how this alters competitive interactions [9]. There are very few studies, to my knowledge, that have
investigated the effects of variable responses to climate change on interspecific interactions between migrants and residents over different geographical areas. The pied flycatcher, European great tits *Parus major*, and collared flycatcher *Ficedula albicollis* are ideal subjects for studying the effects of climate change because extensive long-term studies on their laying dates have been conducted at their breeding grounds in Europe and their interactions in an ecological community are relatively well-known. Here, this study uses mean laying dates across different sites in Europe as a proxy for the egg laying phenology of the studied species, which is obtained from five previously published studies [2, 10-13]. Given these mostly complete time-series of mean laying dates, two-tailed $t$ tests are utilized to analyze the differences in long-term responses of laying dates with respect to geographical region and species. Finally, the implications of differential responses on the interspecific interactions of these species are discussed.

2. Methods

2.1. Study species and area

Pied flycatchers are long-distance migratory birds that overwinter in Western Africa and disperse throughout Europe during the breeding season. They occupy nest boxes on breeding grounds, allowing long-term studies to be conducted regarding their laying dates. Great tits are residents that generally breed earlier than pied flycatchers and actively compete with them for nest boxes, leading to possible influence in on breeding numbers and reproductive success [14]. Collared flycatchers are migratory birds closely related to the pied flycatcher. Although the two flycatchers are allopatric on most of their breeding grounds, there are overlapping ranges in central Europe and on the Gotland island in the Baltic, where they hybridize regularly [15].

Mean laying date (MLD) is defined as the average date of all first clutches that females in a population produce in a given year. In order to avoid reporting bias, all past studies that contain accurate long-term trends of mean laying dates of either of these three species of birds and that were available to the author were incorporated in this study. In total, long-term data from 24 study sites, as shown in Table 1, were used. The value of $n$ refers to the number of years in the time-series for which the laying dates are obtained. The mean MLD is the mean of laying dates in the first five study years. The statistics of MLD-year, as well as the slope, are obtained from linear regression analysis. Experimental methods in these study sites differ, but in most instances, nest boxes are checked weekly in order to determine the laying dates. Since the changes of mean laying dates per year are of particular interest in this study instead of the actual laying dates, different experimental methods do not influence the results significantly as long as they are correct and consistent in each study site.

The study sites were subdivided into three areas: Western Europe includes the Netherlands and Belgium; Central Europe includes southern Germany, Switzerland, Czech Republic, and Hungary; Northern Europe is the region above the Baltic, whose latitude is approximately above 54°N. Firstly, it has been established that pied flycatchers take different migratory routes to each area. For example, a light geolocator study on pied flycatcher individuals confirms that populations in Netherlands and Belgium are originated from the western part of the species’ distribution in Africa [16], whereas populations in central Europe may be originated in the eastern part in Africa [17]. Since migratory routes to each study sites are likely to be different according to their geographical locations, categorizing them into three regions helps reveal clearer, and potentially different, patterns of changes in laying dates. Secondly, since pied flycatchers and collared flycatchers are only sympatric in Central Europe and Gotland, it is only reasonable to use study sites in these regions in order to find variations in their responses to climate change.
Table 1. Long-term data from 24 study sites, obtained from five previous studies [2, 10-13]

| study site | full name       | coordinates      | time period | n  | mean MLD | slope MLD | stats MLD-year |
|------------|-----------------|------------------|-------------|----|----------|-----------|----------------|
| BH         | Lanžhot         | 48° 40' N 16° 56' E | 1961-2007   | —  | —        | -0.20     | CI = 99.9%     |
| LN         | Lednice         | 48° 48' N 16° 46' E | 1961-2007   | —  | —        | -0.19     | CI = 99.9%     |
| VN         | Vranovice       | 48° 56' N 16° 35' E | 1961-2007   | —  | —        | -0.19     | CI = 99.9%     |
| HK         | Horka           | 49° 39' N 17° 11' E | 1961-2007   | —  | —        | -0.16     | CI = 99.9%     |
| MR         | Moravia         | 49° 50' N 17° 15' E | 1973-2002   | —  | —        | -0.193    | p = 0.024      |
| PM         | Pilis mountains | 47° 10' N 19° 09' E | 1983-2002   | 16 | 6 May    | -0.207    | p = 0.13      |
| GL         | Gotland         | 57° 10' N 18° 20' E | 1981-2002   | 22 | 26 May   | -0.284    | p = 0.096      |

