

# Reliability of flipper-banded penguins as indicators of climate change

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In 2007, the Intergovernmental Panel on Climate Change highlighted an urgent need to assess the responses of marine ecosystems to climate change<sup>1</sup>. Because they lie in a high-latitude region, the Southern Ocean ecosystems are expected to be strongly affected by global warming. Using top predators of this highly productive ocean<sup>2</sup> (such as penguins) as integrative indicators may help us assess the impacts of climate change on marine ecosystems<sup>3,4</sup>. Yet most available information on penguin population dynamics is based on the controversial use of flipper banding. Although some reports have found the effects of flipper bands to be deleterious<sup>5–8</sup>, some short-term (one-year) studies have concluded otherwise<sup>9–11</sup>, resulting in the continuation of extensive banding schemes and the use of data sets thus collected to predict climate impact on natural populations<sup>12,13</sup>. Here we show that banding of free-ranging king penguins (*Aptenodytes patagonicus*) impairs both survival and reproduction, ultimately affecting population growth rate. Over the course of a 10-year longitudinal study, banded birds produced 39% fewer chicks and had a survival rate 16% lower than non-banded birds, demonstrating a massive long-term impact of banding and thus refuting the assumption that birds will ultimately adapt to being banded<sup>6,12</sup>. Indeed, banded birds still arrived later for breeding at the study site and had longer foraging trips even after 10 years. One of our major findings is that responses of flipper-banded penguins to climate variability (that is, changes in sea surface temperature and in the Southern Oscillation index) differ from those of non-banded birds. We show that only long-term investigations may allow an evaluation of the impact of flipper bands and that every major life-history trait can be affected, calling into question the banding schemes still going on. In addition, our understanding of the effects of climate change on marine ecosystems based on flipper-band data should be reconsidered.

The effects of climate forcing on primary and secondary production of the short austral food webs may be integrated at higher levels<sup>14,15</sup>, and thus amplified in top-level predators such as seabirds. This has led to a strong interest in studying Antarctic and sub-Antarctic top predators (especially penguins, which are major consumers of the Southern Ocean ecosystem) as sensitive indicators of environmental changes<sup>3,4</sup>. To understand how variability in marine resources affects their demography over the timescale of years, simultaneous investigations of variation in breeding success and survival are necessary and require long-term individual monitoring at the population scale.

Most of our present knowledge on the population dynamics of penguins is based on large flipper-banding schemes. The key advantage is that bands can be identified from a distance, avoiding recapture stress for the birds. In the 1970s, however, bands were observed, both in zoos and in the wild, to injure flipper tissues severely<sup>5</sup>, especially during the moult. Although many research programmes consequently abandoned banding as a precaution in the late 1980s, massive banding

schemes still continued (see references in ref. 5). Yet, as penguins power their swimming exclusively with their flippers, there has been an increasing concern about the hydrodynamic drag effect that may be induced by flipper bands (for example a 24% increase in the energy cost of swimming in captive Adélie penguins<sup>5</sup>). The question was then whether penguins may compensate for such effects<sup>10,11</sup> and whether the impact of flipper bands would be limited in time. Although it had been assumed that the effect of flipper bands lasted for a year at most<sup>12</sup> (until the bird got used to the band), the question remained to be addressed in the long term. In this context, medium-term studies revealed lower breeding success and survival in Adélie penguins<sup>8</sup> and a reduced breeding success in king penguins<sup>7</sup>. However, those pioneering findings did not result in the cessation of ongoing banding schemes. Whether or not flipper bands have a deleterious impact in the long term is, nonetheless, a crucial issue, for “it raises practical and larger ethical questions about costs and benefits of procedures in field studies”<sup>16</sup>. In addition to possibly harming penguin populations already under threat (such as penguins rehabilitated after oil spills; see references in ref. 7), the potentially negative effects of banding on demographic parameters may introduce a bias, which in turn might jeopardize any attempt to use data from banded birds to assess the impact of climate<sup>12</sup> on population dynamics and to predict the future

