

eventual Hector Mine rupture surface. Meanwhile, for both cases, the net (coseismic plus postseismic) changes in Coulomb stress remained negative at and beyond the distal ends of the Hector Mine rupture surface (Fig. 3b and d). Thus, it is possible that, once triggered, the Hector Mine rupture propagated to the north and south until it encountered these regions of negative net stress changes. Propagation part of the way into these negative-stress regions could be explained by the dynamics of the rupture process, which itself could have increased stress levels at the propagation fronts. Alternatively, the lateral extent of the Hector Mine rupture zone may have been controlled by the mechanical heterogeneity of the crust in the region rather than by the spatial patterns of stress changes. These results attest to the importance of considering viscoelastic processes in the assessment of seismic hazard and its migratory pattern^{8–11}. □

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Emperor penguins and climate change

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Variations in ocean–atmosphere coupling over time in the Southern Ocean^{1–3} have dominant effects on sea-ice extent and ecosystem structure^{4–6}, but the ultimate consequences of such environmental changes for large marine predators cannot be accurately predicted because of the absence of long-term data series on key demographic parameters^{7,8}. Here, we use the longest time series available on demographic parameters of an Antarctic large predator breeding on fast ice^{9,10} and relying on food resources from the Southern Ocean¹¹. We show that over the past 50 years, the population of emperor penguins (*Aptenodytes forsteri*) in Terre Adélie has declined by 50% because of a decrease in adult survival during the late 1970s. At this time there was a prolonged abnormally warm period with reduced sea-ice extent. Mortality rates increased when warm sea-surface temperatures occurred in the foraging area and when annual sea-ice extent was reduced, and were higher for males than for females. In contrast with survival, emperor penguins hatched fewer eggs when winter sea-ice was extended. These results indicate strong and contrasting effects of large-scale oceanographic processes and sea-ice extent on the demography of emperor penguins, and their potential high susceptibility to climate change.

Between 1952 and 2000, the emperor penguin colony located near Dumont d'Urville Station (66.7°S, 140.0°E) in Terre Adélie was monitored continuously, generating the longest data set available on an Antarctic marine predator. Data from the meteorological station 500 m from the colony shows that, after a period of stability in the 1960s (average temperatures –17.3 °C), winter temperatures began to vary extensively and were high throughout the 1970s until the early 1980s (average –14.7 °C); they then decreased but remained variable until the present time (average –16.6 °C, $t = 3.2$, $P = 0.004$ (Student's t -test; Fig. 1a). No trend was detectable for the summer temperatures. The breeding population of emperor penguins was stable until the mid-1970s, but declined abruptly by 50% in the late 1970s and has stabilized since (Fig. 1b).

We used capture–mark–recapture data spanning 1969–1989 from ringed breeding emperor penguins to estimate adult annual survival rates (see Methods). Females survived better than males but the survival curves for males and females were parallel (additive time-dependence, see Methods; Fig. 2a). Survival was particularly

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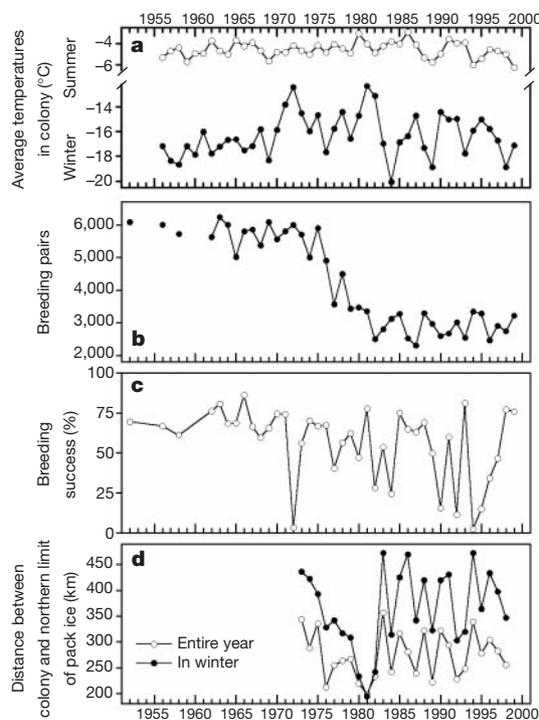


