

UK birds are laying eggs earlier

The evidence for global climate change and for its underlying anthropogenic causes is gathering rapidly. Over the past 11 years the active growing season of plants has advanced by roughly 8 days in northern latitudes¹. This evidence for increased photosynthetic activity is supported by the positive trend in the amplitude of the seasonal cycle in atmospheric CO₂ (ref. 2). The phenology of animal populations should also be affected by climate change, but to date there has been little evidence of this. Here we report that long-term trends in the seasonal distributions of laying dates of birds in the United Kingdom show a tendency towards earlier laying, consistent with the changes reported in growing season.

Since 1939, the nest record scheme of the British Trust for Ornithology has gathered more than a million records on the breeding performance of 225 species of birds in the United Kingdom. A network of 1,000 volunteer ornithologists provided details of nest site, habitat, contents at each visit and evidence for success or failure of each nest found³. Only a proportion of this information is available on computer databases and is sufficiently detailed to provide information on egg-laying dates.

We have now analysed 74,258 records from 65 species to investigate trends in the distributions of laying dates of the first egg in each clutch over the 25-year period from 1971 to 1995. We found significant trends towards earlier laying dates for 20 species (31%) with only one species laying significantly later. The shift towards earlier laying for the 20 species averaged 8.8 days, ranging from 4 to 17 days, s.d. = 3.4 (Fig. 1). The analyses of all species also show a tendency towards earlier laying (Fig. 2).

Species showing significant trends were

Figure 1 Temporal changes in laying dates for early-, mid- and late-season nesters. **a**, *Miliaria calandra*, $F_{1,23.5} = 5.30$, $P = 0.030$. **b**, *Phylloscopus collybita*, $F_{1,271} = 23.00$, $P = 0.0001$. **c**, *Pica pica*, $F_{1,18.9} = 61.89$, $P = 0.0001$. Laying date is numbered such that day 60 is 1 March, 121 is 1 May and so on. Points show annual means \pm s.e.m. We analysed between 150 and 5,700 records per species. Laying dates were estimated with an accuracy of at least ± 5 days (ref. 3). For each species we selected the most significant of three mixed linear models with Year (for example, **a** and **b**), Year² (**c**), or Year and Year² combined, fitted as continuous fixed effects; Year was also fitted as a categorical random effect to contend with the non-independence of observations within years.

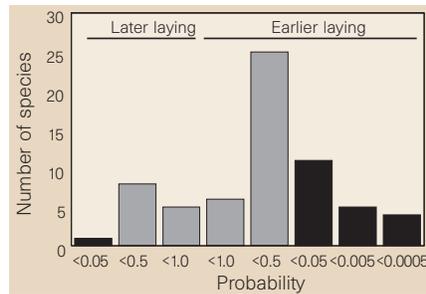
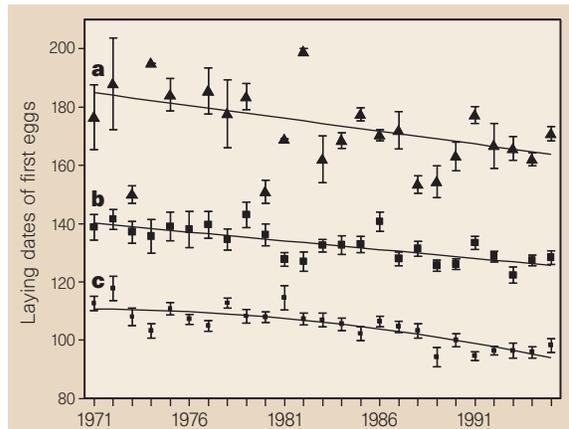


Figure 2 Frequency distribution of P values of temporal trends in laying dates for 65 species of UK birds from 1971 to 1995. Significant trends are shown in black, non-significant in grey. Trends towards earlier laying were found in 51 species and towards later laying in 14 species, a significant difference at $P = 0.000005$ (binomial test).

not confined to any one ecological or taxonomic type, and comprised water birds (*Haematopus ostralegus*, *Numenius arquata*, *Tringa totanus*), resident insectivores (*Cinclus cinclus*, *Troglodytes troglodytes*, *Aegithalos caudatus*, *Sitta europaea*, *Sturnus vulgaris*), migrant insectivores (*Anthus trivialis*, *Phoenicurus phoenicurus*, *Sylvia communis*, *S. atricapilla*, *Phylloscopus sibilatrix*, *P. collybita*, *P. trochilus*), corvids (*Pica pica*, *Corvus corone*) and seed-eaters (*Fringilla coelebs*, *Carduelis chloris*, *Miliaria calandra*).