**Table 1 | Observed differences between life-history traits of banded and non-banded king penguins**

| Parameter   | Non-banded           | Banded               | <i>P</i><br>(banding) |
|---|----------------------|----------------------|-----------------------|
| <b>Early group</b>  |                      |                      |                       |
| Arrival dates   | 21 Nov. ± 2 d (189)  | 7 Dec. ± 3 d (167)   | <0.001                |
| Breeding propensity                                       | 0.95 (189)           | 0.87 (167)           | 0.04                  |
| Laying dates  | 29 Nov. ± 1 d (160)  | 6 Dec. ± 1 d (122)   | <0.001                |
| Breeding success  | 0.44 (160)           | 0.32 (122)           | 0.05                  |
| Foraging trips  | 11.60 ± 0.20 d (512) | 12.70 ± 0.20 d (344) | <0.001                |
| <b>All birds</b>  |                      |                      |                       |
| Overall survival over the decade                          | 0.36                 | 0.20                 | 0.04                  |
| Overall/annual survival over the first period (4.5 years) | 0.62/0.90            | 0.32/0.78            | 0.01                  |
| Overall/annual survival over the last period (5.5 years)  | 0.57/0.90            | 0.60/0.91            | 0.82                  |

Significant results are indicated in bold. Data shows mean ± s.e. The number of events (*N*) is shown in parentheses. Differences in *N* come from differences in studied stages (for example, not every bird arriving at the colony bred). Overall survival corresponds to the number of studied birds present at the colony at the end of the period divided by the number of studied birds present at the colony at the beginning of the period. Breeding propensity corresponds to the proportion of live birds that engaged in reproduction over the ten breeding seasons (that is, the number of reproduction events divided by the sum over the years of live birds). The early group is the group of birds that failed or did not engage in previous reproduction and were free to arrive early in the summer. This group is the one that most affects overall population reproductive success. For breeding analyses, *P* is the *P* value of the banding effect in the mixed model  $Y = \text{banding} + (1 | \text{individual})$ . For survival (investigated through schemes of presence/absence at the colony), *P* is the *P* value obtained from a Cox proportional hazards model with right censoring. Durations of foraging trips were standardized per period and then pooled together to run a single mixed-model analysis.

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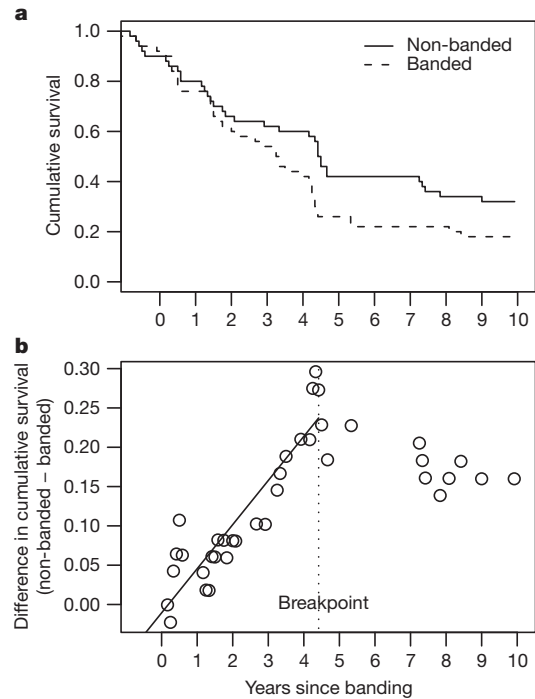
of breeding colonies according to scenarios of the Intergovernmental Panel on Climate Change<sup>13</sup>.

Using a decade-long data set, we analysed differences in reproduction and survival between two groups of electronically monitored king penguins (50 banded and 50 non-banded) breeding on Possession Island in the sub-Antarctic Crozet archipelago. These differences were investigated in relation to the birds' time of arrival for breeding and the duration of their foraging trips. Furthermore, we explored whether and how climate variability might differently affect banded and non-banded penguins.

