

# Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population

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Rapid climate change has been implicated as a cause of evolution in poorly adapted populations. However, phenotypic plasticity provides the potential for organisms to respond rapidly and effectively to environmental change. Using a 47-year population study of the great tit (*Parus major*) in the United Kingdom, we show that individual adjustment of behavior in response to the environment has enabled the population to track a rapidly changing environment very closely. Individuals were markedly invariant in their response to environmental variation, suggesting that the current response may be fixed in this population. Phenotypic plasticity can thus play a central role in tracking environmental change; understanding the limits of plasticity is an important goal for future research.

It is widely acknowledged that recent global changes in climate have had notable effects on the behavior and distribution of numerous plant and animal species (1–3). Less well established is the mechanism by which these effects arise and the consequences that they have for population persistence. Two contrasting, but nonexclusive, mechanisms that can explain population responses to climate change are (i) a microevolutionary response to natural selection and (ii) phenotypic plasticity. Understanding the role that these mechanisms play, and their consequences for population mean fitness, is important for understanding the current and likely future consequences of climate change, because it illustrates the extent to which populations are subject to changing natural selection resulting from changing environments (4). Some recent studies present evidence that climate-driven changes in the mean behavior of populations are genetically based (5–7), but other studies have suggested that individual plasticity can largely account for population responses to climate change (8–10).

Studies of the timing of breeding of birds have been an important model for characterizing the effects of climate change, because long time series are available and because the behavior of individually marked birds can be studied across environments (11–15). In addition, timing of breeding often has a strong connection to reproductive fitness. This is especially true for insectivorous birds that rely on a short period of insect abundance to feed their young; these birds

need to time their reproduction to match the timing of organisms belonging to several different trophic levels, which might easily become dissociated (13, 15, 16). We report exceptionally close tracking of a rapidly changing environment—over almost five decades—by a population of great tits (*P. major*), accomplished by phenotypic plasticity alone.

In common with some other populations for which long time series are available, the population of great tits breeding at Wytham, near Oxford, UK, shows a marked change in mean date of breeding over time. Over the past 47 years (1961–2007), the mean egg-laying date of females has advanced by about 14 days, which is equivalent to a change of more than two SDs in the mean ( $F_{2,44} = 13.89$ ,  $P < 0.0001$ ; Fig. 1A); the advancement of mean breeding date appears to begin in the mid-1970s. Previous work in this population (12, 17) and the current extended data suggest that this is due to a tight relationship between mean laying date in the population and the temperature in the period preceding egg laying ( $r = -0.85$ ,  $n = 47$  years,  $P < 0.0001$ ; Fig. 1B). There has been a marked change in the pre-laying temperature over the period ( $F_{2,44} = 12.26$ ,  $P < 0.0001$ ; Fig. 1C), with a linear increase since the mid-1970s (1975–2007:  $r = 0.66$ ,  $n = 33$  years,  $P < 0.0001$ ).

Over the same period at this site, the half-fall date [a standard measure of the timing of the peak of larval biomass (18)] of winter moth (*Operophtera brumata*) larvae—a key food resource for the rapidly growing offspring of the great tit—has shown a similar pattern of change ( $F_{2,30} = 14.09$ ,  $P < 0.0001$ ; Fig. 1D) to that of the great tit mean laying date. The half-fall date of the winter moth shows a similarly strong correlation with the early spring temperature ( $r = -0.85$ ,  $n = 33$  years,  $P < 0.0001$ ; Fig. 1E), as was found for the mean laying date of great tits. Moreover, the rates of change in the birds' mean laying date with temperature [ $-0.074 \pm 0.007$  ( $\pm$  SE) days  $^{\circ}\text{C}^{-1}$ ] and the caterpillars' half-fall

date with temperature ( $-0.081 \pm 0.009$  days  $^{\circ}\text{C}^{-1}$ ) are similar. The result is that mean laying date and half-fall date are closely matched within years ( $r = 0.79$ ,  $n = 33$  years,  $P < 0.0001$ ; Fig. 1F). Most of the mismatch is explained by differences in spring temperatures after birds have laid but before the caterpillar half-fall date (17), for which birds are partly able to compensate by adjusting the timing of clutch incubation (19). Unlike some other populations of passerine birds (13, 15, 20), there is no evidence that the synchronization of birds' laying dates with the timing of caterpillar emergence has worsened over time, because the interval between the mean laying date and half-fall date has not changed over the course of the study [ $F_{1,31} = 0.03$ ,  $P = 0.86$ ; quadratic ( $F_{2,30} = 2.01$ ,  $P = 0.15$ ) and higher-order ( $F_{3,29} = 1.47$ ,  $P = 0.24$ ) models provide no better fit to the data].

