# Antarctic birds breed later in response to climate change

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**In the northern hemisphere, there is compelling evidence for climate-related advances of spring events, but no such long-term biological time series exist for the southern hemisphere. We have studied a unique data set of dates of first arrival and laying of first eggs over a 55-year period for the entire community of Antarctic seabirds in East Antarctica. The records over this long period show a general unexpected tendency toward later arrival and laying, an inverse trend to those observed in the northern hemisphere. Overall, species now arrive at their colonies 9.1 days later, on average, and lay eggs an average of 2.1 days later than in the early 1950s. Furthermore, these delays are linked to a decrease in sea ice extent that has occurred in eastern Antarctica, which underlies the contrasted effects of global climate change on species in Antarctica.**

Antarctica | phenology | seabirds | sea ice

Climate change is expected to have an impact on the phenology (the study of the timing of seasonal activities of biological events) of organisms living in seasonal environments (1, 2). Analyses of long-term phenological data sets have indeed revealed significant phenological trends linked to large-scale climatic signals, such as the North Atlantic Oscillation, and weather conditions such as spring temperatures (3–5). In general, these trends indicate that spring activities such as first arrival of migrant birds or earlier sprouting of plants have occurred progressively earlier since the mid-20th century in response to increasing temperatures. However, there is a major geographical bias among these phenological studies. Indeed, the overwhelming majority of the studies have been conducted in the northern hemisphere, particularly in Europe and North America. To our knowledge, no such long-term biological time series exist for the southern hemisphere and particularly not for the Antarctic fauna. This bias is problematic because observed climate changes differ between both hemispheres (6), and, consequently, the phenological responses might differ.

Here, we analyze the only long-term record of phenological events for all species of seabirds breeding in continental Antarctica. This record offers an unusual and unique opportunity to observe long-term changes of arrival and egg-laying dates in relation to climate trends in the southern hemisphere.

## Results and Discussion

Of nine seabird species for which dates of first arrival and first egg laying have been recorded at the Dumont d'Urville Station (lat 66°70′S, long 140°00′E) in Adélie Land (Fig. 1) over the period 1950–2004, four species tended to arrive later, with shifts ranging from 5.2 to 30.6 days, and two species bred later, with shifts ranging from 2.8 to 3.7 days (Fig. 2). All other species also tended to arrive and breed later, but the trends were not statistically significant at the 0.05 level. Overall, species now arrive at their colonies an average of 9.1 days (SE of 3.6 days) later and lay eggs an average of 2.1 days (SE of 1.4 days) later than in the early 1950s. In contrast, the only significant trend toward earlier laying (3.8-day shift) was for the south polar skua (*Catharacta maccormicki*), which mainly predates eggs and chicks of Adélie penguins (*Pygoscelis adeliae*), whereas the other species forage at sea for fish, crustaceans, and squid (7).

We found no significant relationship between phenological events and average air temperatures for the month preceding species-specific arrival and laying dates. Large-scale climatic indices that quantify Antarctic climatic conditions [i.e., the Southern Annular Mode (Fig. 3*A*) and the Southern Oscillation Index (Fig. 3*B*) (8, 9)] were also not related to changes in phenological events, except for the Cape petrel (*Daption capense*), for which dates of first arrival and first egg laying were negatively related to the Southern Oscillation Index ($r^2 = 0.196$, $P = 0.0047$ and $r^2 = 0.242$, $P = 0.0058$, respectively). Because sea ice extent has a profound influence on marine productivity and seabird dynamics (10–12), we used the only existing long-term proxy for sea ice extent in East Antarctica before the satellite era (Fig. 3*D*) (13). Regression analyses between sea ice extent and phenological variables indicate that the date of first arrival was negatively related to sea ice extent for four species and that the date of first egg laying was negatively related to sea ice extent for three species (Fig. 4). A metaanalysis in which the slopes of regressions were considered as measures of effect size confirmed that the mean slope of arrival date versus sea ice extent significantly departed from the null model that assumes no change as a function of sea ice extent [one sample Student's *t* test of mean slope against 0; $t(16) = 2.577$; $P$ (two-tailed) $= 0.02$].

