Projected continent-wide declines of the emperor penguin under climate change

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Climate change has been projected to affect species distribution[1] and future trends of local populations[2,3], but projections of global population trends are rare. We analyse global population trends of the emperor penguin (*Aptenodytes forsteri*), an iconic Antarctic top predator, under the influence of sea ice conditions projected by coupled climate models assessed in the Intergovernmental Panel on Climate Change (IPCC) effort[4]. We project the dynamics of all 45 known emperor penguin colonies[5] by forcing a sea-ice-dependent demographic model[6,7] with local, colony-specific, sea ice conditions projected through to the end of the twenty-first century. Dynamics differ among colonies, but by 2100 all populations are projected to be declining. At least two-thirds are projected to have declined by > 50% from their current size. The global population is projected to have declined by at least 19%. Because criteria to classify species by their extinction risk are based on the global population dynamics[8], global analyses are critical for conservation[9]. We discuss uncertainties arising in such global projections and the problems of defining conservation criteria for species endangered by future climate change.

The emperor penguin life cycle depends on sea ice through multiple and non-exclusive mechanisms[10,11] (Supplementary Section 1). Emperor penguins breed and raise their offspring almost exclusively on sea ice (but see ref. 12), and change in sea ice cover impacts the entire Antarctic food web through key organisms, such as krill[13]. Low sea ice concentration (SIC) reduces adult survival through its effect on the food web (low food resources and/or high predation)[7,11,14,15]. High SIC also reduces adult survival and breeding success[7] because it requires longer foraging trips and higher parental energy expenditure, and reduces chick feeding frequency. Thus, there is an optimal SIC for population growth and fitness[7], because neither the complete absence of sea ice (food web interactions) nor heavy and persistent sea ice (longer foraging trip) provide satisfactory conditions[11].

Only one emperor penguin population has been intensively studied: the colony in Terre Adélie (TA), in East Antarctica, at the northern part of the species range[14,16], which has been studied for five decades. A detailed analysis of the effects of climate change on this colony projected a pronounced decline by the end of this century[3,7]. However, 45 colonies are known from direct and satellite observations[5] (Supplementary Section 2). Most of these colonies have never been, and probably never will be visited by humans[17]. Certainly they will never become the focus of long-term demographic studies. Estimates of future global

population dynamics are possible only by making maximal use of the robust and well-tested demographic results from the TA colony, combined with climate change projections from coupled models assessed in the IPCC effort. Generating this global population projection highlights the information needed to analyse species-level effects of climate change, and how difficult it is to obtain.

To project population dynamics of emperor penguins under climate change, a demographic model (1) (refs 3,7) is driven with stochastic projections of SIC anomalies (SICa; Methods and Supplementary Sections 3–6). This is a nonlinear, two-sex, stochastic, seasonal, and climate-dependent matrix population model. The anomaly projections are produced by atmosphere–ocean general circulation models (AOGCMs). When this model was applied to the TA colony using AOGCMs from refs 4,18, the median size of the TA colony was projected to decline by approximately 80% by the year 2100[7].
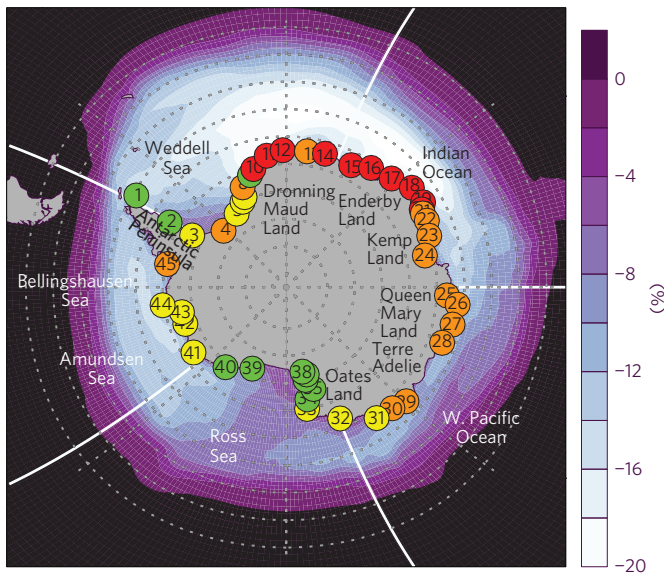
Here, we develop a new analysis of the global, continent-wide emperor penguin population. To do so requires a model that applies local demographic information to global estimates of the vital rates. Since SIC differs among the 45 colonies (Supplementary Section 4.1), we analyse the model (1), using the TA parameter estimates, as a function of the projected SICa at each colony. Because ecological forecasting, especially in conservation settings, requires appropriate treatment of uncertainties[2,19–21], our analysis quantifies uncertainties due to initial conditions, demographic model specification, parameter estimation, environmental stochasticity, and uncertainty arising from AOGCM choice[7,21]. For example, we used both a local and a pan-Antarctic spatial scale method to select a subset of AOGCMs (Supplementary Section 4.2). We treat uncertainties by plotting medians and 90% intervals from large numbers of simulations, and calculate the probability to decline below specific thresholds (Supplementary Section 6).

