

Karine Delord · Christophe Barbraud  
Henri Weimerskirch

## Long-term trends in the population size of king penguins at Crozet archipelago: environmental variability and density dependence?

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**Abstract** We examined the growth rate of the breeding population of king penguins of Crozet archipelago over 41 years. Most colonies showed positive growth rates from the 1960s. However, there was evidence for a decrease in the larger colonies since the early 1990s, and for lower growth rates in the smaller colonies during the 1990s. The overall population size was estimated using log linear models, and the average annual growth rate was +6.3% for the 41-year period. Four change points were detected in the annual growth rate: +21.1% during 1978–1985, +4.3% during 1985–1995, –19.2% during 1995–1999, and +10.9% during 1999–2003. Time-series analyses of the population-size estimates and the relationship between growth rate and population size both indicated density-dependence in population growth rate. Variations in population sizes are also discussed in relation to environmental fluctuations. Our results suggest that important changes occurred over the past 10 years.

### Introduction

Penguins are often at, or close to, the top of the food chain in the Southern Ocean, and the population dynamics of such apex predators are often sensitive indicators of the effects of environmental change in ecosystems (e.g. Aebischer et al. 1990; Furness and Greenwood 1993; Ainley 2002; Gjerdrum et al. 2003; Voigt et al. 2003). King penguins (*Aptenodytes patagonicus*) represent a major component in terms of biomass and energy flux in the sub-Antarctic marine ecosystem (Woehler 1995). A high number of king penguins were

slaughtered by sealers during the nineteenth century on sub-Antarctic islands (Rounsevell and Copson 1982). Since then, there has been a long recovery process, possibly resulting from density-dependence effects at low numbers, and all breeding populations for which long-term data are available have showed a dramatic increase during the twentieth century (Conroy and White 1973; Lewis Smith and Tallwin 1979; Rounsevell and Copson 1982; Gales and Pemberton 1988; Weimerskirch et al. 1992; Woehler and Croxall 1997; Woehler et al. 2001).

Until recently, breeding populations of king penguins have increased at all sites at very high rates, but because populations sizes are at some point limited by extrinsic (environmental) and/or intrinsic (density-dependence) factors (Newton 1998), we may assume that the carrying capacity has been or soon will be reached. Consequently, we expect the rate of increase of king penguin populations to stabilize or decrease. However, until now, there has been no clear evidence of colonies being over-populated and possibly stabilizing since the early 1990s.

King penguins represent the main component of avian biomass and are the major predator species around the Crozet archipelago (Guinet et al. 1996). The high growth rate in breeding numbers of king penguins at this locality has been related to a consistently high adult and immature survival, even though breeding success and breeding frequency were relatively low and variable (Jouventin and Weimerskirch 1990; Weimerskirch et al. 1992). Indeed, being a long-lived species, the population growth rate in king penguins is mostly sensitive to adult survival (Lebreton and Clobert 1991). Recent studies suggest that variations in food availability affect the foraging abilities of the species (Bost et al. 1997; Charrassin and Bost 2001), and therefore poor food conditions might possibly negatively affect the demographic parameters (Olsson and Brodin 1997; Olsson and van der Jeugd 2002).

In this paper, we use a long-term data series of breeding population sizes at Possession Island, Crozet

K. Delord (✉) · C. Barbraud · H. Weimerskirch  
Centre d'Etudes Biologiques de Chizé,  
Centre National de la Recherche Scientifique,  
79360 Villiers en Bois, France  
E-mail: delord@cebc.cnrs.fr  
Fax: +33-5-49096526

archipelago, to examine whether the overall population growth rate of king penguins over 41 years shows any signs of reaching carrying capacity or evidence of density dependence.