Figure 1 Climate and population changes. **a**, Summer and winter average temperatures recorded at Dumont D'Urville meteorological station (1956–1999). **b**, Number of breeding pairs of emperor penguins at Pointe Géologie archipelago, Terre Adélie (1952–1999). **c**, Changes over time in breeding success (number of chicks fledged divided by number of eggs laid). **d**, Changes over time (1973–1999) in the average distance between the emperor penguin colony and the northern extent of pack ice.

low in 1972, in 1976–1980 and in 1985 (Fig. 2a). The prolonged period of low survival during the late 1970s corresponds to the period of rapid decline of the breeding population (Fig. 2a). Interannual per cent changes in the breeding population size were related to annual survival ($P < 0.001$; Fig. 2b) and explained 64% of the variation in survival. The decline in population during the second half of the 1970s was thus caused by this unusually long period of low adult survival. The growth rate of populations of long-lived species is mainly sensitive to changes in adult survival¹². High emigration from this colony to others is unlikely as the nearest colony is 1,000 km away and penguins, like all seabirds, are faithful to their breeding site once they have started to reproduce¹³.

Among the three covariates examined (annual average sea surface temperatures (SST), northward sea-ice extent and atmospheric sea-level pressure; see Methods), SST accounted for most (89.8%) of the yearly variation in survival ($P = 0.0012$). Emperor penguins survived less when SSTs were higher ($P < 0.001$) (Fig. 2c). Sea-ice extent anomalies explained 86.9% of the variation in survival ($P = 0.0022$) and penguins survived better when sea-ice extent was greater ($P < 0.001$). Sea-level pressure did not explain a significant part of the yearly variation in survival ($P = 0.48$). To our knowledge, this is the first time that the consequences of changes in major oceanic parameters on the dynamics of an Antarctic large predator have been identified, and particularly that the proximate and ultimate factors affecting the dynamics of the population have been documented.

Because variables are interlinked, variability is generally assumed to cascade throughout the environment and biological systems. Adult emperor penguins forage only at sea and mainly feed on Antarctic krill (*Euphausia superba*), fish (mainly *Pleuragramma antarcticum*) and squid, in proportions that vary as a function of locality and time^{11,14,15}. Prey availability is influenced by physical parameters such as sea-ice extent or sea-surface temperature (or

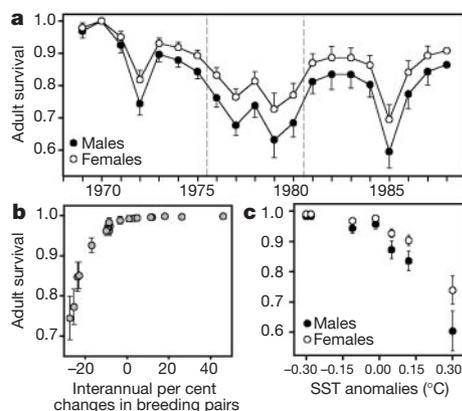


Figure 2 Adult survival of emperor penguins. **a**, Annual survival of male and female emperor penguins (mean \pm 1 s.e., 1969–1988). Dashed vertical lines encompass the period of abrupt decline of the population (see Fig. 1b). The modelling of survival probabilities indicated that adult survival differed between sexes (P -likelihood ratio test (LRT) = 0.065) and varied among years (P -LRT $<$ 0.001). Survival estimates are from model ($\Phi_{a2+s+t}, \rho_{1'm}$) where male and female survival are additive and time-dependent (model with lowest Akaike's Information Criterion (AIC) for the 1969–1989 data set; see Methods). **b**, Survival estimates of emperor penguins (males and females combined) from the covariate model investigating the relationship between survival and inter-annual per cent change in the breeding population size. Survival estimates are from model ($\Phi_{a2 + \text{population change}}, \rho_{1'm}$). Population change accounted for a large part of the annual variation in survival ($\chi^2_{17} = 18.25, P = 0.37$). The slope of the logit-linear relationship of survival Φ with population change (logit $\Phi = a + b \times \text{population change}^{26}$) was 0.42 ± 0.12 (lower