We find that colonies located from the Eastern Weddell Sea to Western Indian Ocean are expected to experience the most pronounced decline (Fig. 1) and highest variability in annual SIC (Supplementary Section 4.2). Colonies in the Ross Sea will experience the smallest sea ice decline and lowest variability. In other regions, projected changes are more complex according to seasons and regions (Supplementary Figs 3–10).

Our results indicate that at least 75% of the emperor penguin colonies are at least vulnerable to future sea ice change, and 20% will probably be quasi-extinct by 2100. Colonies experiencing steeper declines and greater variability in SICa are more likely to be endangered (Supplementary Fig. 11). The projected growth in the number
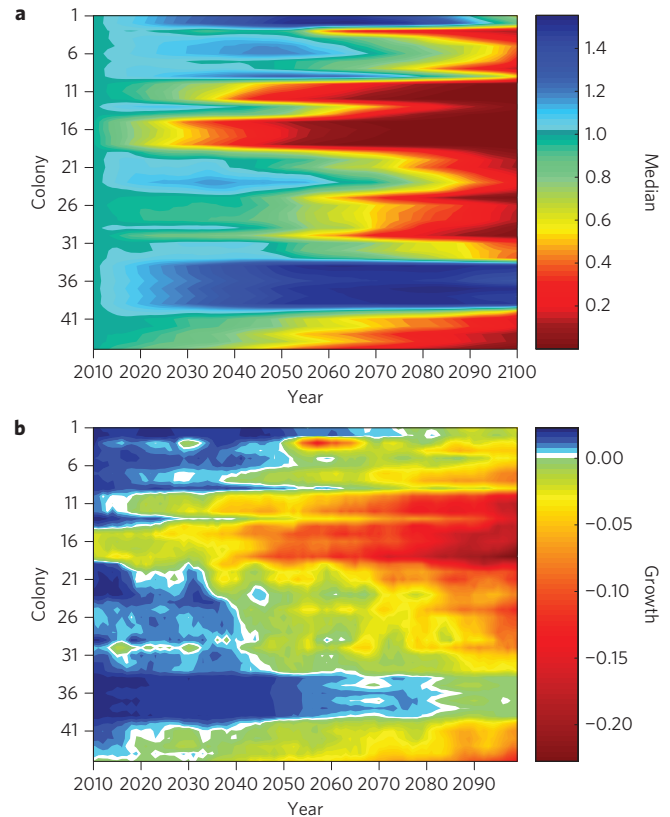
Figure 1 | Annual mean change of sea ice concentrations (SIC) between the twentieth and twenty-first centuries and conservation status of emperor penguin colonies by 2100. SIC projections were obtained from a subset of AOGCMs using a local selection approach (see Supplementary Section 6 for results of alternative AOGCM selections). Dots show the location of colonies from ref. 5, dot numbers refer to each colony and dot colour to the conservation status (Supplementary Table 5). Red refers to 'Quasi-Extinct', orange to 'Endangered', yellow to 'Vulnerable' and green to 'Not threatened'.