The 47-year sequence of our study includes the two warmest early springs (mean of March and April temperatures) in the world's longest-running instrumental temperature record: the 349-year Central England Temperature data set (21). Hence, the great tits have closely tracked the temporal change in the emergence of a key food source over almost five decades, during which there have been marked changes (including conditions that have, in an historical context, been unusual) in the environment and in the behavior of both birds and insects.

The importance of close temporal tracking of the emergence of the main food source is illustrated by the strong relationship between the strength and form of natural selection on laying date, and the interval between mean great tit laying date and winter moth half-fall date. In years in which this interval is relatively short, natural selection on laying date is strongly directional, favoring those birds with the earliest breeding dates [i.e., with the largest intervals between laying and the half-fall date ( $F_{1,30} = 40.27$ ,  $P < 0.0001$ ; Fig. 2A)]; most of the population breeds too late for the peak in food abundance. In years where the interval between egg laying and caterpillar half-fall is relatively large, natural selection is less strongly directional (Fig. 2A), suggesting that more of the population has bred in time for the peak. In addition, the second moment of selection changes from positive to negative as the interval increases. This indicates a switch from a convex relationship between laying date and fitness (such that when caterpillar half-fall occurs soon after mean laying, all but the very earliest birds fare poorly) to a concave one (such that, with a very long interval, fitness is reduced for the very late and very early breeders) ( $F_{1,30} = 6.08$ ,  $P = 0.020$ ; Fig. 2B: insets contrast selection in the most extreme years). This suggests a simple evolutionary mechanism by which a close match in timing of breeding in birds and the emergence of their food supply might be achieved, because years in which birds breed too late on average will be accompanied by the strongest selection for earlier breeding, whereas selection will act

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most strongly against the earliest breeders when the lag between breeding date and the caterpillar timing is largest.

