

A matter of timing: Adélie penguin reproductive success in a seasonally varying environment

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ABSTRACT: Earlier breeding has been shown to be advantageous for the reproductive outcomes of a variety of avian species inhabiting a diverse range of environments. However, it is generally unclear how this advantage translates for polar seabirds that breed in a highly seasonal and restricted breeding season. The present study determined whether there was an overall advantage or disadvantage of early or late breeding on the reproductive outcomes of Adélie penguins *Pygoscelis adeliae* breeding at Béchervaise Island, East Antarctica. We examined this for individual nests within each year as well as for the overall population over a 13 yr period, using between 69 and 166 monitored nests each year. We investigated whether any advantage was related to bird age, and quantified the different environmental conditions (windchill and snow days) that early and late breeders and their eggs and chicks experienced. In just under half of the years, laying eggs late in the breeding season resulted in a reduced chance of chicks crèching, and early egg laying was advantageous in only 2 years. We found no evidence that the advantage of early breeding or the disadvantage of late laying was due to the age and associated experience of the birds. We are unable to generate a consistent explanation for why the timing of clutch initiation in some years was important for reproductive success, yet in others it was not. The years when timing was important were not consistently harsh nor were they particularly favourable for overall reproductive success.

KEY WORDS: Seabird ecology · Breeding phenology · Breeding success · Windchill · Chick rearing · Snow days

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INTRODUCTION

The timing of reproduction for seabirds is driven by physiological, environmental and social cues (Vleck & Vleck 2002). Successful reproduction for seabirds is dependent on the birds adequately responding to these cues to ensure that breeding is undertaken during a period when environmental conditions are favourable (Reed et al. 2009, Hinke et al. 2012). Overall, there appears to be an advantage in early breeding for many avian species, including seabirds (Sydeman et al. 1991, de Forest & Gaston 1996, Arnold et al. 2004, Lewis et al. 2006). Earlier breeding has been associated with a range of benefits, including larger

eggs and clutch sizes and increased chick growth and survival rates in a number of species (e.g. Furness 1983, Moreno et al. 1997, Arnold et al. 2004 and papers therein, Moe et al. 2009). Also, earlier-hatching chicks may have a longer development period before the onset of winter, with later hatching chicks being forced to crèche and/or fledge at a younger age and/or in poorer condition (Viñuela et al. 1996, Moreno et al. 1997), potentially reducing their chances of survival. While the advantages of earlier breeding are more obvious than the disadvantages, the outcome probably also depends on the constraints imposed by the ecosystem, particularly in highly seasonal environments.

Seabirds that breed in the polar regions are constrained to breeding during the short summer season (with the exception of emperor penguins *Aptenodytes forsteri*) when conditions are favourable for reproduction (Viñuela et al. 1996, Ainley 2002, Hodum 2002). Like other seabird species, their reproductive activities need to coincide with maximum prey availability during this period of peak energetic demand, when they need to provision their offspring as well as maintain their own body condition (Hipfner 2008, Watanuki et al. 2009, Ballard et al. 2010). Prey availability is determined by many factors, including sea ice extent, concentration and phenology as well as its influence on phytoplankton concentration and size (Montes-Hugo et al. 2008) and hence krill recruitment (Loeb et al. 1997, Nicol 2006, Murphy et al. 2007). The amount of prey available can also depend on the intensity of intra- and inter-specific competition around seabird breeding colonies (Birt et al. 1987, Ainley 2002, Ainley et al. 2006, Balance et al. 2009). If there is a mismatch between the period of maximum energetic demand and peak prey availability, then offspring survival could be reduced (Durant et al. 2007, Chapman et al. 2010). As a result, responding to cues for initiating breeding is of paramount importance for polar seabirds.

