

RESEARCH/REVIEW ARTICLE

Better late than never? Interannual and seasonal variability in breeding chronology of gentoo penguins at Stranger Point, Antarctica

Mariana A. Juárez,^{1,2} M. Mercedes Santos,² Javier Negrete,^{1,2} M. Rita Santos,³ Jorge A. Mennucci,² Emilce Rombolá,² Lucrecia Longarzo,² Néstor R. Coria² & Alejandro R. Carlini^{†2}

¹ Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917 (C1033AAJ), Buenos Aires, Argentina

² Departamento Biología de Predadores Tope, Instituto Antártico Argentino, Balcarce 290 (C1064AAF), Buenos Aires, Argentina

³ Instituto Multidisciplinario de Biología Celular, Calle 526 y Camino General Belgrano (B1900BTE), La Plata, Buenos Aires, Argentina

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Correspondence

Mariana A. Juárez, Departamento Biología de Predadores Tope, Instituto Antártico Argentino, Balcarce 290 (C1064AAF), Buenos Aires, Argentina.
E-mail: marianajuarez@hotmail.com

Abstract

Rapid climate change recorded in the western Antarctic Peninsula confronts species with less predictable conditions in the marine and terrestrial environments. We analysed the breeding chronology and nesting site selection of gentoo penguins (*Pygoscelis papua*) at King George Island (Isla 25 de Mayo), Antarctica, during four seasons in which differences in snow presence and persistence on the ground were observed. We recorded an overall delay as well as seasonal asynchrony at the beginning of reproduction for those years with higher snow deposition. A redistribution of breeding groups was also observed. Nevertheless, the population breeding success and chicks' weight at fledging remained relatively constant, despite the delay in breeding chronology, the increased duration of foraging trips during the guard stage and the decreased weight of stomach contents during the crèche stage. We suggest that the plasticity of their trophic biology, along with the flexibility of their breeding phenology and relocation of breeding groups, may be complementary reasons why gentoo penguin populations in the region have remained stable in spite of the changing conditions currently registered.

Significant changes in population trends of pygoscelid penguins in the western Antarctic Peninsula have been recently reported (Forcada et al. 2006; Hinke et al. 2007; Sander, Balboa, Costa et al. 2007; Sander, Balboa, Polito et al. 2007; Lynch et al. 2008; Carlini et al. 2009; Lynch et al. 2010; González-Zeballos et al. 2013; among others). These changes have been associated with rapid climate warming observed in the area (Croxall 1992; Fraser et al. 1992; Trivelpiece & Fraser 1996; Croxal et al. 1999; Trivelpiece et al. 2011). The increase in atmospheric (Smith et al. 1999; Vaughan et al. 2003; Ducklow et al. 2007) and sea-surface temperatures (Meredith & King 2005) affects sea-ice dynamics (Fraser et al. 1992; Smith et al. 1999; Smith & Stammerjohn 2001; Ducklow et al. 2007; Stammerjohn et al. 2008). As a consequence,

changes in the abundance, distribution and composition of phytoplankton (Moline et al. 2004; Montes Hugo et al. 2009) and zooplankton have been recorded (Loeb et al. 1997; Loeb et al. 2009). In particular, Antarctic krill (*Euphausia superba*) abundance in the waters of the Scotia Arc has recently declined (Atkinson et al. 2004; Reiss et al. 2008). Biological responses to climate change are complex and vary according to the ecological features and life strategies of each species and also to the different regional or local conditions (Forcada et al. 2006; Trathan et al. 2007; Forcada & Trathan 2009; among others). Shifts in distribution, breeding range, abundance, phenology and predator-prey interactions are the main specific responses so far reported (Trivelpiece & Fraser 1996; Croxall et al. 1999; Barbraud & Weimerskirch 2006;

[†]Deceased.

Trathan et al. 2007; Lynch et al. 2008; McClintock et al. 2008; Miller & Trivelpiece 2008; Forcada & Trathan 2009; McClintock et al. 2010).

The gentoo penguin (*Pygoscelis papua*) is a major predator in the Antarctic ecosystem, consuming Antarctic krill and fishes in different proportions depending on the locations of their breeding sites (Libertelli et al. 2010). This species has a circumpolar distribution and nests between 46° and 65° south latitude (Williams 1995), exhibiting contrasting population trends according to the region considered (Lescroël & Bost 2006). Colonies in the western Antarctic Peninsula have remained stable or increased their breeding population size (Forcada et al. 2006; Hinke et al. 2007; Carlini et al. 2009; Lynch et al. 2010; González-Zeballos et al. 2013) and a southern expansion of their breeding range has recently been reported (Lynch et al. 2008; McClintock et al. 2010).

Gentoo penguin population trends have been related to their lower dependence on sea-ice during winter and the plasticity observed in their feeding strategies (Forcada et al. 2006; Hinke et al. 2007; Miller et al. 2009). The gentoo penguin is an open-water predator that would not be negatively affected by a decrease in sea-ice cover during the winter, when gentoo penguins remain near their natal colony (Trivelpiece et al. 1987; Wilson et al. 1998; Tanton et al. 2004). Indeed, diminishing sea-ice could widen their foraging niche (Trathan et al. 2007; McClintock et al. 2008; Miller et al. 2009). Though Antarctic krill is their main food source at the Scotia Arc (Volkman et al. 1980; Croxall et al. 1999; Miller et al. 2009; Kokubum et al. 2010; Miller et al. 2010), a considerable interannual variation in the trophic ecology of gentoo penguins has been reported, particularly related to prey abundance (Miller et al. 2009). This flexibility has been recently proposed as the principal feature allowing them to withstand changes in prey availability and maintain their breeding success (Miller et al. 2009).