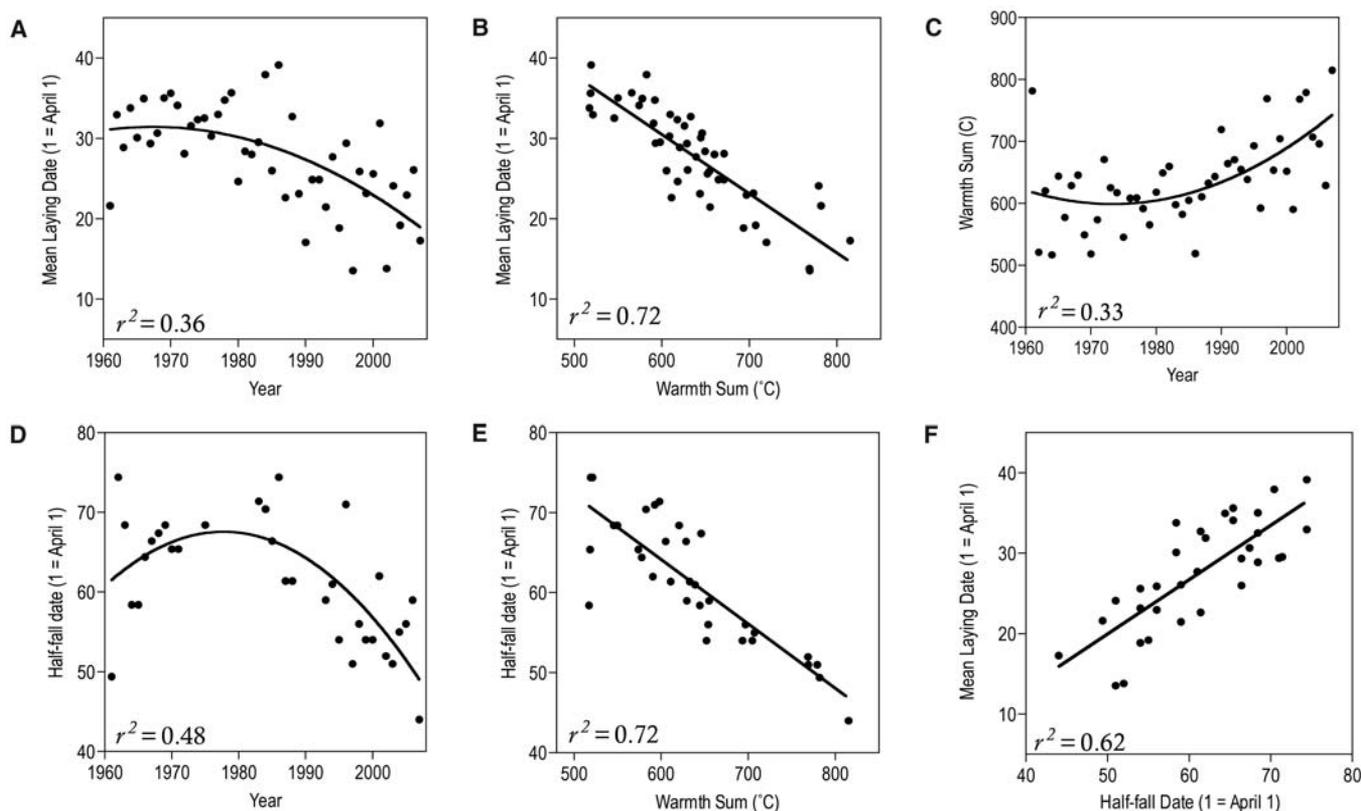
The mean number of offspring recruited per brood was significantly lower in years in which selection was more strongly directional ( $F_{1,44} = 12.56$ ,  $P = 0.0009$ ; Fig. 2C) and tended to be lower in years with a shorter interval between mean laying date and half-fall date ( $F_{1,30} = 3.56$ ,  $P = 0.07$ ). As expected, because of the tracking of the timing of the food source over time, there is no evidence that the strength of selection on laying date has changed with time ( $F_{1,44} = 0.86$ ,  $P = 0.36$ ). Various measures of population fitness suggest that this population is thriving: Population size has increased markedly over time (estimated from 1964 since when there has been a constant availability of nest sites:  $F_{1,42} = 57.56$ ,  $P < 0.0001$ ). Further, the mean recruitment success of birds (mean offspring per breeding attempt recruiting to the adult population) has increased markedly over time, when recruitment rate is corrected for the counteracting negative effect of increased population size (increase in recruitment with time =  $0.019 \pm 0.005$  offspring per year:  $F_{1,43} = 11.74$ ,  $P = 0.0014$ ; effect of population size on mean recruitment =  $-0.0027 \pm 0.0009$ :  $F_{1,43} = 9.52$ ,  $P = 0.0035$ ). The patterns documented for this population are in marked contrast to those from a well-studied Dutch

population of great tits, where caterpillar phenology has shifted forward at three times the rate of great tit laying dates (22), resulting in markedly increased selection for early breeding (13), while mean fitness has declined (14).

Several lines of evidence suggest that the population-level response to spring warming over 47 years in the Wytham great tit population can be entirely explained by individual plasticity in behavior. First, when we considered the potential magnitude of individual plastic responses, which was estimated from individuals that bred in multiple years, the slope of the relationship between within-female changes in breeding date and interannual changes in warmth sum ( $0.071 \pm 0.009$  days  $^{\circ}\text{C}^{-1}$ ;  $F_{1,42} = 57.81$ ,  $P < 0.0001$ ; Fig. 2D)—a direct estimate of phenotypic plasticity—is closely similar to the slope of the relationship between mean breeding date and warmth sum at the population level ( $0.074 \pm 0.007$  days  $^{\circ}\text{C}^{-1}$ ). Second, the strong correlation between mean laying date and spring temperature (Fig. 1B) implies a plastic response and not microevolution, because there would be mismatches in the response in a population where the phenotype in year  $N$  was a function of selection in year  $N-1$ , when the environment varies considerably from year to year (Fig. 1C). Finally, the rate of phenotypic change is too rapid to be explained by natural selection without selection being much