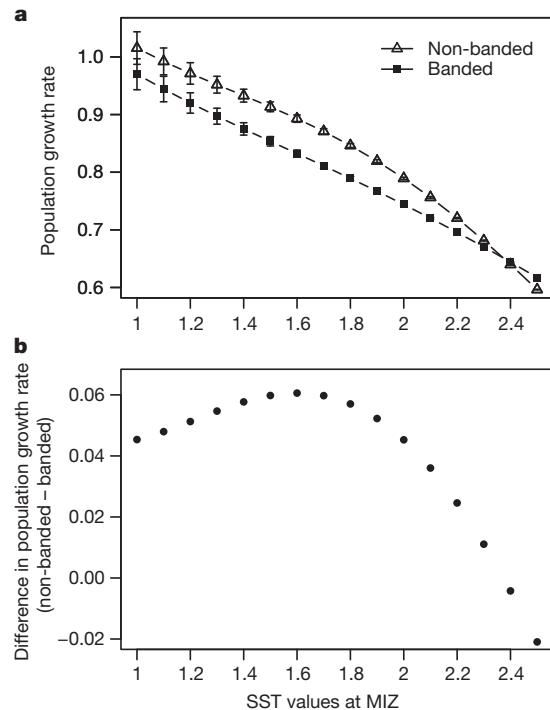
First and foremost, our study underlines a strong negative impact of flipper banding on adult survival, to which population growth rate is most sensitive in long-lived species<sup>17,18</sup> such as king penguins. The average annual survival was 5% lower in banded penguins, leading to an overall 16%-lower survival over a decade (Table 1 and Fig. 1a). Yet a breakpoint analysis revealed that the difference between the cumulative survival of banded penguins and that of non-banded penguins had one breakpoint, after 4.5 years ( $54 \pm 3$  months; Fig. 1b). Before that the mortality was 30% higher for banded birds, whereas afterwards the survival rates of the remaining banded and non-banded birds were not significantly different (Table 1 and Fig. 1). Importantly, those birds that died during the first period (banded or not) had a lower breeding success than those that survived (0.22 versus 0.30,  $P = 0.047$ ) and the annual survival rate of banded penguins increased between the two periods (from 78% to 91%, Wilcoxon rank-sum test,  $P = 0.05$ ). This suggests that banding has a stronger deleterious effect on low-quality birds and thus selects for high-quality individuals.

Second, we show that over the decade banded birds had significantly lower breeding propensity and success than non-banded birds (breeding probability of 0.87 versus 0.95 and breeding success of 0.32 versus 0.44; Table 1 and Supplementary Fig. 1). This could be explained by the significantly later arrival of banded birds to breed (average delay relative to non-banded birds was 16 days; Table 1). Indeed, breeding propensity was negatively affected by arrival dates, meaning that those birds arriving later were less likely to engage in breeding attempts (model 9,  $P < 0.001$ ; Supplementary Table 1). According to life-history trade-offs<sup>18</sup> between reproduction and survival for long-lived species, late-arriving birds may delay reproduction to the following year to avoid breeding costs that may jeopardize their own survival<sup>19,20</sup>. Furthermore, in agreement with previous studies<sup>21,22</sup> we found that the later in the season king penguins arrived to breed, the lower was their breeding success (Supplementary Fig. 2 and model 15,  $P < 0.001$ ; Supplementary Table 1). This suggests an unfavourable timing in chick rearing, which then begins at the end of summer, when prey availability is much lower<sup>23</sup>. The reduced breeding success of banded birds could also be explained by the greater durations of their foraging trips at all summer stages of the breeding cycle (Table 1 and Supplementary Fig. 3). Indeed, a longer trip may either lead to breeding failure (that is, no longer being able to sustain the fasting period energetically, the partner abandons the egg before mate relief<sup>24</sup>) or directly jeopardize the survival of chicks waiting for food. Accordingly, birds failing in reproduction made significantly longer trips at sea than successful birds (21.8 versus 16.1 days,  $P < 0.001$ , for incubation birds and 11.5 versus 8.1 days,  $P < 0.001$ , for birds with chicks). Thus, the longer trip duration of the banded birds suggests that the detrimental effect of the bands can be explained by a reduced swimming and/or foraging efficiency resulting from the effect of flipper-band drag on the hydrodynamics of the bird, such as for Adélie penguins<sup>5</sup>.