Figure 2 | Projected population dynamics of emperor penguin colonies through to 2100. Median of breeding pairs (**a**) and year-to-year population growth rates (**b**) from 2010 to 2100 for each colony. Median and growth rates are based on SICa projections from AOGCMs using the local selection approach. The *y* axis refers to the colony number used on Fig. 1. Blue (red) colours show an increase (decrease) relative to 2010 population size in **a**, and a positive (negative) population growth rate in **b**. The white contour on **b** represents a null growth rate, indicating stable populations.

of breeding pairs among the colonies ranges from an increase by a factor of 2.13 (Fig. 2a), corresponding to an average annual growth rate of 0.84%, to a decrease by a factor of 10,000 (annual growth rate of −9.5%). The year-to-year growth rates are mostly positive for the first 30 years of the simulations, but all become negative by 2080 (Fig. 2b). Colonies in the Ross Sea will have experienced the least loss of sea ice, and thus are projected to increase, relative to their present size, by 2100 (Fig. 2a). However, even these colonies will be declining by 2100 (Fig. 2b). The most threatened colonies are located in Dronning Maud and Enderby lands, where projected SIC declines are largest and conditions are most variable. Colonies in the northern part of the range from Kemp to TA lands are projected to decline by more than 50%, and are thus likely to be endangered. Colonies equatorward of 70° S have a 46% risk to decline by more than 90% by 2100 using AOGCMs selected using a local analysis, and 65% risk using a pan-Antarctic analysis (Fig. 3).

The median global population is projected to increase by 10% up to 2048, but then to decline to 19% below its starting value by the end of the century (Fig. 4 and Supplementary Section 7). By that time, the global population will be declining at 1.1% per year (a half-life of 60 years). However, the median of the global growth rate estimates over the last 10 years of the simulation is a decline of 3.2% per year (a half-life of 22 years). This has serious conservation implications, as discussed below.

Given the absence of demographic data from colonies other than that at TA, the demographic component of our global analysis must be based on an extension of those data. Such analyses are known as population projections; they are expressed as conditional statements based on the structure of the model producing the results. All population viability analyses are projections in this sense[22]. Hence, we apply the life cycle model, with the long-term and statistically rigorous estimates of the TA parameters, to all other colonies, with SICa measured relative to the colony-specific mean values. This gives the benefit of the doubt to other colonies. Because recent ice
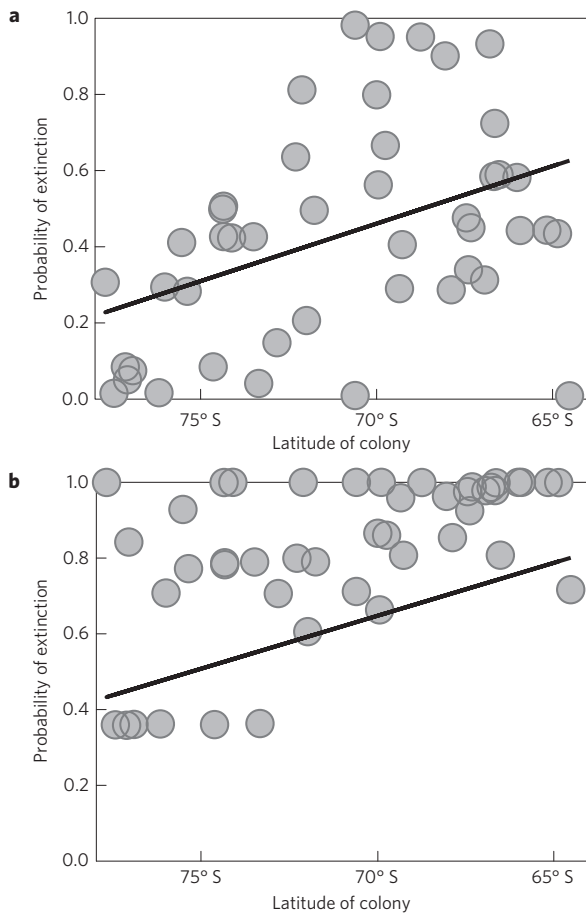
conditions have been close to optimal at TA, to the extent that the penguin demography varies among colonies, we consider it to be in the direction of adaptation towards, not away from, local conditions. This helps to assure that our extension does not artificially inflate the chances of population decline. We recognize that demographic parameters will certainly differ among colonies, and we do not assume otherwise.

We especially underestimate the likelihood of population decline for colonies in the Bellingshausen and Amundsen Seas, which experienced significant decreases in sea ice during the period of satellite observations (1978–2010). As a result, an emperor penguin colony located in Dion Islands, close to the West Antarctic Peninsula, disappeared[10]. We also overestimate the likelihood of population increase in the Ross Sea because population growth is not limited by breeding habitat. However, some colonies in the Ross Sea provide little potential for population expansion, such as Beaufort Island and Cape Crozier, with limited breeding areas and unstable breeding habitat[23].