## Materials and methods

Breeding populations at all five colonies of king penguins at Possession Island (46°25'S, 51°45'E), Crozet archipelago, southern Indian Ocean, have been surveyed intermittently between the austral summers 1961/1962 and 2002/2003. Data from the Baie du Marin colony are also reported here, despite being disturbed by the extension of the French research station, which reduced the colony area by 30% (Weimerskirch et al. 1992). Each count of individuals was made using oblique photographs of colonies taken from promontories overlooking colonies in early January (corresponding to the peak laying period), to count breeders. On the photographs, birds incubating an egg are clearly distinct from non-breeding birds because they are usually regularly spaced. Each individual was pointed with a pen and counted. For all years, except 2002, counts were directly made on printed photographs. In 2002, photographs were scanned at the maximum resolution available (600 dpi) and counts were made on a computer screen. Count repeatability on photographs, estimated with series of three independent counts on the same photographs was high (0.97; C. Guinet, unpublished data). The breeding seasons are given as the years when incubating birds were counted (the summer of 1961/1962 will be referred to as 1962, hereafter).

The data analysis sought to identify statistically significant trends both at the colony and population levels. For each individual colony, we used methods similar to those used by Woehler et al. (2001) for analysing trends. Linear regressions (LR) of  $\log_{10}$  counts against time were performed to yield log-linear trends. Significance of the models was calculated, and we used the proportion of variance explained to summarize the overall fit of the LR models to the data. This approach is designed to estimate an average rate of population change over a time period, although the fit is likely to be poor if the true pattern of change was markedly non-linear (e.g. cyclical). As there were obvious non-linear trends in the data set (see Results), these were modelled by using polynomial regressions (PRs) and generalized additive models (GAMs) (Hastie and Tibshirani 1990; Fewster et al. 2000), all of which were used in an exploratory fashion. PR is a straightforward extension of the linear model used for trend analysis. GAMs are an extension of generalized linear models where a smoother is used to characterize non-linear patterns. Smoothing procedures are built into the model-fitting process, so that inference based on the resulting smooth curve of abundance numbers is made fully within the context of the original model. We used the smoothing span (smoothing

algorithm spline with fixed degrees of freedom) used in the software package R (Ihaka and Gentleman 1996). The degree of freedom was fixed following Fewster et al. (2000), and we used a Poisson error structure. We used the proportion of variance explained to help judge whether or not the PR and GAM were an improvement over the linear model. All analyses except GAM were performed in SPSS (2000); the GAMs were performed in R 1.8.0. To determine the periods of increase and decrease for non-linear trends, we calculated the first derivatives from the fitted model (PR of second-order model). Using derivatives, we estimated inflexion points from which changes in population trajectory were inferred.

Annual population growth rates were estimated using the relationship:

$$\frac{N_t}{N_0} = e^{rt}$$

where  $N_0$  is the number of breeding pairs at the time when the first count of the period was made,  $N_t$  the number at the end of the same period,  $e$  the base of the natural logarithm,  $t$  the number of years elapsed between 0 and  $t$ , and  $r$  the population growth rate (Caughley 1980).  $N_t$  and  $N_0$  were given by the equation of the regression fitted model.

To analyse the overall (41 years) population trend, we combined the time series with missing observations from all the colonies, and made a log-linear regression model with Poisson error terms using the program Trends and Indices for Monitoring Data (TRIM) (Pannekoek and van Strien 1996). The TRIM analysis was restricted to the four undisturbed colonies (i.e. excluding the Baie du Marin colony). To obtain the overall estimated breeding numbers, we used the population size estimates obtained from the TRIM analysis and added the estimates obtained from the best regression model for the Baie du Marin colony. We started the analysis with a model with change points at each time-point, and used the stepwise selection procedure to identify change points with significant changes in slope based on Wald tests with a significance-level threshold value of 0.01 (Pannekoek and van Strien 1996). We took into account over-dispersion and serial correlation since they can have important effects on standard errors, although they have usually only a small effect on the estimates of parameters (Pannekoek and van Strien 1996). No covariate was used.