The species also covered a wide range of nesting times, from early to late season (Fig. 1), which suggests that the recorded trends were not due to changes in the behaviour of observers. The only significant trend towards later laying was for the stock dove (*Columba oenas*), which nests opportunistically throughout the year and may therefore be a special case.

Trends towards earlier laying times are expected if ambient temperatures rise earlier in the year. There are fitness benefits to nesting early, and food availability is often the important determinant of laying date⁴. Average flowering and leafing dates may be advanced by high spring temperatures^{5,6} and these are likely to have pronounced

effects on the availability of the arthropod food supplies for birds. There is evidence that two species of waders in The Netherlands nest earlier in warmer springs⁷. Amphibians in Britain have also been shown to spawn earlier in recent years as spring temperatures have risen⁸.

The tendency to nest or reproduce earlier may be a more general phenomenon for wildlife in Britain. This could have considerable consequences for their ecology and conservation. For birds, earlier nesting could be beneficial if juvenile survival is enhanced by a prolonged period before winter. Conversely, birds may be adversely affected if they become unsynchronized with the phenology of their food supplies.

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CO₂ increases oceanic primary production

The regulation of oceanic primary production of biomass is important in the global carbon cycle because it constitutes 40% of total primary production on Earth¹. Here we present results from short-term experiments in the nutrient-poor central Atlantic Ocean. We find a small but significant stimulation of primary production (15–19%) in response to elevated CO₂ concentrations that simulate the CO₂ rise in surface waters that will occur over the next 100–200 years.

Traditionally, inorganic carbon has not been regarded as a limiting factor for oceanic production^{1–3}. Most inorganic carbon is present as HCO₃⁻ (~2 mM) whereas free CO₂ comprises only ~10 μM at atmospheric equilibrium (25 °C). The main carboxylating enzyme in marine phytoplankton requires 25–35 μM CO₂ to saturate², so phytoplankton species that cannot concentrate CO₂ internally^{2,4} by active transmembrane transport may face rate limitation of photosynthesis by CO₂ diffusion to the cell surface. Even algae capable of using HCO₃⁻ as an external carbon source can be limited by low availability of zinc, owing to its catalytic role

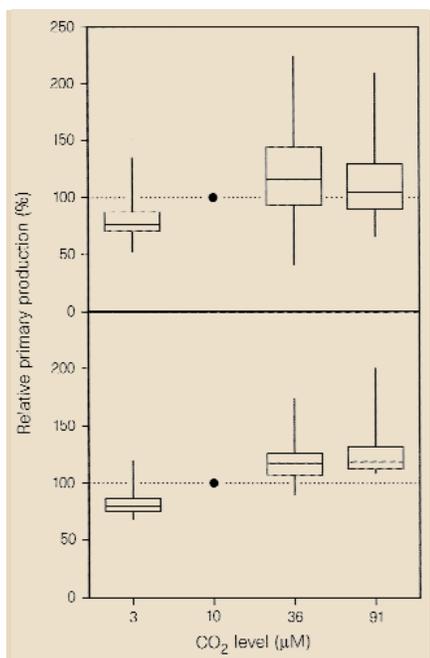


Figure 1 Oceanic primary production at reduced and increased CO₂ concentration (percentage of production at ambient CO₂). Measurements are triplicates at 18 stations along a transect in the Atlantic Ocean (35° S 49° W to 24° N 29° W) on board the Spanish BIO Hesperides. Upper panel, surface layer; lower panel, deeper layer of maximum chlorophyll content. CO₂ concentrations were: ambient 10 ± 0.3 µM, intermediate 36 ± 1.2 µM, high 91 ± 3.1 µM and low 3 ± 0.1 µM. Horizontal lines, median values; boxes, 25 and 75 percentiles; vertical lines include 10–90 percentiles. The coefficient of variation of triplicates for production rates averaged 11% in surface and 7% in deep layers. Primary production rates at elevated intermediate CO₂ concentration (36 µM) were significantly higher than those at ambient levels for surface and deeper layers ($P=0.028$ and $P<0.001$, respectively, one-tailed signed rank test).

in the enzyme carbonic anhydrase⁵. Culture experiments and diffusion models with marine phytoplankton have therefore suggested that photosynthesis and growth can be limited by the supply rate of CO₂ (ref. 4). But culture experiments with a few species cannot provide a fair description of the natural response of the mixed phytoplankton assemblage in the ocean where many species are involved and cell density, nutrient status and physiological acclimation may differ widely from those in culture.