However, climate warming has increased the frequency of years with higher snow accumulation (Turner et al. 2005; Thomas et al. 2008), which may affect nesting site availability and breeding success, and consequently their population size (Croxall 1992; Williams 1995; Trivelpiece & Fraser 1996; Copley & Shears 1999; McClintock et al. 2008; Trathan et al. 2008; among others). Several factors may have an effect on breeding success. Locally, snow plays a significant role in interannual variability at the beginning of the breeding season (Williams 1995; Copley & Shears 1999; Boersma 2008; Lynch et al. 2009). Since the period of optimum weather conditions for breeding is rather short, the delay in egg laying can be quite disadvantageous (Bost & Jouventin 1990a; Bost & Jouventin 1991; Croxall 1992; Trivelpiece & Fraser 1996; Boersma

2008). Furthermore, heavy snow accumulation can drive individuals towards higher sites in the colony (Trivelpiece & Fraser 1996; Boersma 2008), making extra energy demands on adult breeders.

If the plasticity of their trophic parameters gives gentoo penguins an advantage in the face of variation in food availability (Miller et al. 2009), the flexibility of their breeding phenology and selection of breeding sites may also be advantageous. In order to determine whether the flexibility of their breeding phenology allows them to withstand changes in local conditions resulting from environmental warming, we analysed different breeding and feeding parameters of gentoo penguins on King George Island (Isla 25 de Mayo) during four consecutive breeding seasons, 2007/08–2010/11.

Material and methods

Study area

The study was carried out at Stranger Point, King George Island (Isla 25 de Mayo; 62°16'S, 58°37'W), in the South Shetland Islands, within the Antarctic Specially Protected Area No. 132 during four austral summers, from 2007/08 to 2010/11, from October to February. The year in which each breeding season begins hereafter indicates the whole season studied, e.g., 2007 represents the 2007/08 season.

The colony was divided in two contiguous areas, A and B (Fig. 1), according to differences observed in the accumulation and persistence of snow on the ground.

Meteorological data

Daily records of temperature, rain and wind were provided by the meteorological station (Argentine National Weather Service) at Argentina's Carlini Station (formerly, Jubany Scientific Station).

The following parameters were calculated for each season: October average temperature, the number of snowy days, the number of days with moderate to strong north-easterly winds (20 km/h or higher) and the number of days combining the last two parameters (snowfalls and north-easterly winds).

Geographic location of breeding groups

Each breeding group at Stranger Point was georeferenced during the four seasons studied. Following Young (1994), a group of birds breeding as a geographically continuous unit within a larger area was considered

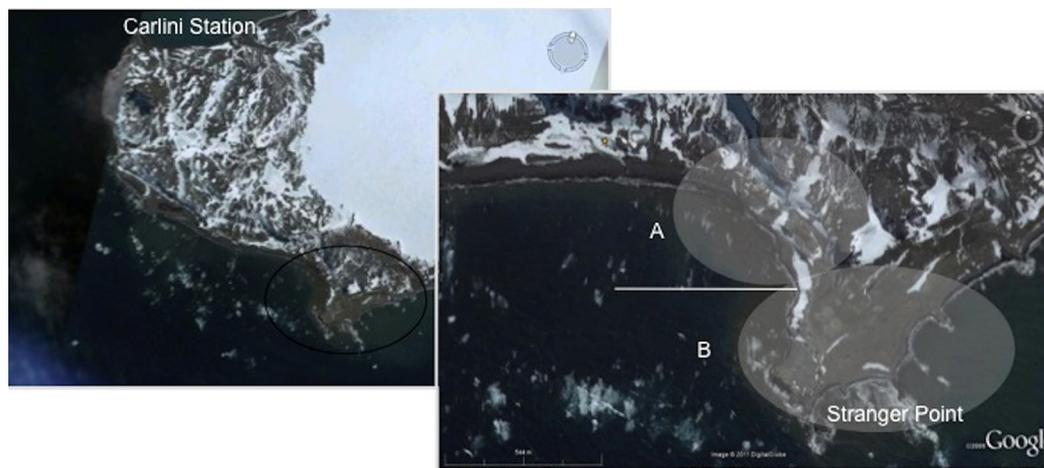


Fig. 1 Study area. Gentoo penguin (*Pygoscelis papua*) colony at Stranger Point, King George Island (Isla 25 de Mayo), South Shetland Islands. The division of the colony into areas A and B is shown.

as a breeding group. The aggregation of breeding groups within a discrete area was regarded as a colony.

A Google Earth image was used and was calibrated using the geographic information system (GIS) software gvSIG. Every breeding group in the field was determined with a global positioning system instrument with eTrex Legend (Garmin, Olathe, KS, USA) and was transferred to the map using Garmin's DNR application.

Breeding chronology and success

When the first egg was observed in the colony, 100 nests from different breeding groups were marked. Nests were followed every five days until the chicks reached 14 days old and then every two days until the chicks reached the crèche stage (CS). At each sampling date, the number of abandoned nests, eggs, chicks in guard and chicks in crèche were recorded according to the Ecosystem Monitoring Program Methods (Method A6, Procedure B) promulgated by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR 2004). The guard stage (GS) involves the presence of chicks in the nest brooded by a parent, whereas during the CS, chicks are alone, aggregated with other chicks, while both parents forage (Williams 1995).

Breeding chronology was estimated according to the number of nests with eggs, chicks in GS and those in CS. The chronology of gentoo penguin was described in two ways: (1) considering the entire colony; and (2) dividing the colony into areas A and B.