Based on population size estimates, we looked for density dependence using the relationship between  $r$  and  $N_t$ . We also used the method of Lande et al. (2002) for estimating density dependence from population time series around an assumed stable equilibrium. From a life history having age at maturity  $\alpha$ , with stochasticity and density dependence in adult recruitment and mortality, this method derives a linearized autoregressive equation with time lags from 1 to  $\alpha$  years. The theory indicates that the total density dependence in a life history,  $D$ ,

should be defined as the negative elasticity of population growth rate per generation with respect to change in population size:

$$D = -\frac{\partial \ln \lambda^T}{\partial \ln N}$$

where,  $\lambda$  is the asymptotic multiplicative growth rate per year,  $T$  is the generation time, and  $N$  is adult population size. This method permits the estimation of the strength of density dependence as the product of the adult mortality ( $\mu$ ), and the total density dependence as one minus the sum of the autoregressive coefficients ( $b_\tau$ ) of the time series:

$$\mu D = 1 - \sum_{\tau=1}^{\alpha} b_\tau.$$

**Table 1** Numbers of breeding pairs in the king-penguin colonies of Possession Island, Crozet archipelago, in January. 1962 = 1961/1962 (see Methods). Gap in the breeding season column or blanks in columns = no census (0 no birds present)

Breeding season	Baie du Marin	Petite Manchotière	Jardin Japonais	Crique de la Chaloupe	Mare aux Eléphants
1962	45,000			0	
1965	43,400	4,000		0	
1967		3,500	5,000	8	
1979				169	0
1981	32,000	11,700	14,700		0
1986	40,500	21,700	33,000	310	100
1987	28,200	17,500	28,000	280	110
1988		18,337	35,100	357	137
1989		21,200	41,600	360	160
1990				676	450
1993		16,525		740	750
1994			51,504		2,901
1996				946	2,886
1997	27,749	14,133	42,033		
1998			25,700	982	4,004
2000		12,981		1,038	5,525
2001	16,073		21,900	1,113	4,282
2003		14,450	34,200	1,650	5,990

**Table 2** Results of LR, PR of second order and GAMs analyses for long-term breeding population data for king-penguin colonies of Possession Island, Crozet archipelago. The best model fitted is indicated in bold characters (*NF* not fitted, *NS* not significant, *df* degree of freedom). All tests had  $P < 0.05$  or less

Colony	Baie du Marin	Petite Manchotière	Jardin Japonais	Crique de la Chaloupe	Mare aux Eléphants
Population trend from linear model	Decrease	Increase	Increase	Increase	Increase
LR: $r^2$	<b>0.65</b>	0.53	0.47	0.91	0.88
Slope	-0.009	0.017	0.020	0.077	0.163
PR: $r^2$	NS	<b>0.93</b>	<b>0.84</b>	<b>0.97</b>	<b>0.89</b>
Quadratic slope		-0.0011	-0.0012	-0.0017	0.00008
GAMs: $r^2$ ( <i>df</i> )	NF	0.92 (4)	0.66 (4)	0.97 (5)	0.93 (5)