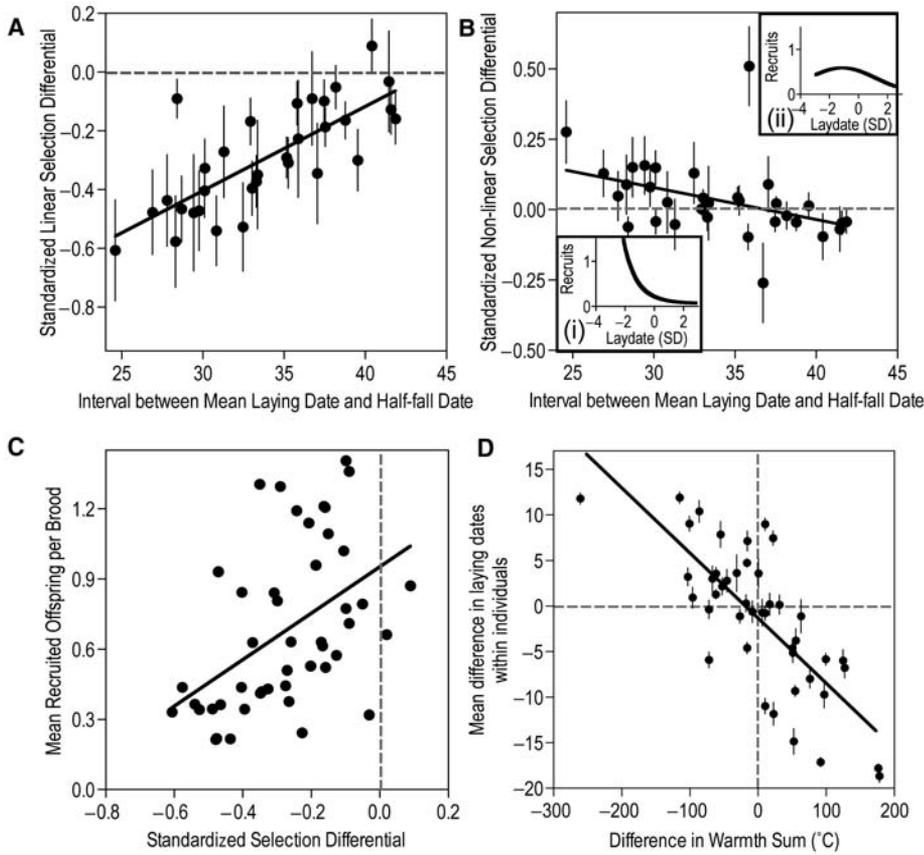
stronger than is observed (Fig. 2A). Because breeding time is sex-limited, with a heritability of  $0.16 \pm 0.06$  (23), and because mean generation time in great tits is about 2 years, a change of 2 SDs in 47 years would require a mean standardized selection differential at least four times that observed (18).

Our analyses show that the sustained response to changing environmental conditions in this population can be explained by adaptive individual phenotypic plasticity alone, but it remains possible that a changing environment may select for differing patterns of plasticity among individuals. Although very little is known about the basis of plasticity in free-ranging populations of animals, a few recent studies of natural populations of vertebrates have estimated individual variability in response to environmental change via a linear mixed modeling approach (14, 24–27). This approach allows the estimation of individual “reaction norms” to environmental variables and hence the quantification of the causes and selective consequences of between-individual variation in plasticity. Although there is a strong response to spring temperature variation at the population level, individual female great tits from the Wytham population show no detectable variation in their response to spring temperature (Table 1). Linear mixed models on laying date that used 2258 breeding records from 644 fe-



**Fig. 1.** Changes over time in temperature during the pre-laying period, assessed by spring warmth sum (sum of daily maximum temperatures between 1 March and 25 April) (C), mean laying date of great tits (A), and half-fall date of winter moth caterpillars (D) at Wytham, near Oxford, UK, between 1961 and 2007, as

well as the interrelationships between spring warmth sum and mean laying date (B), warmth sum and half-fall date (E), and mean laying date and half-fall date (F). The numbers in the panels give the proportion of variance ( $r^2$ ) explained by the regression model; lines are best-fitting linear or quadratic models.