Pied flycatchers *Ficedula albicollis*

| study site | full name       | coordinates      | time period | n  | mean MLD | slope MLD | stats MLD-year |
|------------|-----------------|------------------|-------------|----|----------|-----------|----------------|
| HA         | Harz            | 51° 53' N 10° 37' E | 1980-2002   | 17 | 17 May   | -0.397    | p < 0.001      |
| LR         | Lahr            | 48° 17' N 7° 17' E | 1981-2002   | 2  | —        | -0.53     | CI = 95%       |
| HT         | Harthausen      | 49° 17' N 8° 24' E | 1973-2018   | 46 | —        | -0.31     | CI = 95%       |
| GT         | Goteborg        | 57° 43' N 11° 58' E | 1980-2000   | 17 | 25 May   | -0.157    | p = 0.064      |
| GN         | Gunnebo         | 57° 40' N 12° 05' E | 1980-1998   | 19 | 22 May   | 0.249     | p = 0.15       |
| BL         | Borlange        | 60° 23' N 15° 30' E | 1981-1999   | 19 | 26 May   | 0.128     | p = 0.41       |
| BA         | Baulmes         | 46° 47' N 06° 31' E | 1980-2002   | 23 | 18 May   | -0.312    | p = 0.009      |
| BK         | Buunderkamp     | 52° 01' N 05° 45' E | 1984-2002   | 17 | 12 May   | -0.358    | p = 0.006      |
| DW         | Deelerwoud      | 52° 05' N 05° 55' E | 1980-2002   | 22 | 11 May   | -0.342    | p = 0.004      |
| HV         | Hoge Veluwe     | 52° 02' N 05° 51' E | 1980-2002   | 23 | 14 May   | -0.466    | p < 0.001      |
| SP         | Staphorst       | 52° 37' N 06° 17' E | 1980-2002   | 23 | 12 May   | -0.417    | p < 0.001      |
| WB         | Warnsborn       | 52° 00' N 05° 51' E | 1980-2002   | 23 | 11 May   | -0.287    | p = 0.007      |
| LG         | Lingen          | 52° 27' N 07° 15' E | 1980-2002   | 21 | 16 May   | -0.489    | p < 0.001      |

Great tits *Parus major*

| study site | full name       | coordinates      | time period | n  | mean MLD | slope MLD | stats MLD-year |
|------------|-----------------|------------------|-------------|----|----------|-----------|----------------|
| LH         | Lanžhot         | 48° 40' N 16° 56' E | 1961-2007   | —  | —        | -0.15     | CI = 99%       |
| LN         | Lednice         | 48° 48' N 16° 46' E | 1961-2007   | —  | —        | -0.17     | CI = 99%       |
| VN         | Vranovice       | 48° 56' N 16° 35' E | 1961-2007   | —  | —        | -0.15     | CI = 99%       |
| HK         | Horka           | 49° 39' N 17° 11' E | 1961-2007   | —  | —        | -0.14     | CI = 95%       |
| HP         | Hutsepot        | 51° 01' N 03° 70' E | 1979-1998   | 20 | —        | -0.509    | p = 0.025      |
| BW         | Boswachter      | 51° 27' N 03° 70' E | 1979-1998   | 20 | —        | -0.667    | p = 0.003      |
| LB         | Liesbos         | 51° 35' N 04° 40' E | 1979-1998   | 20 | —        | -0.117    | p = 0.383      |
| OH         | Oosterhout      | 51° 55' N 05° 50' E | 1979-1998   | 20 | —        | -0.101    | p = 0.626      |
| WB         | Warnsborn       | 52° 05' N 05° 50' E | 1979-1998   | 20 | —        | -0.404    | p = 0.017      |
| HV         | Hoge Veluwe     | 52° 05' N 05° 50' E | 1979-1998   | 20 | —        | -0.105    | p = 0.540      |
| VL         | Vlieland        | 53° 18' N 05° 00' E | 1979-1998   | 20 | —        | -0.200    | p = 0.227      |

Note: If the p values are not given, the results are significant under the indicated confident level.
2.2. Data analysis
Past studies have used linear regression to find the slope of MLD versus year in each study site. In this study, these slopes were categorized into four charts according to species and study area in order to make comparisons between differential long-term trends of MLD. In each chart, the study sites were ranked from smallest to largest in terms of the number of days advanced per year. Subsequently, t tests were used to test whether changes in species’ MLD were significantly different from zero in each study area. Then, two-tailed heteroscedastic t tests were used to find whether different species’ changes in MLD were significantly different from each other.

