



Figure 4. Changes in Wild Flycatchers

(A) Annual mean lay dates.
 (B) Ambient temperature during the climate-sensitive window preceding flycatcher breeding.
 (A and B) Solid lines show slopes for the time period between captive studies (delineated by vertical dotted lines); dashed slopes are over the entire study period. Error shading represents 95% confidence limits.
 (C) Timing of the best model-averaged climate window for flycatcher lay dates, identified from 23-year subsets centered on the year indicated on the x axis. Gray circles show the median date of each window. The horizontal dotted lines indicate the start and end of the overall best climate window identified using the entire dataset. Shading represents 95% confidence limits from 1000 reruns of *climwin* after bootstrapping flycatcher lay dates [16].
 See also [Figures S1 and S4](#).

species, we found earlier timing in males during reproductive activation [30].

Climate-associated shifts in autumn migration timing have been reported for many avian species, with variable directionality [31, 32]. In Europe, autumn migration generally advanced in trans-Saharan migrants and single-brooded species, whereas shorter-distance and multi-brooded migrants tended to delay [31]. Flycatchers were among the slightly advancing migrants, but recent observations of increasing late, potentially second, broods (D.H., unpublished data) may indicate shifts to autumnal delays. For winter, data on changing phenology are scarce, but earlier spring departure dates have been reported, for example, for Barn swallows (*Hirundo rustica*) in South Africa [41].

Season-specific changes in phenology in our captive flycatchers imply selective modification of the underlying timing program [8]. One possible mechanism is a change to the photoperiodic response. In spring, increasing day lengths advance the annual cycle and prompt spring phenology in many bird species; in autumn, photoperiodic responses are reversed [9, 37, 43]. A spring advance could be achieved by heightened photoperiodic sensitivity [19, 22, 23], but individuals showed no correlated spring and autumn responses. Furthermore, pied flycatchers and other migrants are largely insensitive to photoperiod in winter, when the flycatchers' phenology advance began [8, 9, 43]. Instead, it is more likely that flycatchers experienced an evolutionary change to the circannual clock itself. By effectively speeding up the clock over winter, the flycatchers' spring phase and concurrent environmental sensitivity were reactivated earlier. Such a change could also explain the advance of the climate window in the wild population.

The selective advance of spring timing also argues against alternative interpretations of the differences between cohorts.

Major influences of developmental factors, for example, hatching date and perinatal conditions, exclusively on spring phenology are unlikely [44, 45], in particular, because within cohorts we found no effect of hatching date on timing after the juvenile phase. Only delayed manifestation of highly specific developmental effects could explain our finding of season-specific timing shifts. Alternatively, cohort differences might have originated from sampling different subsets of the local population. By keeping collection date constant while lay dates advanced, chicks collected in 2002 originated from relatively later-laying parents than those in 1981 (Figure S2). However, this scenario predicts a timing delay in the 2002 cohort instead of the advance we observed [18].

An evolutionary response could have taken several routes seen in other taxa: first, the local population could have experienced selection on existing variation. Selection could have changed allele frequencies of genes involved in circannual rhythms and photoperiodic pathways [23, 46], or modified transgenerational epigenetic effects [45, 47]. Second, the population could have experienced introgression by earlier-timed immigrants [7]. A final possibility is random change due to genetic drift. However, spring timing is linked to fitness in flycatchers [12], and captive data paralleled the climate-linked changes in nearby wild flycatchers. This makes selection a more likely explanation [10, 12, 18, 25], potentially aided by assortative mating for timing [39].

There is growing evidence of evolutionary change in timing in response to warmer springs [2, 5, 6, 10, 15, 25, 29]. Several studies have also detected components of spring advancement that are not explained by plasticity [2, 15, 16, 25]. In a comparison of long-term breeding data of four UK songbird species [25], flycatchers were the least temperature sensitive, and the only species for which the temporal trend in lay date was significantly more extreme than could be explained by plasticity