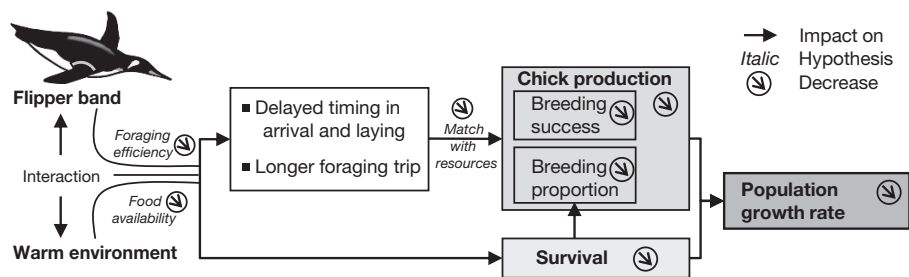
Notably, our data clearly do not accord with the assumption that flipper bands have an impact essentially restricted to the first year after banding, which is the time suggested for birds to habituate to the handicap<sup>6,12</sup>. Indeed, flipper bands also had a deleterious effect during the second half of our study (for example,  $P = 0.008$  for arrival dates). These long-term effects indicate that there is no habituation to the handicap. We conclude that flipper bands lead to delayed breeding



**Figure 1 | Survival of banded and non-banded king penguins during the 10-year study period.** **a**, Cumulative survival was lower for banded birds (dashed line) than for non-banded birds (solid line) (Cox proportional hazard model,  $P = 0.04$ ; assumption of proportional hazards verified,  $P = 0.83$ ). **b**, Difference between the cumulative survivals of banded and non-banded penguins over time. There is a breakpoint at 54 months (4.5 years) and the linear trend is indicated. Differences between banded and non-banded birds tended to disappear after the first 4.5 years.



**Figure 2 | Simulated population growth rates of banded and non-banded penguins as functions of SST.** **a**, Growth rates of both populations according to SST at the marginal ice zone (MIZ). Error bars, s.e.m. **b**, Difference between the two growth rates. A quadratic relation well approximated the difference (Growth rate  $\approx (0.27 \pm 0.01)SST - (0.09 \pm 0.00)SST^2$ ,  $P < 0.001$  for both SST and  $SST^2$ ).



**Figure 3 | Potential mechanisms involved in negative impacts of flipper bands on life-history traits and population dynamics in king penguins.** Flipper bands and climate interact to affect chick production negatively, mostly through delayed timing, survival and, ultimately, population growth rate.

attempts, lower breeding propensities and longer foraging trips, which together explain the large drop observed in chick production between banded and non-banded birds during our study decade (80 versus 47 chicks produced; Supplementary Fig. 1). Moreover, decreasing breeding success in seabirds increases their dispersal<sup>25</sup>, and dispersal of penguins is still studied almost exclusively using flipper-banded birds. The question then arises about the significance of such data, as dispersal may not be representative of actual population dispersal in free-living penguins and may therefore constitute a serious bias.

Finally, banded and non-banded penguins were differently affected by climate. Environmental conditions (Southern Oscillation index (SOI) and sea surface temperature (SST)) are known to affect penguins through changes in food availability (abundance or distribution), compelling individuals to forage for longer periods to reach sufficient body condition when conditions are warmer<sup>26</sup>. In this regard, banded penguins arrived later to breed than did non-banded birds and even more so in years of lower SOI (that is, warmer phases of El Niño/Southern Oscillation<sup>27</sup>; Supplementary Table 2 and Supplementary Fig. 4). Additionally, when compared with that of non-banded penguins, the breeding success of banded birds was similar in years of late arrivals (difference of  $-0.03$ ,  $P = 0.52$ ,  $N = 53$  birds), lower (albeit not significantly) in years of early arrivals (difference of  $-0.13$ ,  $P = 0.32$ ,  $N = 29$ ) and much lower in years of intermediate arrivals (difference of  $-0.19$ ,  $P = 0.01$ ,  $N = 70$ ). Thus, over a single year, differences may not be apparent. Food availability at sea may be so poor in a given year that even non-handicapped birds fail in large numbers. For instance, in 2007 (a year of late arrivals) both banded and non-banded king penguins similarly failed to breed. In contrast, in years of very favourable environmental conditions, the environmental pressure on banded birds may be so weak that they may compensate for the extra cost inflicted by banding, which would explain the absence of (or weakness in) difference observed between banded and non-banded birds in favourable years such as 2004, 2005 and 2006. This accords with data on banded Adélie penguins, whose increase in foraging duration varied according to the year<sup>8</sup>, and on African penguins, which seem to be negatively affected by banding only during periods of reduced prey availability<sup>28</sup>. Similarly, we found that the population growth rates of banded and non-banded king penguins did not respond in the same way to variations in SST. Indeed, the relation between SST and the difference in population growth rates between the two groups was well approximated by a quadratic relationship, highlighting that this difference was most apparent in years of intermediate SST values (Fig. 2).