Our results contrast with phenological changes observed in the northern hemisphere, where increasing spring temperatures are likely to have had pronounced effects on nearly all phenophases. For birds, spring warming is likely to have increased the availability of food supplies, resulting in earlier arrival and laying dates (2). In East (and continental) Antarctica, no major warming or cooling has occurred since the early 1950s, contrary to what has been observed in the northern hemisphere or in western Antarctica (6, 14). However, the large (12–20%) reduction in sea ice extent since the 1950s (13) has been associated with a decline in abundances of krill and other marine organisms (10, 11, 15), which are major food resources for most Antarctic seabirds (7). Their decline may be driving the observed delays in bird arrival and breeding. In addition, the duration of the sea ice season tended to increase by >40 days in eastern Antarctica since the late 1970s (Fig. 3*E*) (16). Although these contrasting trends seem counterintuitive, recent research suggests that sea ice extent is connected to large-scale features of the global climate system (such as the Southern Oscillation Index or the Southern Annular Mode), whereas the length of the sea ice season is connected to more regional features such as temperature (17). Because late sea ice breakup is known to delay access to colonies (18, 19) and food resources at sea, it may also explain Antarctic seabirds' tendency to arrive and reproduce later. Therefore, we suggest that decreasing sea ice extent and

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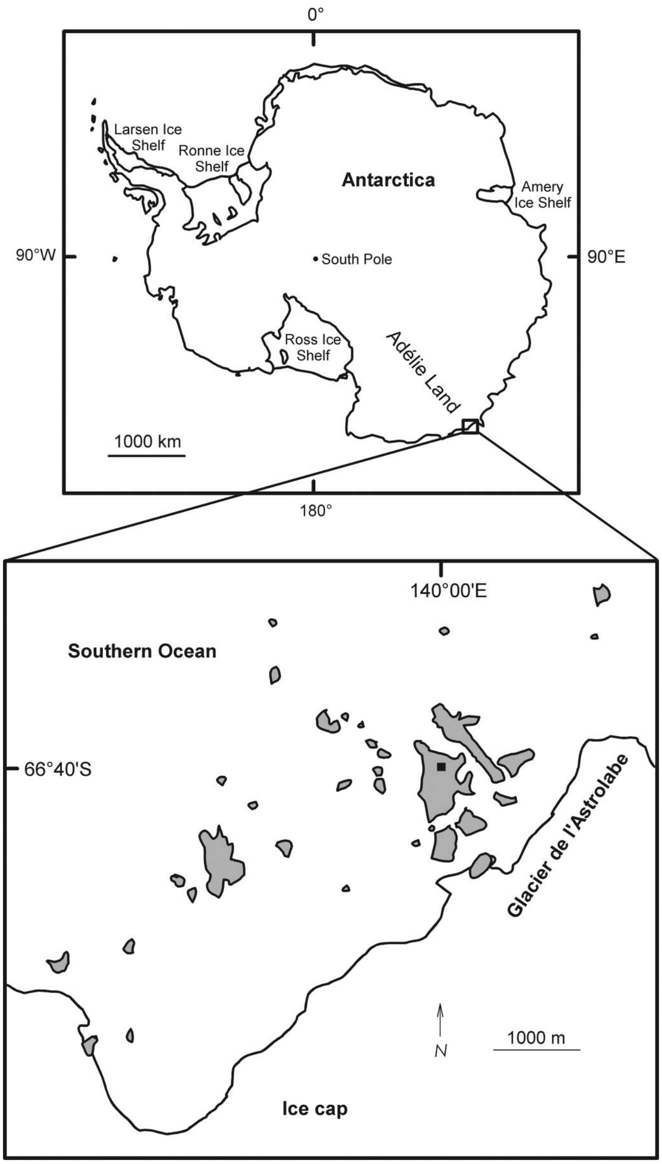


**Fig. 1.** Map indicating the location of Adélie Land in Antarctica and the study sites near Dumont d'Urville. Most seabird species nest and are studied on the largest island, where the Dumont d'Urville research station is located (square).