The measure of breeding success used was as follows: the number of chicks surviving to GS per breeding pair (overall breeding success), the number of eggs laid per breeding pair and the number of chicks hatched per

breeding pair. This estimation was interannually and seasonally compared, considering the entire colony and both A and B areas.

Diet composition and duration of foraging trips

Diet samples were collected from breeding adults following the CCAMLR (2004) sampling protocol (Method A8), using the stomach-flushing method described by Wilson (1984) and carrying out two flushes per bird, in accordance with Gales (1987). Stomach contents were drained and weighed (balance 200 ± 1 g). Individual prey items were then separated and each was weighed and identified to the minimum taxonomic level possible using a binocular magnifying glass and reference material.

The frequency of occurrence expressed as a percentage of each prey item (total number of samples containing the item/total number of samples analysed by 100), and percentage in weight for each item (total weight of the item/total weight of all samples by 100) were estimated for each season.

We determined the duration of foraging trips for the 2008, 2009 and 2010 seasons using time–depth recorders (TDR; Lotek Wireless, Newmarket, ON, Canada) attached on one to six adult breeders during the GS. We used LAT 1110 model TDRs (11 × 32 mm, 5 g, sampling interval 2 s) during 2008, and LAT 1400 TDRs (11 × 35 mm, 4.5 g, sampling interval 3 s) during 2009 and 2010. This last model allowed the device, which was programmed with a conditional pressure (>1 m depth), to achieve higher memory performance and also reduced disturbance of nests, since it only records when birds are in the water. TDRs were attached with epoxy adhesive and duct tape.

The duration of a foraging trip was determined as the time elapsed between the first and last diving recorded (>1 m depth), analysed in conjunction with temperature profiles to confirm that the bird was at sea. Trips were considered independent after more than two hours without a recording of pressure change, in accordance with Miller et al. (2009).

Chick weight at fledging

Fledging chicks were weighed during three periods of five days each, following the CCAMLR (2004) protocol (Method A7).

Statistical analysis

Interannual and seasonal variability in gentoo penguin breeding success was analysed using Chi-square tests after Yates correction. Diet composition variability, particularly the proportion of fish consumed, was analysed by means of Fisher's exact test. Stomach content weights were statistically compared using a generalized linear model (GLM). Since no samples from the 2007 GS were available, the GLM was divided into two stages: (1) two-factor GLM (year and breeding stage) to test the existence of variability among 2008, 2009 and 2010 weights; and (2) one-factor GLM (year) for interannual comparison of content weights during CS for the four seasons studied. Mean and standard deviation (SD) for the duration of foraging trips and fledging weight were calculated. The one-factor GLM (year) was used to test interannual variability. All data were examined for normality with the Shapiro-Wilk test and transformed to logarithmic scale. The post hoc Tukey's test was applied when necessary. The significance level for all tests was set at $P \leq 0.05$.

Results

Meteorological data

During October 2007 and 2009, mean temperatures were lower than those recorded for 2008 and 2010 seasons (-3.7 and -2.3 vs. -0.2 and $+0.2$, respectively). Similarly, more days with snowfall and strong north-easterly winds were also recorded for the same month in the same years (2007: 18; 2008: 6; 2009: 11; 2010: 0).

Though no snow deposition data are available, during 2007 and 2009 a greater presence and persistence of snow were registered in the colony at the beginning of reproduction, being higher for 2009 than for the 2007 season (pers. obs.; Fig. 2). Moreover, local differences

were observed during those seasons: area B showed higher snow accumulation and persistence than area A.

Hereafter, when we refer to "snow accumulation" on the ground, we point out these interannual differences, e.g., the atypical snow presence and persistence recorded in 2007 and 2009 breeding seasons.

Geographic location of breeding groups

Changes in the spatial disposition of breeding groups were observed during each season, with a remarkable redistribution in 2009. In this season, breeding groups were located at a higher altitude snow-free area within the colony, particularly in area A (Fig. 3). During the following breeding season, they remained at the same place.

Breeding chronology

In years with high snow accumulation on the ground (2007 and 2009), the breeding cycle showed a general delay. Considering the entire colony, hatching peaks were registered on 5 January 2007 and 4 January 2009, while for 2008 and 2010 seasons, the hatching peak was recorded on 30 November and 6 December, respectively.

Moreover, during 2007 and 2009, the seasonal breeding asynchrony observed left the colony virtually divided into two zones: areas A and B. In 2007, the difference in the peak of egg laying between areas A and B was 17 days (17 November–4 December), whereas in 2009 it was 15 days (20 November–5 December). In contrast, for 2008 and 2010 seasons, the peak of egg laying was recorded on 28 October and 1 November, respectively, for both zones.

Breeding success

The number of eggs laid per breeding pair was similar between the A and B groups, both interannually (Chi-square test, $df = 3$, $P > 0.05$ for each zone) and seasonally (Chi-square test, $df = 1$, $P > 0.05$ for each season; Table 1). No interannual variability was observed in the number of chicks that hatched, considering the entire colony (χ^2 test = 5.77, $df = 3$, $P = 0.12$). However, the number of chicks hatched in area A was lower for the 2009 season, both interannually (2007–09: χ^2 test = 6.316, $df = 1$, $P = 0.012$; 2008–09: χ^2 test = 4.486, $df = 1$, $P = 0.034$; 2009–10: χ^2 test = 6.757, $df = 1$, $P = 0.009$) and seasonally (χ^2 test = 4.94, $df = 1$, $P = 0.03$; Table 1). During the 2009 season, only 37.8% of chicks hatched in area A, compared with 82.5, 74.4 and 81.6% recorded in the 2007, 2008 and 2010 breeding seasons, respectively, and with 71% registered in area B for the same season.



