# Evolutionary Response to Climate Change in Migratory Pied Flycatchers


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## SUMMARY

**Climate change is rapidly advancing spring phenology [1–3] but at different rates in different species [1, 4]. Whether these advances are solely driven by phenotypic plasticity [2, 5] or also involve evolution is hotly debated (e.g., [5–7]). In some species, including avian long-distance migrants, plastic responses to early springs may be constrained by inherited circannual timing programs [8, 9], making evolutionary adjustment the only viable mechanism for keeping pace with shifting phenology [5, 10]. This constraint may be contributing to population declines in migratory species [5, 10–12]. To test whether a migrant's timing program has evolved [10, 12], we replicated an experimental study of the annual cycle of long-distance migratory pied flycatchers (*Ficedula hypoleuca*) after 21 years of warming. Flycatchers are a model for studying constrained ecological responses to climate change [6, 10, 12, 13]. We show that the phase of the flycatcher circannual clock controlling spring moult, migration, and reproductive timing advanced by 9 days. A nearby wild population mirrored these changes, concurrently advancing egg-laying by 11 days. Furthermore, the time window during which wild flycatcher reproductive timing was most sensitive to ambient temperature advanced by 0.8 days year$^{-1}$. These results support a role of phenotypic evolution [14] in changing spring phenology [15, 16]. We suggest that the timing programs of long-distance migratory birds may have greater adaptive potential than previously thought, leaving some scope for evolutionary rescue in a changing climate.**


## RESULTS AND DISCUSSION

### Replicated Experimental Study

Changing temperature regimes can impart strong selection pressures on annual cycle timing and migration traits [4, 16–19], which are often heritable [20–23]. However, the extent to which climate adjustment requires evolutionary change depends on an organism's timing strategy [3, 23]. For example, in songbirds, populations that can continuously access information about their reproductive environment (e.g., year-round residents [24]) often show high plasticity. Conversely, many migrants use rigid, inherited circannual programs to predict suitable conditions over long distances [2, 8–10, 16]. Although these species show some plasticity (e.g., sensitivity to local temperatures [16, 25]), they require evolutionary adjustment of timing and migration traits to keep pace. Currently, it is unclear whether phenotypic evolution, defined as the change in the mean phenotype of a population over successive generations, can match rapid climate change [5, 14, 17, 18, 26]. Evolutionary changes in timing programs are difficult to detect without experimentation, genetic time series, or longitudinal data from pedigreed populations [5, 17, 19, 22, 24, 26]. Hence, evidence for climate-induced evolution in timing traits is scarce, particularly in vertebrates.

Here we provide experimental evidence for climate-induced evolution in the annual cycle from two studies on the pied flycatcher (hereafter "flycatcher") designed by the late Eberhard Gwinner. We investigated the first full annual cycle of flycatchers in replicated studies of cohorts hatched in 1981 [27] and 2002. In this common garden experiment through time [21], nestlings were collected from the same German field site, on the same dates (Figures S1 and S2), and raised in identical captive settings [13, 27]; thus, we considered any systematic timing changes between cohorts as evidence of evolutionary change in the birds' inherited timing programs. We recorded the timing of annual cycle events and grouped them by season (autumn, winter, spring) [9, 13, 27, 28] (Figure 1).