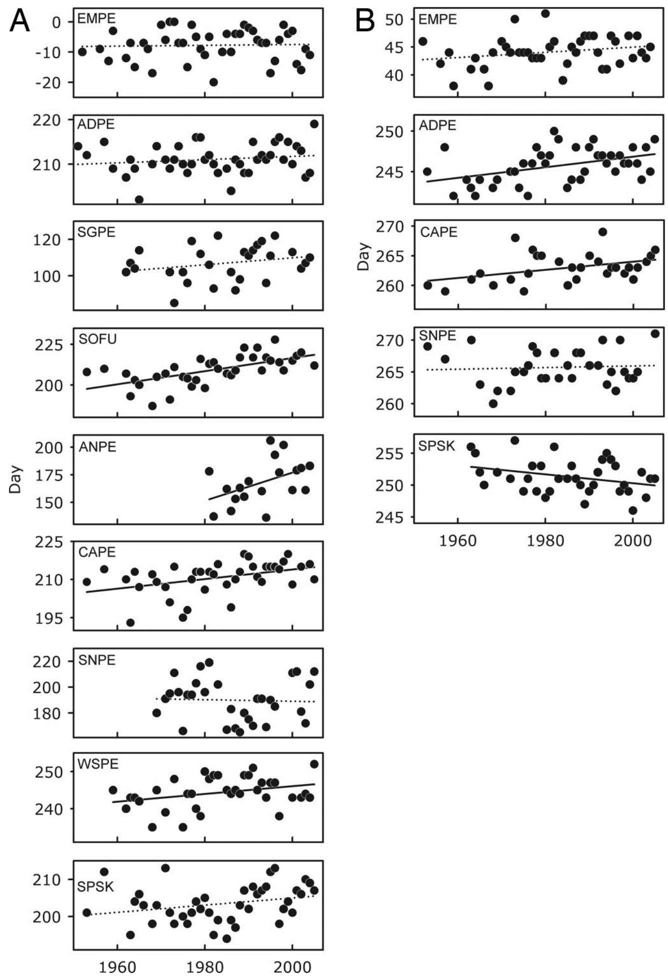


**Fig. 2.** Phenological changes. (*A*) Dates of first arrival for the emperor penguin, *Aptenodytes forsteri* (EMPE) ($r^2 = 0.001$; $P = 0.81$); Adélie penguin, *P. adeliae* (ADPE) ($r^2 = 0.03$; $P = 0.30$); southern giant petrel, *M. giganteus* (SGPE) ($r^2 = 0.06$; $P = 0.20$); southern fulmar, *F. glacialoides* (SOFU) ($r^2 = 0.38$; $P < 0.001$); Antarctic petrel, *T. antarctica* (ANPE) ($r^2 = 0.21$; $P = 0.04$); Cape petrel, *D. capense* (CAPE) ($r^2 = 0.17$; $P = 0.01$); snow petrel, *Pagodroma nivea* (SNPE) ($r^2 = 0.001$; $P = 0.83$); Wilson's storm petrel, *O. oceanicus* (WSPE) ($r^2 = 0.11$; $P = 0.05$); and south polar skua *C. maccormicki* (SPSK) ($r^2 = 0.07$; $P = 0.09$). (*B*) Dates of laying of first eggs. Data are shown for EMPE ($r^2 = 0.12$; $P = 0.11$), ADPE ($r^2 = 0.19$; $P < 0.01$), CAPE ($r^2 = 0.16$; $P = 0.03$), SNPE ($r^2 = 0.004$; $P = 0.73$), and SPSK ($r^2 = 0.11$; $P = 0.05$). Regression lines indicate significance of the trends (solid line, $P < 0.05$; dotted line, $P > 0.05$).

increasing sea ice season duration have reduced the quantity and accessibility of the food supplies available in early spring and may partly explain the delays observed in arrival and laying dates, with seabirds needing more time to build up the reserves necessary for breeding (20). However, sea ice extent only explained up to 24% of the variance in arrival or egg-laying dates. Given that none of the other climatic factors examined were related to arrival date or to laying date of first eggs, there are other factor(s) that are more important than sea ice extent in determining arrival and laying dates.