Fig. 2 Interannual comparison of local conditions recorded at the Stranger Point colony, from 2007/08 to 2010/11: (a) 2007: first week of November; (b) 2008: 10 November; (c) 2009: 5 December; (d) 2010: last week of November.

Considering the entire colony, overall breeding success remained relatively stable and high (Table 2), without any interannual differences (χ^2 test = 5.768, $df = 3$, $P = 0.155$). However, pairs nesting in area A showed interannual variability in their breeding success (χ^2 test = 10.704, $df = 3$, $P = 0.013$). The 2009 season had the lowest production of CS chicks (2007 vs. 2009: χ^2 test = 8.664, $df = 1$, $P = 0.003$; 2008 vs. 2009: χ^2 test = 4.226, $df = 1$, $P = 0.04$; 2009 vs. 2010: χ^2 test = 6.088, $df = 1$, $P = 0.014$). During 2009, only 27.6% of chicks reached CS, while 72.5, 56.4 and 61.2% of chicks reached it in 2007, 2008 and 2010, respectively. However, no interannual variability was observed in the success of pairs nesting in area B (χ^2 test = 1.16, $df = 3$, $P > 0.05$). When comparing seasonal breeding success, differences between A and B groups were found only for 2009, in which the breeding success of area A pairs was significantly lower (χ^2 test = 5.503, $df = 1$, $P = 0.019$).

Diet composition and duration of foraging trips

Antarctic krill represented the main prey in terms of frequency of occurrence (100%) as well as percentage in weight (>98%) for each year and breeding stage (Table 3). The frequency range of fish found in the

samples was 13.33–50%, representing in all cases a non-significant fraction by weight (<1.6%). With regard to the proportion of fish consumed, no significant variability was recorded between breeding stages for the same season (GS-CS: Fisher's exact test, 2008: $P = 0.06$; 2009: $P = 0.22$; 2010: $P = 0.60$) or interannually (Fisher's exact test, $P > 0.05$ for GS: 2008 to 2010, and for CS: 2007 to 2010). Other prey in diet samples (i.e., other euphausiids, amphipods, squid, algae, mollusc shells, unidentified material) represented <1% of the diet by weight in all cases, and were considered accidental ingestion.

The stomach content weight did not differ between breeding stages (GS-CS: GLM, $F_{2,97} = 1.36$, $P = 0.89$), though it did interannually (GLM, $F_{2,97} = 8.95$, $P < 0.001$). Although there were no interannual differences in GS (post hoc Tukey's test, $P > 0.05$ for each season), interannual variability was found in stomach content weight during CS. Stomach content weights decreased after each season, being significantly lower in 2010 than in 2008 (post hoc Tukey's test, $P < 0.001$). This was most evident when the 2007 season was included in the analysis (GLM, $F_{3,79} = 22.99$, $P < 0.001$; post hoc Tukey's test: 2007–08, $P = 0.022$; 2007–09, $P < 0.001$; 2007–10, $P < 0.001$; 2008–10, $P < 0.001$).

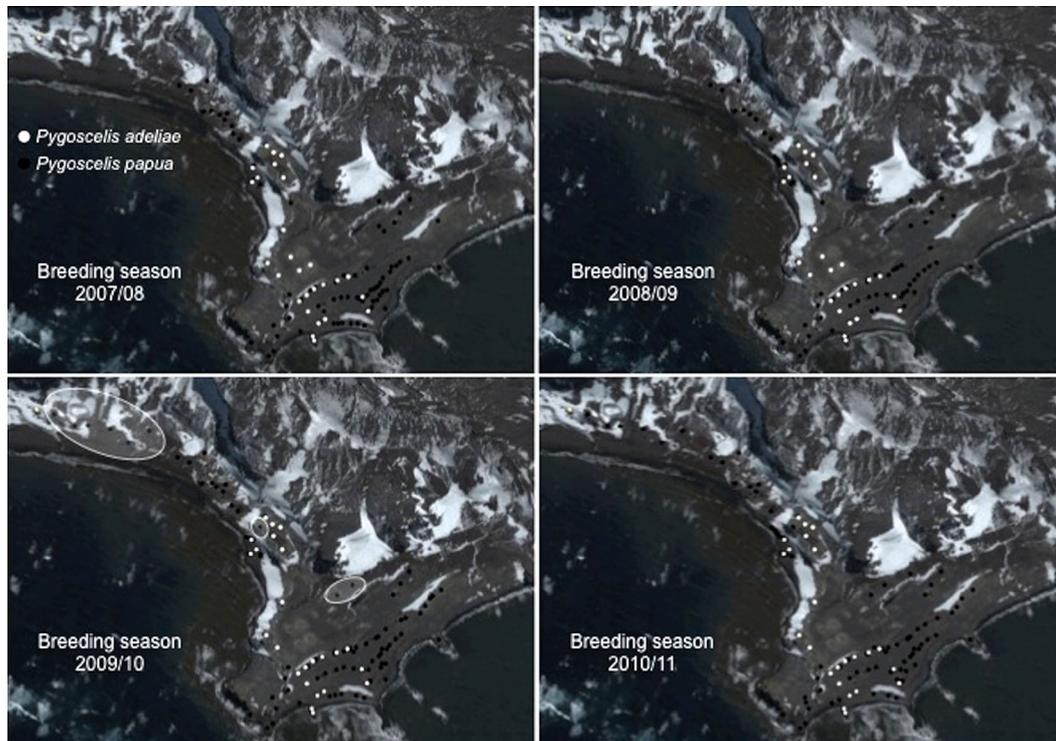


Fig. 3 Comparison of the spatial distribution of the breeding groups of gentoo penguin (*Pygoscelis papua*) at Stranger Point, from 2007/08 to 2010/11. The ovals show the notable redistribution observed during the 2009/10 breeding season. The locations of the breeding groups of Adélie penguin (*Pygoscelis adeliae*) are included for comparison.