and upper 95% confidence limits were 0.19 and 0.66, respectively), indicating lower survival when the population decreased. Error bars, \pm 1 s.e. **c**, Survival estimates of male and female emperor penguins plotted against sea-surface temperature anomalies for the period 1982–1988, when both parameters were available. Survival estimates are from model ($\Phi_{s+SST}, \rho_{1'm}$) with the lowest AIC value. The AIC-differences between this model and models ($\Phi_{s+t}, \rho_{1'm}$) and ($\Phi_s, \rho_{1'm}$) were, respectively, 4.48 and 50.51, and SST accounted for a large part of the annual variation in survival ($\chi^2_5 = 5.942, P = 0.312$). The slope of the logit-linear relationship of survival Φ with SST was -6.02 ± 1.01 (lower and upper 95% confidence limits -7.99 and -4.05 , respectively), indicating lower survival with higher SST. Errors bars, \pm 1 s.e. The slope of the relationship of survival Φ with sea-ice extent was 0.38 ± 0.10 (lower and upper 95% confidence limits 0.18 and 0.58, respectively), indicating higher survival with greater sea-ice extent.

both)¹⁶. Decreased frequency of krill recruitment associated with a decreased frequency of extensive winter sea-ice may be responsible for low population sizes of krill¹⁷, and lower krill abundance is associated with areas with less winter sea-ice cover⁵. In years with high SSTs, emperor penguins probably have difficulties in finding food, which could increase mortality. It is not known when the survival of adult emperor penguins is affected by warm water events: whether during winter when males and females undertake long incubation and chick brooding fasts^{18,19}, or during the summer when they disperse to moult²⁰.

Breeding success varied extensively throughout the period, and its variability has increased progressively since the 1970s (Fig. 1c). A combination of local factors has probably contributed to the high variability in breeding success. Complete or extensive breeding failures in some years resulted from early break-out of the sea-ice holding up the colony, or from prolonged blizzards during the early chick-rearing period²¹. Overall breeding success was not related to SST anomalies or sea-ice extent, possibly because variation was the result of a combination of confounding factors related to sea-ice conditions or weather conditions. However, the proportion of eggs that hatched a chick was negatively related to the extent of pack ice in winter ($r^2 = 0.284$, $P = 0.02$), with wider pack ice resulting in lower hatching success.

One paradoxical and unexpected result of this study is that the extent of pack ice, which is a key factor in the Antarctic ecosystem⁷, has two opposite effects on the demographic parameters of emperor penguins. Sea-ice extent in winter negatively affects hatching success, by increasing the distance between the colony and feeding grounds. Conversely, annual sea-ice extent positively affects adult survival by increasing food availability. Therefore there exists in emperor penguins a trade-off between the advantages and disadvantages of extensive pack ice. In population terms, the trophic advantage of extensive pack ice, by favouring higher survival and further reproduction, outmatches its physical disadvantage of reducing fecundity.

Whereas time series on emperor penguins and on meteorological conditions in the colony are available since 1952, data on the extent of sea-ice are available only from 1972 onwards, and on SST from 1982. Given the strong relationship between survival and SST anomalies related to the Antarctic Circumpolar Wave² in 1982–1989, low survival during 1976–1980 (and the 50% population decrease) was probably associated with high SSTs, but remote-sensing satellite data were not available at this time. The temperature recorded in winter in the colony, however, indicates a prolonged warm period during the 1970s (Fig. 1a) associated with a prolonged period of decreasing extent of ice¹ (Fig. 1d). This anomaly is probably connected to the abrupt decline in Antarctic sea-ice extent that is apparent from whaling records during the 1960s and 1970s^{1,3}. The exact timing of the decline is not known because of the lack of records during this period³. Our results indicate that this major event may have occurred during the 1970s rather than during the 1960s as suggested earlier. Our results also indicate that emperor penguins may be very susceptible to environmental variability and that further long-lasting coupled anomalies are likely to affect their populations. □

Methods

We determined the number of breeding pairs from the number of chicks fledged plus the number of eggs and chicks found dead. Dead chicks and eggs remain frozen on sea-ice around the colony and were collected and counted daily during the entire breeding season. The number of breeding pairs represents 80% of the overall population size.