3. Results and discussions

3.1. Differential response of pied flycatchers and great tits
On average, pied flycatchers advanced their MLDs by 0.387 days per year (SD = 0.10; \( t_3 = 7.49, p < 0.01 \)) across study sites in Central Europe. Great tits advanced their MLDs by an average of 0.153 days per year (SD = 0.01; \( t_3 = 24.2, p < 0.01 \)). Similarly, pied flycatchers advanced MLDs by an average of 0.382 days per year (SD = 0.08; \( t_6 = 13.1, p < 0.01 \)) in Western Europe, and the great tits by 0.3 days per year (SD = 0.23; \( t_6 = 3.50, p < 0.02 \)).

Through comparison of these two species, some general trends were found. In Central Europe, pied flycatchers advanced their laying dates at a significantly faster rate than great tits, as shown in figure 1, which was corroborated by a two-tailed heteroscedastic t test (\( t_6 = 4.5, p = 0.019 \)). Alternatively, long-term trends of MLDs between these two species vary from site to site in Western Europe, as shown in figure 2. For example, the pied flycatchers advanced their laying dates faster than did great tits by an average of 0.361 days per year in Hoge Veluwe (HV) populations, yet the trend reverses nearby in the Warnsborn (WB) populations. This variability in Western Europe can be largely attributed to the varied patterns on a small spatial scale exhibited by the MLDs of great tit populations. It was suggested that variations in microclimate or vegetation and the great tit’s life-history, instead of the temperature, might account for the highly varied pattern in laying date [2]. The timing of egg laying for female pied flycatchers, however, is restricted by the timing of arrival at breeding grounds, which is likely to be determined by both the endogenous programme of migration and the environmental conditions on the wintering grounds in Africa. These differences between the two species may explain why great tits advance egg laying faster than pied flycatchers in some sites in Western Europe, whereas not in others.

3.2. Implications on competition for nesting holes
In general, the resident great tits occupy the nest holes for quite some time in advance of the migratory flycatchers. The pied flycatchers then seize nesting holes from great tits in two ways: intense attacks against a great tit when it flies to and from the nest, resulting in nest desertion by the tit; or rapid nest-building in a hole already occupied by a tit when the tit is foraging during the day [14]. The flycatcher’s chances of wresting nest holes successfully are likely to decline as the nesting period of great tits progresses. Once the incubation period of great tits starts, takeover attempts are often fatal for pied flycatchers. Therefore, when the interval between the onset of the breeding period between the two species is short, the flycatcher is at an advantage.

Differential advancement in times of egg-laying of the two species has important implications on their competition for nest holes. In Central Europe and few sites in Western Europe (e.g., HV), pied flycatchers are likely to be favored because the interval between the onset of their breeding periods is reduced as a result of pied flycatchers’ faster advancement. Conversely, in other sites in Western Europe
(e.g., WB), the flycatchers are disadvantaged because they fail to advance laying dates at a similar pace compared to the great tits. This result agrees with an empirical study of a Dutch population, in which Samplonius and Both find increased pied flycatcher fatalities in great tit nest boxes because tits adjusted egg laying phenology significantly more than pied flycatchers [18].

**Figure 1.** Differential advancement of MLD per year in great tits *Parus major* and pied flycatcher *Ficedula hypoleuca* in Central Europe

**Figure 2.** Differential advancement of MLD per year in great tits *Parus major* and pied flycatcher *Ficedula hypoleuca* in Western Europe

**Note:** In Fig. 1 and 2, black bars represent great tit populations and gray bars are from pied flycatcher populations. The study sites are indicated (Table 1).
3.3. Differential response of pied flycatchers and collared flycatchers

Collared flycatchers advanced their MLDs by an average of 0.19 days per year in Central Europe (SD = 0.02; $t_5 = 28.9$, $p < 0.01$). In approximately the same geographical region, pied flycatchers advanced their laying dates consistently and significantly faster compared to collared flycatchers, as shown in figure 3, which was confirmed by a two-tailed heteroscedastic $t$ test ($t_5 = 3.78$, $p = 0.031$).