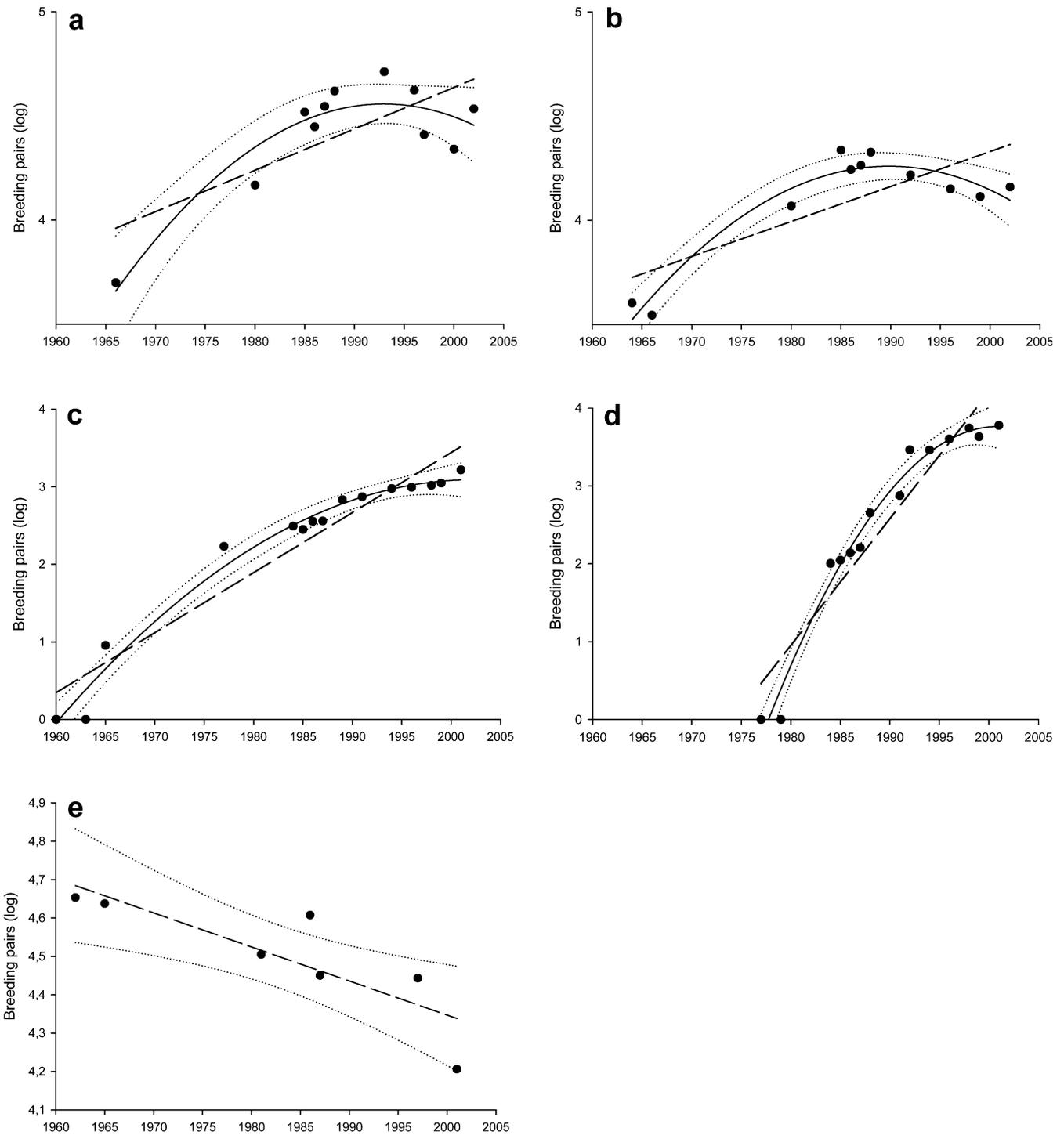
**Table 3** Periods and intrinsic population growth rate ( $r$ ) of breeding pairs for the five colonies of king penguin of Possession Island, Crozet archipelago

Colony	Period of decrease	$r$ (%)	Period of increase	$r$ (%)
Baie du Marin	1962–2001	-2.04		
Petite Manchotière	1992–2003	-3.39	1965–1991	+6.53
Jardin Japonais	1995–2003	-2.89	1967–1994	+7.67
Crique de la Chaloupe	–		1965–2003	+15.58
Mare aux Eléphants	–		1981–2003	+32.02

## Results

The number of king penguin colonies increased from three in 1962 to five in 2003 (Table 1). Except for one large colony (Baie du Marin), which shows a significant decreasing trend, the four other colonies have increased significantly over the 41-year period (Table 1). In all but one case (the Baie du Marin colony), the best fit was obtained using non-linear models (Table 2). Quadratic models performed at least as well as GAM models in three of four cases (Table 2).