We do not consider movement among populations; it is unlikely to be demographically important in this species. The Antarctic continent prevents southward range expansion, and even the southernmost locations in the Ross Sea will not provide a viable refuge by the end of the twenty-first century (Fig. 2b). Inter-colony dispersal is extremely unlikely; because of the unique breeding behaviour of the species, colonies are inaccessible except during breeding, and so cannot be encountered 'accidentally' while foraging during the non-breeding season. Emperor penguins are unlikely

Figure 4 | Global number of breeding pairs of emperor penguins from 2009 to 2100. This global population size is calculated using SICa projections from AOGCMs selected with the local selection approach (see Supplementary Section 7 for results of alternative AOGCM selections). The red line is the median and the grey area is the 90% envelope from stochastic simulations of population trajectories.
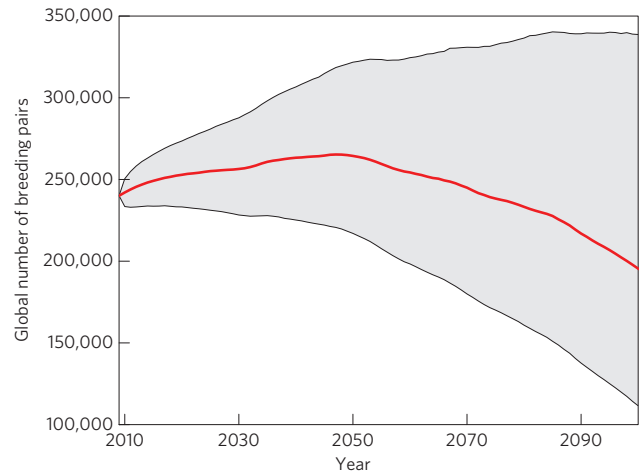
Figure 3 | Probability of quasi-extinction according to colony latitude. Probability of quasi-extinction is the probability of a decline greater than 90% relative to the initial population size in 2009. It is calculated using a subset of AOGCMs selected using the local (**a**) and pan-Antarctic approaches (**b**). The black line is the linear regression fit ($p < 0.05$).

to massively colonize new habitats such as stable, long-lasting fast ice for breeding, and new polynyas (open area within sea ice for feeding) may not appear[11]. Breeding on land or on ice shelves[12] would result in higher energy expenditure (longer foraging trips, greater exposure to cold and wind) and would still be subject to the negative effects of declining sea ice through the food web. Thus, neither dispersal nor demographic source–sink dynamics will change our main conclusion about global population declines.

A previous qualitative pan-Antarctic study[11] suggested that projected sea ice decline is likely to reduce emperor penguin habitat and may jeopardize half of the breeding colonies equatorward of 70° S, but provided no quantitative estimates of population trends or their associated uncertainties. Our results do so. Like all viability analyses, ours is a projection conditional on the clauses that make up the model. If seasonality, trends, and interannual variability in future climate follow the patterns in the AOGCMs, and if the emperor penguin life cycle and its responses to sea ice are similar to our estimates, then the global population is seriously threatened by the end of the century.

The conservation status of the emperor penguin as a species depends on our judgment of those trends and uncertainties. We have found that population growth will be slightly positive until 2050, but will be negative at all colonies, and for the global population, by the end of the century. At the global level, large population declines at most colonies are buffered by increases in the Ross Sea until 2080, but by the end of the twenty-first century there will no longer be any viable refuges.

Projected population declines are among the criteria used by the International Union for Conservation of Nature (IUCN) to assign conservation status (for example, 30% decline over three generations implies Vulnerable; 50% decline over three generations implies Endangered[8]). The generation time of the emperor penguin is approximately 16 years (Supplementary Section 8). Thus, within three generations (that is, by 2061) the population will not have declined sufficiently for IUCN Vulnerable status.

However, by 2100 the median growth rate (−3.2% per year) implies a projected population decline of 78% over three generations, far exceeding the threshold for Endangered status. This suggests that the IUCN projected decline criteria may not be optimally formulated to capture threats from long-term, directional trends such as climate change.