Thus, our decade-long monitoring demonstrates the detrimental effect of flipper banding and its interaction with climate on the major life-history traits of king penguins (Fig. 3). The effects of extensive banding schemes on penguin populations can on ethical grounds no longer be neglected, and studies considering population trajectories with regard to climate change seriously need to reconsider the biases inherent in studies using flipper-banded birds.

## METHODS SUMMARY

King penguins from a breeding colony on Possession Island ( $46^{\circ} 25' S$ ,  $51^{\circ} 45' E$ ; Crozet archipelago) were monitored from 1998 to 2008 using automatic

identification (see ref. 26 for details). One hundred birds were randomly sampled in their breeding area and 50 of them were fitted with a metal flipper band<sup>7</sup> (banding every second bird).

We established breeding propensity and phenology by analysing bird movements between their breeding area and the sea<sup>29</sup>. Breeding propensity and success were defined as binary variables respectively depending on whether or not a bird attempted to breed and whether or not a breeding bird fledged its chick. In king penguins, egg laying is not synchronized within the colony, owing to a breeding cycle lasting over a year<sup>21,29</sup>. Here we present results of early breeders only, because they are the ones that most affect population reproductive success. We investigated survival as a function of decline in animal presence. Population growth rates were estimated as dominant eigenvalues of transition matrices<sup>30</sup> and simulated according to varying SST.

Monthly fluctuations in SOI, SST and chlorophyll *a* concentration ([Chl *a*]) both around Crozet archipelago and around the polar front were the three environmental descriptors used in this study<sup>26</sup>. SOI was used as a global index of El Niño/Southern Oscillation, whereas SST and [Chl *a*] were used as proxies of the prey availability of important feeding locations of king penguins.

We computed all statistics using the R statistical environment (version R-2.8.0). Survival was investigated using a Cox proportional hazards model with right censoring. Changes in cumulative survival over time were determined using breakpoints in segmented regression analysis. We analysed breeding data using mixed models computed with the individual as a random effect, enabling us to account for repeated measures, as birds were tracked over multiple breeding seasons. Years were added as random effects when we did not investigate differences between years.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Author Contributions** C.S. did the analyses and co-wrote the paper; C.L.B. helped in the analyses, the organization of the paper and the writing; Y.L.M. designed the study and co-wrote the paper; V.A.V. provided ideas on the analyses and co-wrote the paper; N.G.Y. proposed one of the analyses and helped with statistics; J.M.D. supplied ideas on the analyses and the organization of the paper; M.G.-C. and N.C.S. added some very useful comments and modifications to the manuscript; D.B. ran some pre-analyses; and Y.-H.P. provided climatic data.

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## METHODS

We confirm that all work followed approval by an ethics committee and conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare.