Among the colonies monitored since the 1960s, Baie du Marin decreased at an average rate of -2.04% per year (Table 3, Fig. 1e). The lowest number of breeding pairs was observed in 2001. The two other large colonies (Petite Manchotière and Jardin Japonais) increased



**Fig. 1a–e** Comparison of population models fitted to counts of breeding pairs (expressed as logarithm) on photographs, 1962–2003, for **a** Jardin Japonais, **b** Petite Manchotière, **c** Crique de la Chaloupe, **d** Mare aux Eléphants, and **e** Baie du Marin colonies. Lines indicate predictions of LR models (*dashed line*), and PR models of second order (*solid line*) with the 95% CIs (*dotted line*)

rapidly in size from the mid-1960s up to the 1980s (+6.53 and +7.67% per year, respectively), reached a maximum number of breeding pairs in the late 1980s, and decreased until 2003 (–3.39 and –2.89% per year,

respectively) (Table 3 and Fig. 1a,b). Two small colonies established during the study period (Chaloupe and Mare aux Eléphants) showed a very rapid increase until the 1990s (+15.58 and +32.02% per year, respectively) (Table 3 and Fig. 1c,d). There is some evidence of a decrease in the rate of increase of breeding pairs during the second half of the 1990s (Fig. 1c,d).

The stepwise procedure for selection of change points indicated four significant change points (1978, 1985, 1995 and 1999; all  $P < 0.0052$  for Wald tests), where the

**Table 4** Multiplicative slopes standing for the changes in population size (all colonies except Baie du Marin), and their 95% CIs for king penguins at Possession Island, Crozet obtained from the model selected in the TRIM analysis

Period	Trend	Multiplicative slope $\pm$ SE	95% CI
1962–1978	Stable	1.0 $\pm$ 0.0	–
1978–1985	Increase	1.235 $\pm$ 0.054	1.129–1.341
1985–1995	Increase	1.044 $\pm$ 0.025	0.995–1.093
1995–1999	Decrease	0.825 $\pm$ 0.050	0.727–0.923
1999–2003	Increase	1.114 $\pm$ 0.064	0.989–1.239

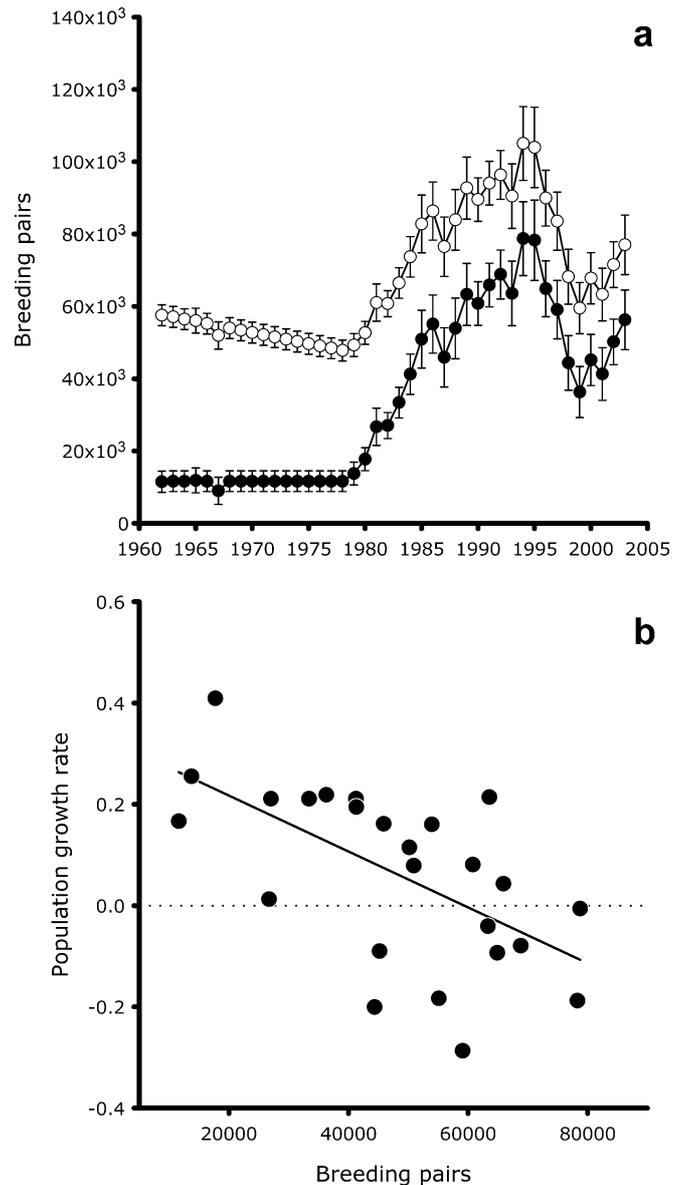
trend in population size was significantly different before and after the change points (Table 4, Fig. 2a). The population size estimates computed from this model with four change points (Fig. 2a) indicate an average population growth rate of +6.3% per year between 1978 and 2003 for the four colonies combined. This rate was +21.1% per year between 1978 and 1985, +4.3% per year between 1985 and 1995, –19.2% per year between 1995 and 1999, and +10.9% per year between 1999 and 2003. When the estimated breeding numbers of the Baie du Marin colony were added to the TRIM estimates, the signs of the population growth rates were similar, but the absolute values were lower, due to the long-term decrease of the Baie du Marin colony. The overall average rate of increase was of +1.9% per year between 1978 and 2003 for all five colonies combined, which incorporates human impact on the population.