Environmental parameters

We used three types of data: the annual average SST calculated from a combination of *in situ* and satellite-radiometer measurements obtained on a 1° grid²²; the annual average northward sea-ice extent calculated from space-borne microwave sensors on a 25-km grid²³; and the annual averages of atmospheric sea-level pressure calculated from data produced by the European Centre for Medium Range Weather Forecasts on a 1.875° grid²⁴, all spanning 1982–1989. Data were extracted for the 200-km radius (from latitude 66.7° S)

surrounding the Pointe Géologie colony, an area consistent with the foraging radius of emperor penguins^{11,19}. Physical parameters were determined relative to the applicable record length annual mean values and filtered to suppress seasonal and possible biennial signals².

Survival modelling

Adults were ringed each year between 1967 and 1980 using metal bands placed at the base of the flippers. Ringing and ring readings were made in April and May when birds arrived on the breeding grounds forming columns and during pair formation from 1968 until today⁹. Because during the first year after banding, and to a lesser extent during the second year, bands are more likely to be lost or to affect survival²⁵, we have excluded data from the first two years after banding. We estimated adult survival rate using recent developments of the Cormack–Jolly–Seber model^{26,27} implemented in the MARK software²⁸ for the period 1969–1988. This method allows the estimation of unbiased capture and survival probabilities. Parameters that may explain time-variation in survival were then examined using the capture–mark–recapture data set over the period 1982–1989, when data were simultaneously available with adult survival (before 1982, no physical data were available). The 1982–1989 data set was used to test the effects of physical parameters on survival. Details of survival modelling procedures are available as Supplementary Information.

Changes in breeding population size from year to year should be correlated with survival if variations in the latter are a principal cause of the former. To test whether the temporal variation in survival is likely to have been a significant cause of changes in population size we used a covariate model in which the interannual per cent change in the breeding population size was added to the selected model as an annual covariate²⁹ with a one-year lag, as the breeding population size of emperors was determined in May.

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Supplementary Information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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Host recognition by the tobacco hornworm is mediated by a host plant compound

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It is generally believed that animals make decisions about the selection of mates, kin or food on the basis of pre-constructed recognition templates. These templates can be innate or acquired through experience¹. An example of an acquired template is the feeding preference exhibited by larvae of the moth, *Manduca sexta*. Naive hatchlings will feed and grow successfully on many different plants or artificial diets, but once they have fed on a natural host they become specialist feeders^{2–6}. Here we show that the induced feeding preference of *M. sexta* involves the formation of a template to a steroidal glycoside, indioside D, that is present in solanaceous foliage. This compound is both necessary and sufficient to maintain the induced feeding preference. The induction of host plant specificity is at least partly due to a tuning of taste receptors to indioside D. The taste receptors of larvae fed on host plants show an enhanced response to indioside D as compared with other plant compounds tested.

By manipulating the diets of larvae, we examined the strength of induced feeding preferences. *Manduca sexta* larvae were reared from hatching until the early fourth instar on either solanaceous or non-solanaceous diets. The solanaceous diets consisted of foliage from potato (*Solanum tuberosum*) or tomato (*Lycopersicon esculentum*); the non-solanaceous diets were either foliage of cowpea (*Vigna sinensis*, Fabaceae), or a wheat-germ-based artificial diet⁷. After the molt to the fourth instar, larvae from these four groups were removed from their original diet, and randomly assigned to one of the two solanaceous plants, or to the non-solanaceous cowpea. Within 24 h, all larvae reared on solanaceous foliage had begun feeding on solanaceous leaves; however, only 21.5% (11/51) of the solanaceous-reared larvae had fed on the foliage of the non-solanaceous cowpea (Fig. 1a). After 96 h, the percentage of solanaceous-reared larvae feeding on cowpea had increased to 45.1% (23/51), although by this time 35.3% (18/51) of the larvae had starved to death, having never fed on cowpea (Fig. 1b). In contrast, after only 24 h, all the larvae reared on non-solanaceous diets had accepted

either the solanaceous or non-solanaceous foliage equally (Fig. 1a), and no mortality was observed among these larvae. These results show that once host plant specificity is induced, some *M. sexta* larvae will actually starve to death rather than change from a solanaceous to a non-solanaceous diet.