We tested whether primary production was limited by ambient CO₂ concentration at 18 stations along a transect in the Atlantic Ocean. Primary production was measured as short-term ¹⁴C-incorporation into organic matter in samples collected from the surface waters (~5 m) and from the deeper layer (30–150 m) with maximum chlorophyll content. We illuminated surface samples at 350 µmol photon m⁻² s⁻¹ and deeper samples at 50 µmol photon m⁻² s⁻¹ for 2 h in an incubator kept at ambient temperature.

We elevated or reduced the CO₂ concentration relative to the ambient level by slightly changing the pH, adding HCl or NaOH. This procedure is straightforward and can change CO₂ concentrations without altering the total inorganic carbon pool. The decline in pH along with the CO₂ rise may influence primary productivity, but this pH decline would also occur naturally with the future CO₂ rise. The alteration of pH may also influence trace metal bioavailability⁵, but the duration of the experiments was so short (2 h) that they are unlikely to influence ¹⁴C incorporation.

Overall, primary production at the 18 sites responded significantly to manipulation of the CO₂ concentration (Fig. 1). In surface waters, median primary production at low CO₂ (3 µM) was 75% of the level at ambient CO₂ (10 µM) and median primary production at elevated CO₂ (36 µM) was 115% of the ambient level. Likewise, in deeper chlorophyll-rich layers, median primary production was 78% at low CO₂ and 119% at elevated CO₂ as compared with ambient primary production. We saw no further increase in primary production at the highest CO₂ level tested (91 µM).

The response to CO₂ manipulation varied substantially among different sites, as expected considering that the composition of the phytoplankton communities was likely to vary along the transect. At some sites primary production did not respond to CO₂ elevation whereas at other sites primary production more than doubled. Rates of primary production at ambient CO₂ in the surface (0.02–0.44 mg C m⁻³ h⁻¹) and deeper layers (0.05–0.86 mg C m⁻³ h⁻¹) also varied considerably. There was no systematic relationship between the response of primary production to CO₂ manipulation and the geographical location or magnitude of primary productivity.

The CO₂ concentration elevation to 36 µM corresponds roughly to the level expected in the surface ocean at atmospheric equilibrium (855 p.p.m., 25 °C) in year 2100, according to the IPCC ‘business as usual’ model⁶. Our results indicate that the median primary production could increase by about 15–19% in response to the CO₂ rise, with other factors remaining constant. The variable response to CO₂ elevation along the transect also suggests that the stimulation could be markedly higher (perhaps double) in some instances, probably dominated by phytoplankton species without CO₂-concentrating mechanisms. However, the long-term growth response to CO₂ elevation is usually much lower than the short-term photosynthetic response determined here. This has been shown frequently for terrestrial plants³.

We propose that the overall response of oceanic primary production to the CO₂ rise would be relatively small, whereas the influ-

ence on the species composition of the phytoplankton assemblages could be profound, depending on the kinetics of carbon use.

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Structural biology and phylogenetic estimation

When reconstructing evolutionary trees from DNA sequences, it is often assumed that increasing the amount of sequence will improve the phylogenetic estimate^{1,2}. This is based on the notion that historical ‘signal’ will rise above misleading ‘noise’ as more sequence is gathered. Our analysis of mitochondrial genomes fails to support this assumption, but suggests a way to select objectively for data with maximum ‘signal-to-noise’ potential.

We carried out a phylogenetic parsimony analysis³ of the entire protein-coding portion (12,234 base pairs) of the mitochondrial genome of 19 taxa whose interrelationships are widely accepted (Fig. 1a). Not only did we fail to obtain the expected phylogenetic tree from this large data set, but found compelling bootstrap support for the incorrect placements (Fig. 1b). This suggests that misleading signals will not always disappear as more data are collected.

When a subset of sites associated with residues important for protein folding was subjected to phylogenetic analysis, the expected tree resulted with strong bootstrap support. Phylogenetic analysis of DNA sequences might therefore be improved by incorporating structural and functional considerations into inference models^{4–6}.

To determine which of our 12,234 sites were responsible for the misleading signal, we superimposed the sequence data onto the accepted tree and measured, using the retention index^{7,8}, how well each site fitted that tree. We found that among codons, nucleotides at third positions produced the poorest fits; among genes, *NADH2* produced the poorest fit; and isoleucine, leucine and valine produced the poorest fits of the amino acids. Sites coding for residues with aliphatic side chains produced poorer fits than did those coding for any other type