To look for density dependence, we first plotted the population growth rate calculated from the estimates obtained from the TRIM analysis against the population size estimates for the period 1978–2003, during which the population size varied. The relationship (Fig. 2b) was negative ( $r = -0.60$ ,  $n = 25$ ,  $P = 0.0015$ ; even when considering only the point estimates based on real counts:  $n = 14$ ,  $P = 0.023$ ) and linear, indicating that the population growth rate decreased as the population size increased. Second, the time-series analysis was performed on the population size estimates for the period 1981–2003 to test the assumption of relative stability of the population (Lande et al. 2002). Estimates of the autoregression coefficients and density dependence in the life history are shown in Table 5. For all values of  $\alpha$ , the total density dependence was strong.

## Discussion

### Changes in breeding numbers

When analysed individually, all colonies except Baie du Marin showed positive population growth rates from the 1960s. However, there is clear evidence for a decrease in at least the two larger colonies since the early 1990s, and for lower growth rates for the two smaller colonies during the 1990s. Some of the  $r$  values found for individual colonies are beyond the scope of the intrinsic



**Fig. 2** **a** Estimates of the breeding population size of king penguins at Possession Island, Crozet archipelago, between 1967 and 2003. Estimates (filled circles) were computed from a model with four change points using program TRIM (see Methods) and are imputed estimates. Errors bars indicate  $\pm$ SE. Unfilled circles indicate the number of breeding pairs estimated from the TRIM analysis plus the number of breeding pairs estimated from the linear model for the Baie du Marin colony. **b** Relationship between the population growth rate and the number of breeding pairs between 1978 and 2003:  $r = 0.3277 - 5.521 \times 10^{-6} \times N$ , where  $N$  is the number of breeding pairs. Estimates are from the model selected in the TRIM analysis

growth rate (max  $r < 0.2$ , even assuming unrealistically high survival and fecundity values), indicating that growth of some colonies was driven at least in part by immigration (as is evident from the formation of two new colonies during the study period, and from few observations of ringed birds that were observed breeding in different colonies during successive years, C.-A. Bost, personal communication). When colonies are considered

**Table 5** Parameter estimates (SE) for the 23-year population time series of king penguins (1981–2003) fitted to the stage-structured life-history model of Lande et al. (2002), using different mean ages of first reproduction  $\alpha$ , and with an adult survival  $(1-\mu)$  of 0.952 (Weimerskirch et al. 1992)

$\alpha$	$b_1$	$b_2$	$b_3$	$b_4$	$b_5$	$b_6$	$R^2$	$\mu D$	$D$
3	0.891 (0.270)	-0.231 (0.379)	-0.019 (0.252)				0.62	0.359	7.5
4	0.744 (0.257)	-0.181 (0.319)	0.504 (0.329)	-0.498 (0.227)			0.69	0.432	9.0
5	0.937 (0.286)	-0.337 (0.331)	0.612 (0.320)	-1.023 (0.356)	0.520 (0.266)		0.74	0.291	6.1
6	1.397 (0.287)	-0.890 (0.424)	0.706 (0.396)	-1.044 (0.409)	1.075 (0.494)	-0.509 (0.301)	0.77	0.266	5.5

altogether, the population growth rate appears to increase from the late 1970s, being close to zero earlier (Fig. 2). Although this may reflect reality, it may also have been caused by too many missing data between the 1960s and the 1970s. Because of the high proportion of missing data prior to the late 1970s, some change points may have occurred and remained undetected. Nevertheless, the growth rate of the overall population was lower between 1985 and 1995 than between 1978 and 1985, and became negative between 1995 and 1999. There is some indication for a positive growth rate since 1999, since the 95% CI of the multiplicative growth rate only marginally includes 0.