**Fig. 2.** Synchrony between great tit laying and caterpillar emergence: consequences for natural selection, population recruitment, and the mechanism underlying synchrony. **(A and B)** Relationship between synchrony of great tit egg laying and caterpillar half-fall date and the standardized selection differential on egg-laying date (A) or the standardized nonlinear selection differential on egg-laying date (B). Error bars indicate  $\pm 1$  SE. The interval between mean laying date and the half-fall date explains a large amount of the annual variation in the strength of directional selection [(A)  $r = 0.76$ ,  $n = 32$  years,  $P < 0.0001$ ], but as the interval changes from small to large, selection on laying date changes in form from strongly directional [(B): inset (i) from 1964, the year with the smallest interval] to stabilizing [(B): inset (ii) from 1983, the year with the largest interval]; curves are fitted values from a general linear model with Poisson error. **(C)** Years with strong directional selection are years with reduced recruitment to the breeding population. **(D)** Relationship between the mean difference in laying date for individuals observed in successive years and the difference in spring warmth sum in the same pair of years ( $r = -0.76$ ,  $n = 44$  years,  $P < 0.0001$ ). Error bars indicate  $\pm 1$  SE.

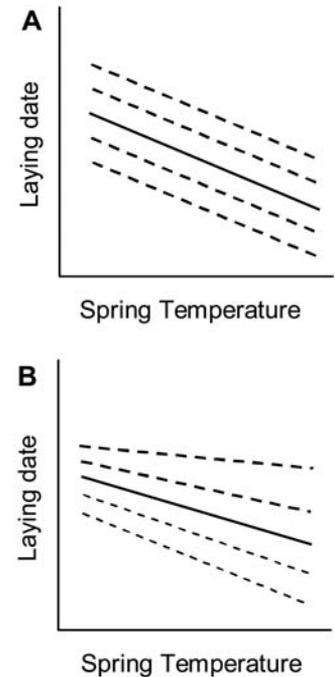
**Table 1.** Linear mixed-effects models of plasticity in egg-laying date with response to spring warmth sum for 644 females that bred in three or more years, observed on a total of 2258 occasions between 1961 and 2004. All three models control for several fixed effects (18). Model comparison is hierarchical, from the most simple to the most complex. There is strong support for differences between years in mean egg-laying date, and for differences between females across years, but there is no evidence that individual females differ in their response to spring temperature. NA, not applicable; df, degrees of freedom.

Random terms in model	Log (likelihood)	Likelihood ratio test	
		$\Delta$ df	Likelihood ratio
NA	-5382.0	NA	NA
<i>Linear mixed-effects models</i>			
Year	-5195.4	1	373.2***
Year, female	-5089.9	1	210.9***
Year, female, female $\times$ warmth sum	-5088.1	2	3.7

\*\*\* $P < 0.0001$ .

males with three or more breeding attempts between 1961 and 2004 showed significant variation between females in their average laying date but not in the slope of their response to changes in spring temperatures (Table 1). This conclusion is independent of several alternative methods of expressing individual plasticity, alternative methods of analysis, and expansion of the data to include all females ( $n = 1746$ ) that were observed breeding in multiple years (18).

Our results contrast with those reported by Nussey *et al.* (14) for a Dutch great tit population in which there was considerable individual variation in the slope of the laying-date temperature reaction norm (Fig. 3). In the absence of evidence for significant individual variation in response to the environment, the value of further analyses of individual reaction norms is debatable at best (27). In any case, such analyses yield no evidence of heritability of, or selection on, variation in the response mechanism in this population of great tits, again in marked contrast to results from the Dutch population (18). Hence, these two populations differ markedly in the extent to which individuals vary in their response to spring temperature. In the British population, females are relatively invariant, but the mean population response is highly adaptive; in the Dutch population, there is marked variation among females, but the mean population response does not track the environment sufficiently closely,



**Fig. 3.** Illustrative plots of the variance and covariance in average laying date (intercept) and slope (plasticity) in the laying-date response to increasing spring temperatures for UK **(A)** and Dutch **(B)** great tit populations. Dashed lines represent examples of reaction norms for four individual females, whereas solid lines represent the average population response.

with the result that the reaction norm is under increasingly strong selection for increased responsiveness, and fitness has declined correspondingly (14, 22).