An increase of approximately two hours per season was observed in the average duration of foraging trips of breeding adults during GS (2008 [one bird; $N=19$]: $07:10 \pm 04:17$; 2009 [six birds; $N=40$]: $09:15 \pm 03:29$; and 2010 [four birds; $N=31$]: $11:54 \pm 06:14$ hr: min) and significant interannual differences were recorded between the 2008 and 2010 seasons (GLM, $F_{2,87} = 6.20$, $P = 0.003$; post hoc Tukey's test: 2008–10, $P = 0.003$).

Table 1 Measures of breeding success: number of eggs laid/breeding pairs and number of chicks hatched/breeding pairs, for the entire colony and separated by zones: areas A and B.

	Breeding season			
	2007	2008	2009	2010
Eggs laid/breeding pairs				
Entire colony	1.87	2.00	1.87	1.99
A	1.90	2.00	1.86	1.98
B	1.85	2.00	1.88	2.00
Chicks hatched/breeding pairs				
Entire colony	1.44	1.50	1.09	1.70
A	1.65	1.49	0.76 ^a	1.63
B	1.30	1.51	1.42	1.76

^aInterannual significant differences in area A (χ^2 tests, $df=3$, $P < 0.05$); seasonal differences significant between areas A and B (χ^2 tests, $df=1$, $P < 0.05$).

Chick weight at fledging

The descriptive statistics of fledging weight are shown in Table 4. No interannual variability was found in the weight of fledging chicks (GLM, $F_{1,702} = 1.44$, $P = 0.229$).

Discussion

Penguins can be highly sensitive to climate change, which could alter the weather, oceanographic conditions and wintering or breeding habitats (Forcada & Trathan 2009). Species are confronted with variable conditions through time and space, and only those with plasticity in one or more aspects of their biology will be able to cope with this variability (Forcada 2007; Forcada & Trathan 2009). Phenology changes can contribute to the understanding of penguin responses to climate variation. Gentoo penguins show features, such as non-migratory behaviour, the absence of a fasting period prior to egg laying, and short nest reliefs, which probably increases their phenological flexibility in the face of less predictable conditions (Bost & Jouventin 1991; Forcada & Trathan 2009).

In response to snow accumulation, gentoo penguins at Stranger Point showed less nest-site fidelity compared to

Table 2 Overall breeding success (chicks in crèche stage/breeding pairs) for the entire colony and by zone: areas A and B.

Overall breeding success	Breeding season			
	2007	2008	2009	2010
Entire colony	1.27	1.21	0.87	1.35
A	1.45	1.13	0.55 ^a	1.22
B	1.15	1.27	1.18	1.48

^aInterannual significant differences in area A (χ^2 test, $df=3$, $P<0.05$); seasonal differences significant between areas A and B (χ^2 tests, $df=1$, $P<0.05$).

the sympatric *Pygoscelis adeliae* (Fig. 2). Notably some entire breeding groups moved to higher altitudes in 2009, a fact that was also observed by Boersma (2008) during years of unusual amounts of snow. Several authors (Bost & Jouventin 1990a; Bost & Jouventin 1991; Copley & Shears 1999; Boersma 2008; Lescroël et al. 2009) found that, under unfavourable conditions, gentoo penguins may delay the beginning of reproduction, which may be related to lower availability of nest sites or food, affecting their reproductive success. The chronology delay and low breeding success registered for area A during 2009, but not for area B during the same year, could indicate a reduced availability of snow-free sites to start reproduction. In addition to the importance of age or experience and the body condition of individual birds at the beginning of their breeding season (Bost & Jouventin 1990a; Bost & Jouventin 1991; Croxall 1992; Williams 1995), behaviour is also crucial for breeding performance, because the selection of partners as well as nesting sites can determine their breeding success (Lescroël et al. 2010). At Stranger Point, it is likely that the flexibility of gentoo penguin in the selection of nesting site helped buffer the impact of unfavourable local conditions.

To reduce the disturbance generated by observers (see Trathan et al. 2008), the breeding chronology was estimated with an error margin of two to five days, depending on the breeding stage. While this makes our findings unsuitable for comparison with other colonies, the method reliably detected changes in the phenology of

gentoo penguins within the studied colony during different years, since the error was constant. Moreover, using the same methodology, no variability was found for the gentoo penguin's congener *P. adeliae*, for the same study area and years (unpubl. data). Lynch et al. (2009) suggested that mean October temperatures constitute a predominant factor at the beginning of reproduction, given the need to find snow-free areas for nest building. During the 2007 and 2009 seasons, local conditions were similar: area B showed higher snow deposition and ice persistence, possibly related to heavy north-easterly snow storms and low temperatures recorded in October for these years. During these seasons, interannual variability in reproductive phenology was recorded for the entire colony, and seasonal asynchrony was observed for all breeding pairs nesting in area B, which represents 63% of the breeding population.

Variability in the breeding chronology of gentoo penguin has been previously reported (Williams 1990; Bost & Jouventin 1990a; Bost & Jouventin 1991; Williams 1995; Copley & Shears 1999; Boersma 2008; Forcada & Trathan 2009; Lescroël et al. 2009; Lynch et al. 2009; Lynch et al. 2010). In some cases, the delay in the breeding cycle is related to a previous failure in reproduction and second egg laid, as well as to low food availability (Bost & Jouventin 1990a; Bost & Jouventin 1991; Lescroël et al. 2009). Since this study did not include the replacement clutches in the description of chronology, we have ruled out that the delay observed here is due to reproductive failure. Also, if low food availability is a factor contributing to reproduction delay, this was not reflected during the periods studied (see below). On the other hand, variability in reproductive timing has also been associated with the age or experience of individual birds or the social structure of the population (Williams 1990; Bost & Jouventin 1990a; Williams 1995). The interannual variability reported here involved the entire colony, and the asynchronism involved much of the colony, results which appear to be independent of the age or experience of

Table 3 Diet composition of gentoo penguins rearing chicks at Stranger Point during four study seasons. Frequency of occurrence (as percentage) and percent in weight of the items; the mean (g) \pm SD of the stomach contents weights are shown.