It can be argued that varying proportions of breeding adults may have affected our population estimates. Indeed, given the complex breeding cycle of king penguins (Weimerskirch et al. 1992), it is possible that the breeding success in a given year partly determines the number of breeders during the following year. Although our data on breeding success are too sparse to control for such an effect, we think that it is unlikely that breeding success variations generated the observed pattern in the number of breeders. This would require the existence of trends on breeding success, which was not suggested by our fragmentary data (1987: 29.4%; 1988: 25.5%; 1989: 26.3%; 2003: 40%). Another possibility is that varying proportions of birds skipped breeding during poor years, but the extent of this strategy is unknown in the king penguin at present.

The population increase between the 1960s and the 1990s appears to be a general trend for the species (Woehler et al. 2001). It has been suggested that king penguins are recovering from past exploitation during the nineteenth century, and that these increases were linked to the cessation of slaughter (or to density-dependent rates of increase associated with low post-slaughter populations), although they may also be correlated with an increased food availability (mainly fish and cephalopods), which in turn may have increased as a result of higher krill production due to reduction in stocks of baleen whales (Conroy and White 1973; Rounsevell and Copson 1982).

#### Evidence for density dependence

Using the overall population estimates, we found evidence for strong density dependence. The relationship between the population growth rate and population size

permits estimation of a theoretical maximum growth rate of +32.77%, and a carrying capacity of at least 59,000 breeding pairs for all the colonies, excluding Baie du Marin. This maximum growth rate appears too high given the demographic parameters of the king penguin, and is probably overestimated due to immigration, particularly during the early phase of increase of the population. The surface area of the Baie du Marin colony was reduced in 1965 and in 1982 because of human activities. Given that the maximum number of breeding pairs in the Baie du Marin colony after 1982 reached 40,500 (1986), the total carrying capacity for Possession Island is at least 99,500 breeding pairs. However, this is an underestimate because of the unique breeding phenology of king penguins (Barrat 1976; Weimerskirch et al. 1992; Jiguet and Jouventin 1999). The total carrying capacity may be 40% higher than our estimate (Guinet et al. 1995) and thus may reach ca. 140,000 breeding pairs. The population of Possession Island represents only part (ca. 10–15%; Guinet et al. 1995) of the Crozet archipelago population, since large colonies occur on Ile des Cochons and Ile de l'Est. The huge colony of Ile des Cochons (700,000 breeding pairs in 1988; Guinet et al. 1995) has increased similarly to the Possession Island colonies, but recent visits suggest that the numbers of pairs may have decreased, since the borders of the colony were not occupied (H. Weimerskirch et al., unpublished data). These results suggest that the observed trends on Possession Island may be indicative of the trends on the whole Crozet archipelago.

Evidence for density dependence also comes from the time-series analysis. The average age of first breeding is 6 years for king penguins (Weimerskirch et al. 1992). However, the estimated autoregression coefficients for  $\alpha = 5$  and 6 years are unreliable, probably because there were too many coefficients for the length of the time series. We thus consider the estimate for  $\alpha = 4$  years (the minimum age of first breeding for king penguins is 3 years, Weimerskirch et al. 1992). The estimated adult survival for king penguins ( $0.952 \pm 0.037$ ; Weimerskirch et al. 1992) is not significantly different from the first autoregression coefficient  $b_1 = 0.74$ , and the intermediate autoregression coefficient does not differ significantly from zero. Consequently, we cannot reject the hypothesis of no density dependence in survival beyond the 1st year (Lande et al. 2002). However, the last autoregression coefficient was significant, suggesting density dependence in adult fecundity. Based on estimates from

Table 5 for  $\alpha = 4$ , the estimated characteristic return rate is  $\gamma = D/T = 0.517$ , where  $T$  is the generation time (the mean age of mothers of newborn individuals when the population is in a stable age distribution) estimated at 17.4 years using the matrix population model established by Weimerskirch et al. (1992). Since  $0 < \gamma < 1$ , the population appears to be undercompensated (Begon et al. 1996), and one may expect the population to approach the carrying capacity smoothly without overshooting.