This unique data set for the southern hemisphere shows clearly that responses of Antarctic seabirds are opposite to those observed in the northern hemisphere and the Arctic but consistent with climatic and oceanographic changes in eastern Antarctica. The consequences of delayed phenology could be serious for these top predators if they become less synchronized with the phenology of their food supplies (21). Interestingly, the 9.1-day delay in arrival at the colonies and the 2.1-day delay in the date of laying of the first egg represent, on average, a 7-day compression of the prelaying period when birds set up territories and court and females make their egg(s). The time needed by females to make their egg is probably under strong physiological constraints, and thus, presumably, the duration needed for setting up territories and/or courting decreased, suggesting some plasticity in the timing of these activities. The fact that Antarctic top predators already respond to environmental changes by shifts in their population dynamics (12, 22, 23) and phenology raises some fascinating questions about how they will be affected by ongoing climatic trends. Because southern shifts in the distribution of Antarctic species are extremely limited by the presence of the Antarctic ice cap, unless microevolutionary responses to climate change progress with sufficient speed, these species may be unable to respond appropriately to changes occurring in their breeding area and therefore may be

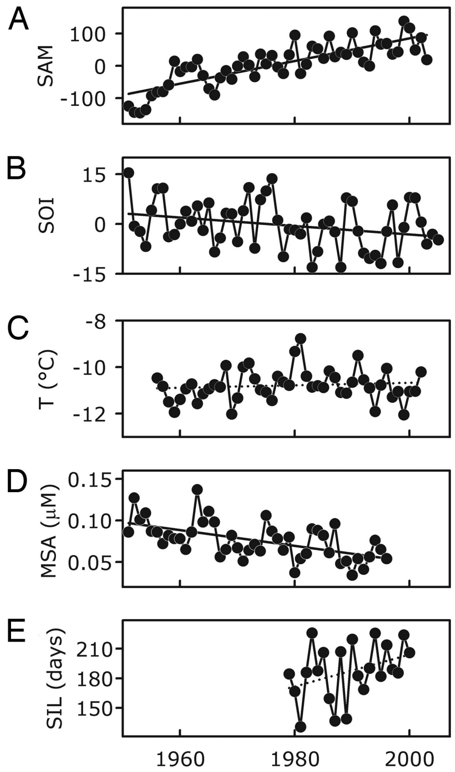


**Fig. 3.** Climate changes. (*A*) Southern Annular Mode (SAM) ($r^2 = 0.65$; $P < 0.001$) as defined in ref. 9. (*B*) Southern Oscillation Index (SOI) ($r^2 = 0.08$; $P = 0.03$). (*C*) Average annual air temperatures recorded at the Dumont d'Urville meteorological station (1956–2002) ($r^2 = 0.01$; $P = 0.47$). (*D*) Methanesulfonic acid concentration (MSA) ($r^2 = 0.32$; $P < 0.001$) as a proxy for sea ice extent from an ice core in East Antarctica (13). Values were redrawn from ref. 13. (*E*) Sea ice season length (SIL) for the sector 136°E to 142°E and north of 65°S ($r^2 = 0.13$; $P = 0.09$). Data are from ref. 16; updates were kindly provided by C. L. Parkinson (NASA Goddard Space Flight Center, Greenbelt, MD). Regression lines indicate significance of the trends (solid line, $P < 0.05$; dotted line, $P > 0.05$).