Season	Breeding stage	N	Frequency of occurrence		Percent in weight		Stomach contents weights (g)
			Krill (%)	Fish (%)	Krill (%)	Fish (%)	
2007	CS ^a	25	100	28.00	99.87	0.09	572.82 \pm 170.67
2008	GS ^b	15	100	13.33	99.95	0.02	392.00 \pm 180.16
	CS	24	100	41.67	99.20	0.77	442.32 \pm 190.74
2009	GS	15	100	26.67	99.83	0.11	310.71 \pm 171.74
	CS	10	100	50.00	98.37	1.56	307.79 \pm 110.67
2010	GS	15	100	26.67	99.42	0.54	301.18 \pm 99.54
	CS	24	100	25.00	98.38	1.49	248.31 \pm 81.66

^aCrèche stage.

^bGuard stage.

Table 4 Descriptive statistics of chicks fledging weight of gentoo penguins during 2007–10.

Fledging weight	Breeding season			
	2007	2008	2009	2010
N	150	161	165	230
Mean \pm SD (kg)	5.09 \pm 0.64	5.01 \pm 0.52	5.05 \pm 0.62	5.13 \pm 0.58
Range (kg)	3.00–6.50	3.95–6.27	3.65–6.85	3.75–6.60
Sampling period	11/02 to 25/02	21/01 to 4/02	06/02 to 20/02	31/01 to 14/02

breeding birds. Moreover, if chronology variability were determined mainly by the presence of inexperienced birds, it is reasonable to expect low reproductive success for those years in which differences in the chronology were more pronounced (Williams 1990; Williams 1995).

There is general consensus about the negative impact of rainfall and snow precipitation on the breeding success of penguins (Williams 1995; Trivelpiece & Fraser 1996; Cogley & Shears 1999; Boersma 2008; McClintock et al. 2008; Trathan et al. 2008; Forcada & Trathan 2009; Lynch et al. 2009; Lynch et al. 2010; among others), resulting in the loss of nests due to flooding or desertion, and loss of chicks to hypothermia. While in each season birds laid eggs in the same proportion, there was a significant decrease in the number of chicks that hatched and chicks that reached the crèche for birds nesting in area A during the 2009 season. However, when considering the general population, reproductive success was relatively stable and high during the periods analysed, similar to findings reported by Carlini et al. (2009) for the same study area, suggesting that the high breeding plasticity of gentoo penguins enables them to face successfully different environmental conditions.

The abundance and quality of food have a strong influence on reproductive chronology (Bost & Jouventin 1990a; Bost & Jouventin 1991; Lescroël et al. 2009) and breeding success (Croxall 1992; Croxall et al. 1999; Boyd & Murray 2001; among others). The gentoo penguin exhibits behavioural plasticity with respect to diet composition and feeding and this favours their adjustment to changes in food availability (Bost & Jouventin 1990b; Pütz et al. 2001; Miller et al. 2009). During the study period, Antarctic krill was the principal prey in the diet of gentoo penguins breeding at Stranger Point. The percentage in weight of fish in samples was extremely low. These results are consistent with those reported for other colonies of gentoo penguins breeding on the same island (Hinke et al. 2007; Kokubum et al. 2010; Miller et al. 2010). Our study showed no changes either in diet composition or in the amount of food delivered to the chicks during GS for all seasons, though an increase in the duration of foraging trips in GS (2008–10) and a gradual weight decline in stomach contents during CS (2007–10) was observed. This may reveal a gradual

decrease in the availability or quality of food with each season (Croxall et al. 1999; Fraser & Hofmann 2003; Miller et al. 2009; Salihoglu et al. 2001). Declining prey availability could substantially alter the breeding success and survival of krill-dependent species (Croxall 1992; Croxall et al. 1999; Fraser & Hofmann 2003; among others). However, this decline in food abundance was reflected in neither the phenology nor the breeding success of the studied gentoo penguins; in fact, the breeding population increased by 91% between 1995/96 and 2011/12 (unpubl. data). On the one hand, only two of the four seasons analysed (2007 and 2009) showed a delay in reproduction, coinciding with high snow deposition on the ground. On the other hand, both reproductive success and fledging weight – considered by Hinke et al. (2007) to be measure of reproductive performance – remained constant despite the variability in the breeding chronology, the apparent decline in prey availability and the increased foraging effort of adults.

In summary, it has been previously demonstrated that plasticity in the diet composition and foraging behaviour of the gentoo penguin contributes to maintain their relatively constant breeding success, despite the effects of climate change on their main prey, Antarctic krill. Similarly, according to our results, the flexibility in their reproductive phenology and their low nesting site fidelity are advantageous characteristics that help support their breeding success, buffering against such changes observed in local environmental conditions as increased snowfall. Separately or together, these biological responses allow gentoo penguins to cope with the great environmental variability, both marine and terrestrial, and possibly influence the current population trends recorded in the western Antarctic Peninsula.