The complexity of climate change (nonlinear dynamics, multiple feedbacks, low resilience) and its large spatial and temporal scales may require new international conservation paradigms[9]. We believe that such a paradigm should consider five factors. First, there are uncertainties, which must be acknowledged and communicated[24]. Second, climate change varies regionally and potential refuges (or the lack thereof) are important. Third, climate change resulting from increases in CO_2 is largely irreversible for up to 1,000 years after emissions stop[25,26]; thus, the IUCN three-generation period should be allowed to start in the future. Fourth, international climate mitigation strategies will probably require a long time for implementation[27]. Last, because ecological responses to climate change are complex, conservation status criteria should accommodate patterns of temporary increase followed by long-term declines, such as projected here for many of the emperor penguin colonies (Fig. 2) and the global population (Fig. 4). In the light of these issues, we propose that the emperor penguin is fully deserving of Endangered status due to climate change, and can act as an iconic example of a new global conservation paradigm for species threatened by future climate change.

Methods

Population model[6,7]. The population model (Supplementary Section 3) can be written as

$$\mathbf{n}(t+1) = \mathbf{A}\,[\mathbf{n}(t),\mathbf{x}(t)]\,\mathbf{n}(t) \qquad (1)$$

where $\mathbf{n}$ is the population vector and $\mathbf{x}(t)$ denotes environmental conditions at time t. The projection matrix $\mathbf{A}$ is a periodic product that incorporates seasonal

development of the penguin through the breeding and nonbreeding seasons of the year. The nonlinear dependence of **A** on **n** accounts for the monogamous breeding system and the effects of the operational sex ratio on reproduction. The vital rates depend on sea ice concentration anomalies (SICa) measured relative to the period 1979–2007 (Supplementary Section 4). The parameters, including the effects of SICa on the vital rates, were estimated from the TA colony using maximum likelihood mark-recapture methods and multi-model inference applied to long-term data on marked individuals. The model has been extensively compared with data, shown to successfully resolve the dynamics of the TA colony[6,7] and provides a coherent pattern of past population trends (Supplementary Section 5).

SIC projections. SIC projections were developed for each colony, for the four seasons of the emperor penguin breeding cycle (Supplementary Sections 3 and 4). For each colony, we employed a subset of AOGCMs for which the climatology of the simulated sea ice cover agreed well with the observed climatology at that colony. We call this a local model selection. For comparison, we also considered a pan-Antarctic selection that applied the same subset of AOGCMs to each colony, and an analysis using all AOGCMs without regard to their agreement with observations. Results of the local selection approach are shown here (see Supplementary 4.2.1 for alternative approaches). The AOGCMs were forced with a middle range emissions scenario (SRES A1B; ref. 28), which assumes a future socio-economic development depending on fossil and non-fossil energy sources in balanced proportions. Under this scenario, the CO_2 level would double by 2100, from 360 ppm to 720 ppm.

Colony specific population trajectories. Colony specific population trajectories were obtained using these SIC projections as environmental drivers (Supplementary Section 6). We generated 10,000 simulations for each colony, for each AOGCM. These simulations included uncertainties from the choice of AOGCMs, from stochastic sea ice sequences, and from estimated parameter values. For each simulation, we calculated the number of breeding pairs relative to the starting population in 2010, and the one-year growth rates of the breeding population for each year. Based on the ensemble of simulations for a colony, we calculated the probability of population decline by more than a specific threshold by 2100, and defined conservation status accordingly (Supplementary Table 5).

Global population. The global population size consists of the sum of sizes of the 45 local populations. To project future changes in the global population, we generated 100,000 simulations for each colony, starting from the estimated numbers of breeding pairs in 2009[5] (Supplementary Section 7). The sampling distribution of global size is the convolution of the distributions of the colony sizes; we approximated this by resampling from the distributions of colony population size and summing the results.