Because contact with solanaceous foliage seems necessary to induce a preference for the host plant, the larvae may acquire the ability to recognize a specific compound(s) in the host plant. To test this possibility, we began to isolate a compound(s) from solanaceous plants that the larvae might use as a host plant recognition cue. As an assay, we tested solanaceous-reared larvae for their acceptance of non-solanaceous cowpea leaf discs that were treated with extracts of potato leaves. The larvae clearly discriminated between treated and control discs, taking the first bite from cowpea discs treated with potato extract in more than 95% of the cases ($n = 75$, $\chi^2 > 200$, degrees of freedom (d.f.) = 1, $P < 0.001$), in a period of less than 2 h (Fig. 2a).

An active fraction was isolated from an aqueous extract of potato foliage by solvent partitioning and flash chromatography. This active fraction was subjected to further fractionation and exhaustive chromatographic separation. At each step, activity was monitored using choice assays with fraction-treated cowpea leaf discs and ten or more solanaceous-reared larvae. This approach yielded a single fraction that accounted for all the feeding stimulant activity of potato foliage. Analyses by ¹H NMR spectroscopy showed that this fraction comprised one single steroidal glycoside of more than 96% purity. A standard set of two-dimensional NMR experiments⁸ and additional mass spectroscopic analyses using negative-ion electrospray ionization established the structure (Fig. 2c) of this compound as (25R)-26-O-(β -D-glucopyranosyl)-furost-5-en-3 β ,22 ξ ,26-triol-3-O-(α -L-rhamnopyranosyl-(1 \rightarrow 2)-[β -D-glucopyranosyl-(1 \rightarrow 3)]- β -D-galactopyranoside) (indioside D), which was isolated previously from the solanaceous *Solanum indicum*⁹.

Whereas considerable attention has focused on the theoretical aspects of template recognition, little is known about its proximate mechanisms^{1,10,11}. Our behavioural data suggest that induced *M. sexta* larvae use indioside D to recognize their host plant. Evidence suggests that the lateral and medial sensilla styloconica on the mouthparts (Fig. 3a, b) of *M. sexta* have a key role in taste and food preferences^{12–16}. To examine the role of these taste sensilla in host recognition, we recorded their electrophysiological responses to indioside D. The sensilla recordings were carried out on fifth instar larvae that were reared on either solanaceous foliage or wheat germ diet. Each recording electrode contained either control solu-

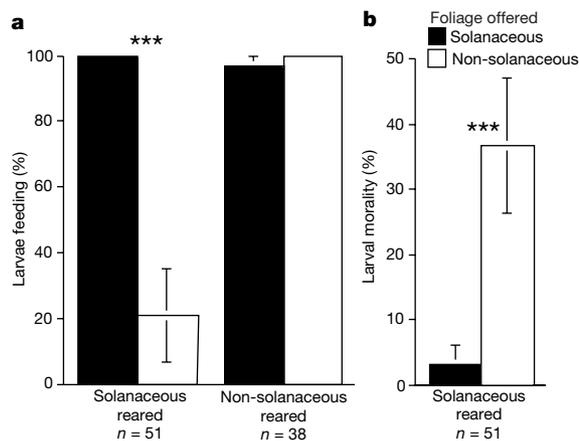


Figure 1 Host-restricted feeding behaviour is determined by dietary experience. **a**, Percentage of larvae feeding on foliage in no-choice tests, after a 24-h exposure to novel food item (Fisher's exact test). **b**, Percentage of larval mortality among solanaceous-reared larvae after a 96-h exposure to fresh foliage (Fisher's exact test). Error bars, 95% confidence interval. Triple asterisk, $P < 0.001$.