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References

- Atkinson A., Siegel V., Pakhomov E. & Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Barbraud C. & Weimerskirch H. 2006. Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the United States of America* 103, 6248–6251.
- Boersma P.D. 2008. Penguins as marine sentinels. *BioScience* 58, 597–607.
- Bost C.-A. & Jouventin P. 1990a. Laying asynchrony in gentoo penguins on Crozet Islands: causes and consequences. *Ornis Scandinavica* 21, 63–70.
- Bost C.-A. & Jouventin P. 1990b. Evolutionary ecology of the gentoo penguin (*Pygoscelis papua*). In J.T. Darby & L.S. Davis (eds.): *Penguin biology*. Pp. 85–112. Orlando: Academic Press.
- Bost C.-A. & Jouventin P. 1991. The breeding performance of the gentoo penguin *Pygoscelis papua* at the northern edge of its range. *Ibis* 133, 14–25.
- Boyd I.L. & Murray W.A. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology* 70, 747–760.
- Carlini A.R., Coria N.R., Santos M.M., Negrete J., Juárez M.A. & Daneri G.A. 2009. Responses of *Pygoscelis adeliae* and *P. papua* populations to environmental changes at Isla 25 de Mayo (King George Island). *Polar Biology* 32, 1427–1433.
- CCAMLR 2004. *CCAMLR ecosystem monitoring program. Standard methods*. North Hobart: Commission for the Conservation of Antarctic Marine Living Resources.
- Cobley N.D. & Shears J.R. 1999. Breeding performance of gentoo penguins (*Pygoscelis papua*) at a colony exposed to high levels of human disturbance. *Polar Biology* 21, 355–360.
- Croxall J.P. 1992. Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society of London B* 338, 319–328.
- Croxall J.P., Reid K. & Prince P.A. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series* 177, 115–131.
- Ducklow H.W., Baker K., Martinson D.G., Quetin L.B., Ross R.M., Smith R.C., Stammerjohn S.E., Vernet M. & Fraser W. 2007. Marine pelagic ecosystems: the west Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B* 362, 67–94.
- Forcada J. 2007. The impact of climate change on antarctic megafauna. In C.M. Duarte (ed.): *Impacts of global warming on polar ecosystems*. Pp. 85–110. Madrid: Fundación BBVA.
- Forcada J. & Trathan P.N. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15, 1618–1630.
- Forcada J., Trathan P.N., Reid K., Murphy E.J. & Croxall J.P. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12, 411–423.
- Fraser W. & Hofmann E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* 265, 1–15.
- Fraser W.R., Trivelpiece W.Z., Ainley D. & Trivelpiece S.G. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of ice due to environmental warming? *Polar Biology* 11, 525–531.
- Gales R.P. 1987. Validation of the stomach flushing technique for obtaining stomach contents of penguins. *Ibis* 129, 225–243.
- González-Zeballos D., Santos M.M., Rombolá E.F., Juárez M.A. & Coria N.R. 2013. Abundance and reproductive distribution of marine birds in the northern area of Danco Coast, Antarctic Peninsula. *Polar Research* 32, article no. 11133, doi: 10.3402/polar.v32i0.11133.
- Hinke J.T., Salwicka K., Trivelpiece S.G., Watters G.M. & Trivelpiece W.Z. 2007. Divergent responses in *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153, 845–855.
- Kokubum N., Takahashi A., Mori Y., Watanabe S. & Shin H.-C. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology* 157, 811–825.
- Lescroël A., Bajzak C. & Bost C.A. 2009. Breeding ecology of the gentoo penguin *Pygoscelis papua* at Kerguelen Archipelago. *Polar Biology* 32, 1495–1505.
- Lescroël A., Ballard G., Toniolo V., Barton K.J., Wilson P.R., Lyver P.O. & Ainley D.G. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91, 2044–2055.
- Lescroël A. & Bost C.-A. 2006. Recent decrease in gentoo penguin populations at Iles Kerguelen. *Antarctic Science* 18, 171–174.
- Libertelli M.M., Juárez M.A., Santos M.M., Favero M. & Coria N.R. 2010. Variation in the diet of gentoo penguin at Cierva Point and Esperanza Bay (Antarctic Peninsula) and Stranger Point (South Shetland Islands), Antarctica. Poster presented at the XXXI SCAR & Open Science Conference. 3–6 August. Buenos Aires, Argentina.
- Loeb V., Siegel V., Holm-Hansen O., Hewitt R., Fraser W., Trivelpiece W. & Trivelpiece S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900.
- Loeb V.J., Hofmann E.E., Klinck J.M., Holm-Hansen O. & White W.B. 2009. ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. *Antarctic Science* 21, 135–148.
- Lynch H.J., Fagan W.F. & Naveen R. 2010. Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula. *Polar Biology* 33, 493–503.
- Lynch H.J., Fagan W.F., Naveen R., Trivelpiece S.G. & Trivelpiece W.Z. 2009. Timing of clutch initiation in *Pygoscelis* penguins on the Antarctic Peninsula: towards an improved