Relative invariance in the individual response to temperature is conceivably the result of past selection to optimize the reaction norm of the British population of great tits. As documented from the close association between the timing of their food supply and the egg laying of the birds over almost five decades—despite marked changes in the typical early spring temperatures (an increase in the mean warmth sum by 127 degree days from 1961 to 2007: a change of 1.8 SDs)—the current response mechanism appears to be adaptive. However, the relative lack of variation in plasticity in British great tits suggests that although birds are currently very well adapted to present environmental conditions and to the rate of change in those conditions over the past three decades, selection for an altered pattern of plasticity would be very inefficient. The difference between two well-studied populations of the same species in their response to similar cues, and indeed even in the presence of variation in this response, is notable and suggests that within-species variation in responses to climate change deserves further investigation (15, 28). More generally, the role of phenotypic plasticity in allowing populations to track environmental changes deserves further attention. Whereas some populations are poorly adapted to changes that have occurred (5), with potential

consequences for their range and persistence (3), other species may be able to cope with a wider range of environments. Studies of the phenology of different parts of trophic systems offer an important opportunity to determine whether changes occur at appropriate rates and whether the close matching demonstrated in the British population is unusual (4). Long-term studies of marked individuals in wild populations, for which detailed knowledge of ecological processes relevant to these populations can be combined with measures of fitness, offer many opportunities to increase our understanding of the importance of this process.

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#### Supporting Online Material

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Materials and Methods  
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References

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## Temperature Sensing by an Olfactory Neuron in a Circuit Controlling Behavior of *C. elegans*

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Temperature is an unavoidable environmental cue that affects the metabolism and behavior of any creature on Earth, yet how animals perceive temperature is poorly understood. The nematode *Caenorhabditis elegans* “memorizes” temperatures, and this stored information modifies its subsequent migration along a temperature gradient. We show that the olfactory neuron designated AWC senses temperature. Calcium imaging revealed that AWC responds to temperature changes and that response thresholds differ depending on the temperature to which the animal was previously exposed. In the mutant with impaired heterotrimeric guanine nucleotide-binding protein (G protein)-mediated signaling, AWC was hyperresponsive to temperature, whereas the AIY interneuron (which is postsynaptic to AWC) was hyporesponsive to temperature. Thus, temperature sensation exhibits a robust influence on a neural circuit controlling a memory-regulated behavior.

If wild-type *C. elegans* individuals are cultivated at a certain temperature, ranging from 15° to 25°C, for 3 hours with bacteria as food source and are then placed on a temperature gradient from 15° to 25°C, most of the animals migrate to the previous cultivation temperature (Fig. 1) (1). This behavior is called thermotaxis, and its plasticity provides an opportunity to

understand molecular and neural circuit mechanisms of thermosensation, learning, and memory (1–3). By ablation of particular cells with a laser microbeam and evaluation of the consequent behavioral effects, a simple neural circuit essential for thermotaxis has been identified (Fig. 2A) (3).

Although wild-type animals migrate up or down the temperature gradient until reaching their

cultivation temperature, *nj8* mutants that were isolated in a genetic screen for thermotaxis-defective mutants migrated toward colder temperatures than those to which they were previously exposed (Fig. 1, B, D, and E). The *nj8* mutation corresponded to a nearly loss-of-function mutation in the *eat-16* gene encoding a homolog of the mammalian regulator of G protein signaling (RGS) proteins, which are negative regulators for the  $\alpha$  subunit of the G proteins (4).

A fusion gene encoding wild-type EAT-16 fused to green fluorescent protein (*eat-16::gfp*), which is under the control of the *eat-16* promoter, was broadly expressed in neurons (fig. S2A). To

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