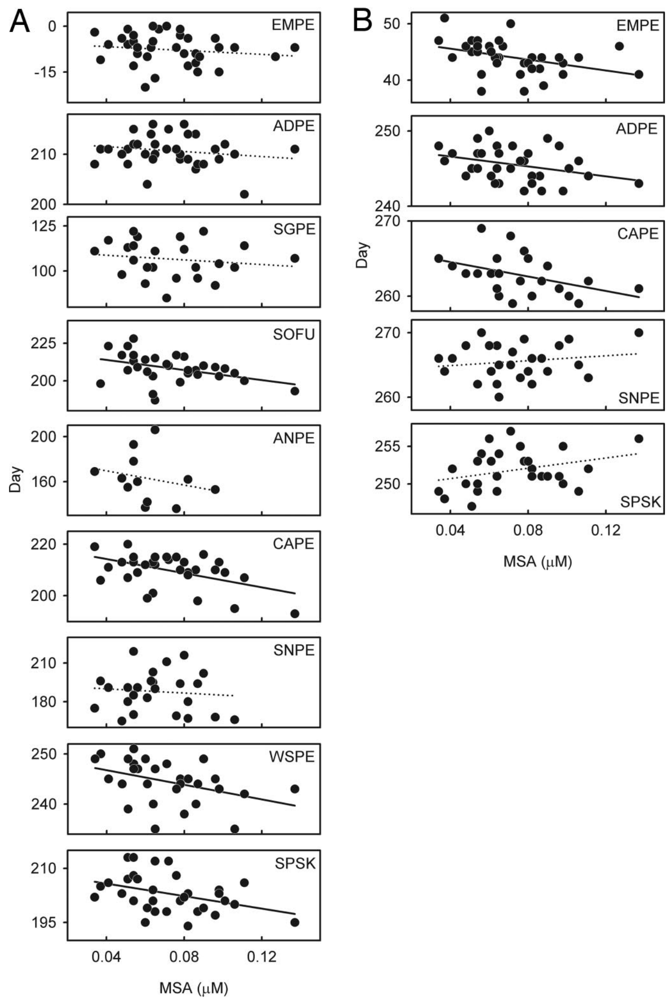


**Fig. 4.** Phenological changes and sea ice extent. (*A*) Dates of first arrival advanced significantly with increasing sea ice extent for the southern fulmar ($r^2 = 0.17$; $P = 0.02$), Cape petrel ($r^2 = 0.24$; $P = 0.004$), Wilson's storm petrel ($r^2 = 0.17$; $P = 0.02$), and south polar skua ($r^2 = 0.16$; $P = 0.03$). (*B*) Dates of laying of first eggs advanced significantly with increasing sea ice extent for the emperor penguin ($r^2 = 0.15$; $P = 0.02$), Adélie penguin ($r^2 = 0.12$; $P = 0.05$), and Cape petrel ($r^2 = 0.19$; $P = 0.04$). Solid lines indicate significant ($P < 0.05$) regressions. Abbreviations are as described in the legend of Fig. 2.

disproportionately negatively affected by current climate changes.

## Materials and Methods

**Phenological Data.** Since 1950, the dates of first arrival of the nine seabird species breeding in Antarctica and the dates of laying of first eggs from five of these species have been recorded by ornithologists wintering almost each year at the Dumont d'Urville Station in Adélie Land, Antarctica, generating the longest phenological data set available for Antarctic species. First arrival dates and first egg-laying dates were recorded as part of a long-term study of top predators at Adélie Land. The Antarctic petrel (*Thalassoica antarctica*) is the only Antarctic seabird species not breeding at Dumont d'Urville. However, a large breeding colony (nearly 4,000 breeding pairs) is situated ≈110 km from Dumont d'Urville (24), and the species is regularly seen in the surroundings of the station. Consequently, first arrival dates for all of the nine species of Antarctic seabirds were used in the analysis. For three species (southern giant petrel, *Macronectes giganteus*; southern fulmar, *Fulmarus glacialoides*; and Wilson's storm petrel, *Oceanites oceanicus*), egg-laying dates were not recorded either because these species breed in low numbers, and access to colonies was limited to minimize disturbance, or because of their cryptic nesting. Because all breeding colonies are situated in the vicinity of the research station and because the observer was permanently in the field (weather permitting), we are very confident in the precision of arrival and egg-laying dates. Although the methodological uncertainties for the observations have not been quantified, the precision of the observations is probably ±1 day.

**Statistical Analyses.** To correct for fluctuations in the calendar date of the vernal equinox over the study period, phenological events were reported and expressed as the time elapsed since the vernal equinox for each year of the data set (25). In the metaanalysis, the slopes of regressions were considered as measures of effect size, and Kolmogorov–Smirnov tests confirmed that the slopes were distributed normally ($P > 0.66$).

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