**Demographic survey.** Our study was conducted on king penguins breeding in the colony of La Grande Manchotière at Possession Island (46° 25' S, 51° 45' E) on Crozet archipelago. We used automatic identification and data-logging systems (the ANTAVIA system<sup>31</sup>) to follow, from 1998 to 2008, 100 king penguins implanted with a passive transponder tag under the skin of their leg. The transponder tags weigh 0.8 g and have no known adverse effects. They were shown not to affect survival of king penguins<sup>32</sup> or breeding success, recruitment or survival of tits<sup>33</sup>. Furthermore, concerns about infections should be minimal, as transponder tags were kept sealed sterile in iodine capsules (Betadine) and were removed from the capsules only by the process of injecting them into the bird. Moreover, Vétédine soap and alcoholic antiseptic solutions were used to disinfect the skin and the injecting needle before each insertion. Flesh wounds did not seem infected thereafter (personal observations on recaptured birds). Penguins were randomly sampled in their breeding area (only breeding birds were taken, to make sure that they were mature birds). Fifty of them were also fitted with a metal flipper band<sup>7</sup>, with the simple rule of banding every second bird to randomize the treatment. Automatic identification systems allow for continuous, automatic data collection of bird movements into and out of the colony. The system is completed by video recording of the passageways over the antennas. Banded birds were thus monitored during the whole study, and only one bird lost its flipper band. This bird was not considered in further analyses.

**Biological variables.** The breeding propensities and phenologies of the birds were established by analysing recorded movements of the 100 studied penguins between the breeding area and the sea<sup>29</sup>. We assumed that those birds which were recorded leaving the colony went to sea. The specificity of the king penguins' breeding cycle allows us to determine whether and when birds attempted to breed, and whether and when they failed (stop in the sex-specific shifts). We were thus able to obtain arrival and laying dates, lengths of sojourns at sea and breeding variables, over all years and for each bird.

The sex of the birds was established by analysing the chronology of sex-specific incubating shifts<sup>29</sup>. Because sex had no significant effect on the date of arrival at the colony or on the propensity to breed, gender was not incorporated in our models. The presence of couples in the sample was controlled to avoid double-counting the same reproductive event and to keep independent our data on each individual. The data recorded during 1998 (that is, the year the birds were marked) were not included, to avoid eventual bias induced by handling.

**Breeding success, sea trips and survival.** We defined breeding propensity as a binary variable considering the onset of a breeding cycle (breeding propensity equals 1 if the bird attempted reproduction and equals 0 otherwise, that is, if no egg was laid). We defined breeding success as successful chick fledging for birds that laid an egg (breeding success equals 1 if the chick is fledged and equals 0 otherwise).

Lengths of sea trips were investigated for all birds still incubating or brooding, whether successfully fledging their chick or not. Different shifts have different mean durations<sup>29</sup> and we thus separated them into different groups: one group per incubation shift, one for the first guard trip, one for all subsequent guard trips pooled together and a last one for all post-guard trips. To be able to run a single model on foraging trips, we standardized trips per group and then pooled them all together.

Yearly chick production was investigated as the number of fledglings (that is, 14-month-old chicks) produced per individual present in the colony each year. It combines breeding success and propensity into a single parameter representative of yearly reproduction at the population level. The total number of chicks produced over the 10-year period, integrating both breeding and survival over the number of penguins present in the colony, was also studied to give a better representation of the success of the considered sample (that is, banded or non-banded).

Survival was investigated as a function of decline in bird presence at the colony. We conducted analyses on both annual and overall survival. Overall survival corresponds to the number of studied birds present at the colony at the end of the period divided by the number of studied birds present at the colony at the beginning of the period.

**Early breeders and late breeders.** Because the king penguins' breeding cycle lasts for more than 1 year (around 14 months on Crozet archipelago<sup>21,29,34</sup>), bird arrival at the colony depends on the success and timing of the previous year's breeding attempt. The laying period of king penguins therefore extends for over four months, with two peak periods<sup>34,35</sup>: one for 'early breeders' (before 1 January) and another for 'late breeders' (after 1 January). To account for the dependence on the previous breeding attempt, we separated our data into two timing groups

and conducted separate analyses on them. The first corresponded to penguins that did not fledge a chick the previous breeding season (failed or skipped reproduction) and which were thus free to arrive early in the summer (early group), and the second corresponded to birds that succeeded in fledging a chick the previous breeding season and which were consequently late breeders the subsequent season (late group).

As birds in the late group have a very small impact on the chick production of the colony, we did not present their data in our breeding analyses. Their late arrival almost always results in breeding failure as they do not breed early enough to allow their chick to meet normal phases of the chick growth period<sup>21,22</sup>. Moreover, the pool of these birds is very small in comparison with the early group, and the production of chicks and, therefore, the renewal of the population is thus mostly dependent on the success of early breeders.