- understanding of off-peak census correction factors. *CCAMLR Science* 16, 149–165.
- Lynch H.J., Naveen R. & Fagan W.F. 2008. Censuses of penguin, blue-eyed shag *Phalacrocorax atriceps* and southern giant petrel *Macronectes giganteus* populations on the Antarctic Peninsula, 2001–2007. *Marine Ornithology* 36, 83–97.
- McClintock J., Ducklow H. & Fraser W. 2008. Ecological responses to climate change on the Antarctic Peninsula. *American Scientist* 96, 302–310.
- McClintock J.B., Silva-Rodriguez P. & Fraser W.R. 2010. Southerly breeding in gentoo penguins for the eastern Antarctic Peninsula: further evidence for unprecedented climate-change. *Antarctic Science* 22, 285–286.
- Meredith M.P. & King J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32, L19604, doi: 10.1029/2005GL024042.
- Miller A.K., Kappes M.A., Trivelpiece S.G. & Trivelpiece W.Z. 2010. Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Island, Antarctica. *The Condor* 112, 683–695.
- Miller A.K., Karnovsky N.J. & Trivelpiece W.Z. 2009. Flexible foraging strategies of gentoo penguins *Pygoscelis papua* over 5 years in the South Shetland Islands, Antarctica. *Marine Biology* 156, 2527–2537.
- Miller A.K. & Trivelpiece W.Z. 2008. Chinstrap penguins alter foraging and diving behavior in response to the size of their principle prey, Antarctic krill. *Marine Biology* 154, 201–208.
- Moline M.A., Claustre H., Frazer T.K., Schofield O. & Vernet M. 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology* 10, 1973–1980.
- Montes-Hugo M., Doney S.C., Ducklow H.W., Fraser W., Martinson D., Stammerjohn S.E. & Schofield O. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323, 1470–1473.
- Pütz K., Ingham R.J., Smith J.G. & Croxall J.P. 2001. Population trends, breeding success, and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. *Polar Biology* 24, 793–807.
- Reiss C.S., Cossio A.M., Loeb V. & Demer D.A. 2008. Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. *ICES Journal of Marine Science* 65, 497–508.
- Salihoglu B., Fraser W.R. & Hofmann E.E. 2001. Factors affecting fledging weight of Adélie penguin (*Pygoscelis adeliae*) chicks: a modeling study. *Polar Biology* 24, 328–337.
- Sander M., Balbao T.C., Costa E.S., dos Santos C.R. & Petra M.V. 2007. Decline of the breeding population of *Pygoscelis antarctica* and *Pygoscelis adeliae* on Penguin Island, South Shetlands, Antarctica. *Polar Biology* 30, 651–654.
- Sander M., Balbao T.C., Polito M.J., Costa E.S. & Carneiro A.P.B. 2007. Recent decrease in chinstrap penguin (*Pygoscelis antarctica*) populations at two of Admiralty Bay's islets on King George Island, South Shetland Islands, Antarctica. *Polar Biology* 30, 659–661.
- Smith R.C., Ainley D., Baker K., Domack E., Emslie S., Fraser S., Kennet A., Mosley-Thomson E., Stammerjohn S. & Vernet M. 1999. Marine ecosystem sensitivity to climate change. *Bioscience* 49, 393–404.
- Smith R.C. & Stammerjohn S.E. 2001. Variations of surface air temperature and sea-ice extent in the western Antarctic Peninsula region. *Annals of Glaciology* 33, 492–500.
- Stammerjohn S.E., Martinson D.G., Smith R.C. & Iannuzzi R.A. 2008. Sea ice in the western Antarctic Peninsula region: spatio-temporal variability from ecological and climate change perspective. *Deep-Sea Research Part II* 55, 2041–2058.
- Tanton J.L., Reid K., Croxall J.P. & Trathan P.N. 2004. Winter distribution and behavior of gentoo penguins *Pygoscelis papua* at South Georgia. *Polar Biology* 27, 299–303.
- Thomas E.R., Marshall G.J. & McConnell J.R. 2008. A doubling in snow accumulation in the western Antarctic Peninsula since 1850. *Geophysical Research Letters* 35, L01706, doi: 10.1029/2007GL032529.
- Trathan P.N., Forcada J., Atkinson R., Downie R.H. & Shears J.R. 2008. Population assessments of gentoo penguins (*Pygoscelis papua*) breeding at an important Antarctic tourist site, Goudier Island, Port Lockroy, Palmer Archipelago, Antarctica. *Biological Conservation* 141, 3019–3028.
- Trathan P.N., Forcada J. & Murphy E.J. 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society of London B* 362, 2351–2365.
- Trivelpiece W.Z. & Fraser W.R. 1996. The breeding biology and distribution of Adélie penguins: adaptations to environmental variability. *Antarctic Research Series* 70, 273–285.
- Trivelpiece W.Z., Hinke J.T., Miller A.K., Reiss C.S., Trivelpiece S.G. & Watters G.M. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences of the United States of America* 108, 7625–7628.
- Trivelpiece W.Z., Trivelpiece S.G. & Volman N.J. 1987. Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68, 351–361.
- Turner J., Lachlan-Cope T., Colwell S. & Marshall G. 2005. A positive trend in western Antarctic Peninsula precipitation over the last 50 years reflecting regional and Antarctic-wide atmospheric circulation changes. *Annals of Glaciology* 41, 85–91.
- Vaughan D.G., Marshall G.J., Connolley W.M., Parkinson C., Mulvaney R., Hodgson D.A., King J.C., Pudsey C.J. &

- Turner J. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climate Change* 60, 247–274.
- Volkman N.J., Presler P. & Trivelpiece W.Z. 1980. Diets of pygoscelid penguins at King-George Island Antarctica. *Condor* 82, 373–378.
- Williams T.D. 1990. Annual variation in breeding bird biology of gentoo penguins, *Pygoscelis papua*, at Bird Island, South Georgia. *Journal of Zoology* 222, 247–258.
- Williams T.D. 1995. *The penguins*. New York: Oxford University Press.
- Wilson R.P. 1984. An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* 55, 109–112.
- Wilson R.P., Alvarez B., Latorre L., Adelung D., Culik B. & Bannasch R. 1998. The movements of gentoo penguins *Pygoscelis papua* from Ardley Island, Antarctica. *Polar Biology* 19, 407–413.
- Young E. 1994. *Skua and penguin; predator and prey*. Cambridge: Cambridge University Press.