References

1. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145–148 (2004).
2. Hunter, C. *et al.* Climate change threatens polar bear populations: A stochastic demographic analysis. *Ecology* **91**, 2883–2897 (2010).
3. Jenouvrier, S. *et al.* Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proc. Natl Acad. Sci. USA* **106**, 1844–1847 (2009).
4. Meehl, G. *et al.* in *IPCC Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) (Cambridge Univ. Press, 2010).
5. Fretwell, P. T. *et al.* An emperor penguin population estimate: The first global, synoptic survey of a species from space. *PLoS ONE* **7**, e33751 (2012).
6. Jenouvrier, S., Caswell, H., Barbraud, C. & Weimerskirch, H. Mating behavior, population growth, and the operational sex ratio: A periodic two-sex model approach. *Am. Nat.* **175**, 739–752 (2010).
7. Jenouvrier, S. *et al.* Effects of climate change on an emperor penguin population: Analysis of coupled demographic and climate models. *Glob. Change Biol.* **18**, 2756–2770 (2012).
8. *IUCN Red List Categories and Criteria* (International Union for Conservation of Nature, 2012).
9. Hannah, L. A global conservation system for climate-change adaptation. *Conserv. Biol.* **24**, 70–77 (2010).
10. Trathan, P. N., Fretwell, P. T. & Stonehouse, B. First recorded loss of an emperor penguin colony in the recent period of Antarctic regional warming: Implications for other colonies. *PLoS ONE* **6**, e14738 (2011).
11. Ainley, D. *et al.* Antarctic penguin response to habitat change as Earths troposphere reaches 2 degrees above preindustrial levels. *Ecol. Monogr.* **80**, 49–66 (2010).
12. Fretwell, P. T., Trathan, P. N., Wienecke, B. & Kooyman, G. L. Emperor penguins breeding on iceshelves. *PLoS ONE* **9**, e85285 (2014).
13. Loeb, V. *et al.* Effects of sea-ice extend and krill or salp dominance on the Antarctic food web. *Nature* **387**, 897–900 (1997).
14. Barbraud, C. & Weimerskirch, H. Emperor penguins and climate change. *Nature* **411**, 183–186 (2001).
15. Jenouvrier, S., Barbraud, C. & Weimerskirch, H. Long-term contrasted responses to climate of two Antarctic seabirds species. *Ecology* **86**, 2889–2903 (2005).
16. Croxall, J., Trathan, P. & Murphy, E. Environmental change and Antarctic seabirds populations. *Science* **297**, 1510–1514 (2002).
17. Wienecke, B. Review of historical population information of emperor penguins. *Polar Biol.* **34**, 153–167 (2011).
18. Meehl, G. A. *et al.* The WCRP CMIP3 multi-model dataset: A new era in climate change research. *Bull. Am. Meteorol. Soc.* **88**, 1383–1394 (2007).
19. Caswell, H., Fujiwara, M. & Brault, S. Declining survival probability threatens the North Atlantic right whale. *Proc. Natl Acad. Sci. USA* **96**, 3308–3313 (1999).
20. Clark, J. S. Ecological forecasts: An emerging imperative. *Science* **293**, 657–660 (2001).
21. Jenouvrier, S. Impacts of climate change on avian populations. *Glob. Change Biol.* **19**, 2036–2057 (2013).
22. Caswell, H. *Matrix Population Models* (Sinauer, 2001).
23. Kooyman, G., Ainley, D., Ballard, G. & Ponganis, P. Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. *Antarct. Sci.* **19**, 31–38 (2007).
24. Reto, K. & Sedláček, J. Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Clim. Change* **2**, 1–5 (2012).
25. Solomon, S., Plattner, G-K., Knutti, R. & Friedlingstein, P. Irreversible climate change due to carbon dioxide emissions. *Proc. Natl Acad. Sci. USA* **106**, 1704–1709 (2009).
26. Teng, H., Buja, L. E. & Meehl, G. A. Twenty-first-century climate change commitment from a multi-model ensemble. *Geophys. Res. Lett.* **33**, L07706 (2006).
27. Ricke, K. L. & Caldeira, K. Natural climate variability and future climate policy. *Nature Clim. Change* **4**, 333–338 (2014).
28. Nakicenovic, N. & Swart, R. (eds) in *IPCC Special Report Emissions Scenarios* (Intergovernmental Panel on Climate Change, 2000).

Author contributions

This research was designed and coordinated by S.J., M.H., M.S., H.W. and H.C. Analyses were performed and coordinated by S.J. with the support of H.C. (demographic analysis), M.H. (climate models analysis), J.S. and M.S. (sea ice observations), C.B. and H.W. (emperor penguin observations). S.J. and H.C. contributed new analytic tools. Figures were created by S.J. (emperor penguin projections) and M.H. (sea ice maps). S.J., M.H. and H.C. wrote the paper. J.S., M.S., C.B. and H.W. contributed equally to the study. All authors discussed the results and commented on the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to S.J.

Competing financial interests

The authors declare no competing financial interests.