**Environmental descriptors.** The three environmental descriptors used in this study were the SOI, calculated from the monthly fluctuation in the air pressure difference between Tahiti and Darwin, Australia; the SST (in degrees Celsius); and the concentration of chlorophyll ([Chl *a*], in milligrams per cubic metre) (see ref. 26 for details). Negative SOI values indicate a warm phase of El Niño/Southern Oscillation<sup>27</sup>. SST and [Chl *a*] were used as a proxy of prey availability both around the breeding site and near the polar front, which are two locations known to affect the breeding of king penguins in the Crozet archipelago.

**Growth rate estimates and simulations.** To integrate breeding success and survival into one single parameter, we established population growth rates for both banded and non-banded groups, as the dominant eigenvalues of stage-structured population transition matrices<sup>30</sup>. Different population matrix structures were tested and the obtained growth rates were almost identical, seeming insensitive to this structure. For simplicity, we present results of only one model. Briefly, we used a four-stage structured matrix with three first stages of immature birds and a last one of breeding adults. This supposes that every penguin began breeding at age five (average breeding age of the colony, unpublished data). An example of such a matrix is

$$M = \begin{pmatrix} 0 & 0 & 0 & \text{GBS} \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & \text{Adult survival} \end{pmatrix}$$

where GBS stands for global breeding success (that is, the product of breeding proportion and breeding success) and  $\alpha$  represents annual juvenile survival.

As birds were followed only from adult age in this study, we fixed annual juvenile survival for both populations at 0.89 (C. Saraux *et al.*, unpublished observations, where the authors studied the return rates and survival of juveniles in king penguins). Breeding success is affected by the SST of the area around Crozet archipelago as far south as the polar front and survival is affected by SST at the MIZ with a 2-year lag<sup>26</sup>. We computed two different models explaining breeding success in terms of SST around Crozet, one for banded birds and one for non-banded birds. Similarly, survival was modelled using the SST at the MIZ for banded and non-banded birds. Significant relationships were obtained in each of these four cases and were implemented in the matrix of each group as follows:

$$M_{\text{non-banded}} = \begin{pmatrix} 0 & 0 & 0 & \frac{1}{1 + e^{4.1207\text{SST}_{\text{Cro}} - 30.6312}} \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & \frac{1}{1 + e^{1.845\text{SST}_{\text{MIZ}} - 8.6676}} \end{pmatrix}$$

$$M_{\text{banded}} = \begin{pmatrix} 0 & 0 & 0 & \frac{1}{1 + e^{3.386\text{SST}_{\text{Cro}} - 24.981}} \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \\ 0 & 0 & \alpha & \frac{1}{1 + e^{1.1304\text{SST}_{\text{MIZ}} - 5.5565}} \end{pmatrix}$$

SSTs averaged over the two different areas were highly correlated ( $\rho = 0.97$ ,  $P < 0.001$ ), and we thus decided to let both SSTs vary the same way, differing only by a constant:  $\text{SST}_{\text{Cro}} = \text{SST}_{\text{MIZ}} + \text{mean}(\text{SST}_{\text{Cro}} - \text{SST}_{\text{MIZ}})$ . Finally, we simulated the variation of these population growth rates in relation to varying SST. Standard errors of growth rates were calculated using Caswell's method<sup>30</sup>, by adding standard errors of all parameters of the matrix, these having previously been calculated bootstrapping over 1,000 repetitions of the models used in the matrix.

**Statistics.** All statistics were computed using the R-2.8.0 statistical environment (R Development Core Team, 2008). Survival was investigated using a Cox proportional hazards model with right censoring. Changes in survival over time were determined

using breakpoints from segmented regression analysis ('segmented' package). Breeding data was analysed using a mixed-effect model fitted using maximum likelihood ('lme4' package<sup>36</sup>). Generalized linear mixed models were computed with the individual (bird) as a random effect, enabling us to account for repeated measures, as birds were tracked over multiple breeding seasons. The most appropriate model was selected by using the Akaike information criterion. Variables were considered significant for  $P < 0.05$ .

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