In Northern Europe, collared flycatchers advanced egg laying by 0.284 days per year on Gotland. In contrast, all surveyed pied flycatcher populations responded slower in study sites near Gotland ($t_2 = 2.97$, $p = 0.097$), with two of the three populations delaying egg laying dates, as shown in figure 4. One possible explanation of the lack of response in pied flycatcher populations is that Northern Europe did not experience significant warming during the study period from 1980 to 2000; therefore, an advancement in laying dates was unwarranted.

![Figure 3](image1.png)

**Figure 3.** Differential advancement of MLD per year in collared flycatcher *Ficedula albicollis* and pied flycatcher *Ficedula hypoleuca* in Central Europe.

![Figure 4](image2.png)

**Figure 4.** Differential advancement of MLD per year in collared flycatcher *Ficedula albicollis* and pied flycatcher *Ficedula hypoleuca* in Northern Europe.

**Note:** In Fig. 3 and 4, black bars represent collared flycatcher populations and gray bars are from pied flycatcher populations. The study sites are indicated (Table 1).
3.4. Implications on hybridization

Pied flycatchers and collared flycatchers potentially shared a smaller overlap in breeding dates in Northern Europe as a result of asymmetrical response to climate change. Since the collared flycatcher started egg laying relatively earlier than the pied flycatcher in sympatric breeding grounds in Northern Europe [19], their laying dates could potentially continue to diverge, considering the result that collared flycatcher advanced their MLDs at a faster rate per year. This trend provides both costs and benefits to the pied flycatchers. On one hand, the divergence in the timing of egg laying may reduce the temporal coincidence of mate choice between the two closely related species [20], hence decreasing the occurrence of hybridization. Less frequency of hybridization benefits both species mainly because hybrid individuals hatch fewer eggs and therefore fledge fewer offspring. On the other hand, both clutch size and fledgling success in flycatchers decline as the breeding season progresses [15]. Since pied flycatchers are projected to breed relatively later than collared flycatchers, their overall reproductive success may be negatively impacted due to a later start.

Unexpectedly, the two flycatchers potentially shared a greater overlap in breeding dates in Central Europe, as the laying dates of the two species converged in this region, where the pied flycatchers advanced their MLDs faster. It is perhaps noteworthy that a comparison between the pied flycatcher population in southern Germany (Lahr (LR)) and collared flycatcher populations in the Czech Republic (LH, LN, VN, and HK) revealed that the difference in mean laying dates diminished by several days from 1980 to 2000 due to asymmetric responses between the two species. As a result, the frequency of hybridization is expected to increase in Central Europe.

4. Conclusions

Based on the analysis and discussion, pied flycatchers may be favored in the competition with great tits in Central Europe and certain study sites in Western Europe because they advanced laying dates at a faster rate, whereas this result reverses in other sites in Western Europe. Additionally, the mean laying dates of pied flycatchers and collared flycatchers diverged in Northern Europe and converged in Central Europe due to asymmetrical responses to climate change. Therefore, it is expected that the frequency of hybridization between the two species may decline in Northern Europe and increase in Central Europe. Overall, these results indicate that the effects of differential changes in phenology on interspecific interactions are varied depending on geographical locations, hence more complex than previously thought.

This study has limitations. Firstly, although data from 26 sites are used, the relatively small sample size and absence of empirical studies prevent the author from making definitive conclusions about the consequences of variable responses on interspecific interactions. Secondly, there still exist understudied areas in Europe that are not accounted for in this study due to the absence of long-term trends. As a result, the generality of the results on a large geographical scale may be negatively affected. Thirdly, this study covers wide geographical regions, hence the validity of the results and implications must be confirmed at a local level. Finally, it remains uncertain whether these interspecific interactions could substantially impact community structure and population dynamics.

In the future, field research should be conducted in order to provide empirical evidence for the effects of differential adjustments of laying dates on interspecific interactions outlined in this study. Furthermore, future studies on climate change and its effects on ecological communities should be replicated in different locations in order to account for geographical variability.
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