#### Mechanisms regulating the population size of king penguins at Crozet archipelago

However, this is not what is observed in the population size estimates, where the population appears to have oscillated since 1995 (Fig. 2a). One candidate hypothesis to explain this discrepancy is that the population approached carrying capacity during the early 1990s, as suggested by the decreasing growth rate estimates, but that an external factor perturbed the population trajectory and caused a decrease in the growth rate until 1999. After 1999, conditions went back to pre-1995 conditions and the population is again increasing towards carrying capacity. A possible external (climate) force may be the Southern Oscillation, which affects the southwest of the Indian Ocean with a 3-year lag (Xie et al. 2002). Between 1991 and 1994, the southern oscillation index (SOI) remained negative, which corresponds to El Niño-like conditions, for the longest period in the SOI historic record (<http://www.cpc.ncep.noaa.gov/data/indices>). Negative SOI conditions correspond to higher sea-surface temperatures and a lower thermocline depth, which in turn may negatively affect the abundance of penguin prey. King penguin breeding on Possession Island feed mainly at the polar and sub-Antarctic fronts (Bost et al. 1997) on myctophid fish (Cherel et al. 1993) whose distribution depends on the water temperature (Charrassin and Bost 2001). Satellite tracking studies indicate that when frontal zones move southwards during warm anomalies such as in 1996, 1997, 1998 and 2001, king penguins drastically increased their foraging trip lengths (distance covered) and durations (time spent) (C.-A. Bost, unpublished data). This increased reproductive effort over consecutive years may negatively affect breeding success, recruitment and possibly adult survival (Olsson and van der Jeugd 2002), thereby affecting the population growth rate.

Density-dependence may arise if breeding numbers reach a level where competition (for food or nest site) becomes important (Newton 1998). Other regulating processes affecting population growth rates, such as predation or parasites and pathogens cannot be rejected. For king penguins, competition for breeding sites may be a population regulating process. King penguins are territorial, and early arriving breeders tend to occupy the centre of the colony, perform aggressive behaviours, and experience a higher reproductive success than delayed-

arriving pairs (Côté 2000; Bried and Jouventin 2001). Nesting space limitation may force some early-arriving breeders to establish in poorer sites where reproductive success is lower. In addition, the larger colonies (Petite Manchotière and Jardin Japonais) show clear signs of a plateau in population density and space limitation, with all flat areas without vegetation being occupied (H. Weimerskirch et al., unpublished data). There is also evidence for deleterious levels of haematophagous ectoparasite infestations (Mangin et al. 2003). During years of high infestation rates, king penguins showed a lower incubating success (ratio number of breeding penguins at the beginning of the incubation period/at the beginning of the brooding period) in highly infested areas, and adults infested by ticks had a lower breeding success in rearing a 1-year-old chick. This negative effect of ticks on local breeding success can lead to low local recruitment, breeding site fidelity or timing of breeding the year after in highly infested areas (Weimerskirch et al. 1992). However, a cause-and-effect relationship between the presence of ticks and colony trends remains difficult to demonstrate.

The results of this study infer that important changes in king penguins' breeding numbers have occurred since the mid-1990s. Two factors have probably contributed to the last 10 years' changes. Populations have probably started to reach a plateau, due to density-dependence feedbacks, and at the same time, a strong environmental anomaly may have negatively affected the population. The last 3 years increase correspond to the rebuilding of the population after the decline, probably the population returning to the plateau level reached in the early 1990s. The results again show the high value of monitoring top predators like seabirds as indicators of environmental changes.

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