Higher reproductive success in relation to earlier breeding, however, is not only due to the timing of breeding per se or how it relates to environmental conditions or peak prey supply. Previous studies on seabirds (e.g. Ainley & Schlatter 1972, Coulson & Horobin 1976, Weimerskirch 1990, de Forest & Gaston 1996) have shown that age and/or experience can have an important role in influencing reproductive success. Experience, which is often positively correlated with bird age, is important as it enhances foraging ability (Limmer & Becker 2009) and the capacity to co-ordinate between pairs (Weimerskirch 1990, Lewis et al. 2006). As a result, earlier and/or more experienced breeders often have better body condition at the beginning of the season and are less likely to desert the egg(s) or chick(s) (Gauthier-Clerc et al. 2001).

For the circum-Antarctic breeding Adélie penguin *Pygoscelis adeliae* (the subject of this study), inter-annual phenological variability has been linked to broad-scale sea ice extent and temperature as well as local conditions such as snow cover (Barbraud & Weimerskirch 2006, Emmerson et al. 2011, Hinke et al. 2012, Lynch et al. 2012). Adélie penguins return to the breeding colony when the sea ice is near, or at, its maximum extent (Emmerson et al. 2011), enabling them to complete breeding in time to moult by early

autumn (Trathan et al. 1996). Once at the colonies, the timing of clutch initiation and the length of the incubation and guard periods can be influenced by wind speed and snow cover (Ulbricht & Zippel 1994, Emmerson et al. 2011, Hinke et al. 2012, Lynch et al. 2012). Breeding success can vary between birds within a year because older, more experienced birds arrive earliest and often have higher reproductive success (Ainley 2002). However, the limited number of years and locations where this has been examined hinders generalisations as to whether earlier nesting within a breeding season is consistently advantageous for this species. For example, in contrast to the results of Ainley (2002) and Marks et al. (2010), which demonstrated a clear advantage for early breeding or arrival, other studies in the Ross Sea found that early and late breeders were more likely to have failed nests (Davis 1982). It could be that, in line with other seabird species, the pattern and strength of selection on the timing of breeding for Adélie penguins could vary in relation to environmental conditions, being prominent in some years and absent in others (Reed et al. 2009).

The synchronous breeding of Adélie penguins may provide advantages for chick survival which could be compromised if breeding was less concurrent (Hinke et al. 2012). However, the 3 wk variability in the timing of clutch initiation between individuals within a year (Emmerson et al. 2011) could still result in early and late eggs being laid (or chicks being hatched) into fundamentally different environmental conditions because of the rapid transition to the austral summer. Combined with age and/or experience, differences in the environment associated with the timing of nesting could confound any advantages of breeding early. On the basis of this, it is unclear whether Adélie penguins at this location express the advantage of early breeding reported for many avian species and, if they do, whether it is consistent across years.

In this study, we explore whether the benefits of earlier breeding hold for Adélie penguins breeding at Béchervaise Island, East Antarctica, over a 13 yr period. We investigate whether there is an overall advantage in terms of reproductive outcomes for early or late clutch initiation or whether the optimal time for egg laying occurs at some intermediate date. Emmerson et al. (2011) previously examined Adélie penguin phenology at this site at the population level but did not examine differences between individuals within a year. Here, we rectify this and ask 3 key questions: (1) Is there a reproductive advantage associated with the timing of clutch initiation between

individuals within a year? (2) Could any advantage be a consequence of age-related differences in breeding timing and ability? (3) Is the importance of timing consistent across years or are there particular conditions when it is important? We also determine whether laying eggs early or having early hatching chicks results in the eggs or chicks experiencing different conditions compared to eggs laid and chicks hatched later in the breeding season. Our expectation is that during colder years, or if birds breed earlier, the length of the incubation and guard periods would increase as eggs take longer to incubate in colder conditions and chicks divert more energy towards thermoregulation than growth compared with warmer years.

MATERIALS AND METHODS

The Adélie penguin data used in this study were collected at Béchervaise Island (67°35' S, 62°49' E), situated approximately 2 km NW of Mawson Station in East Antarctica. At this location, there are approximately 2000 breeding Adélie penguins spread across 18 sub-colonies (Kerry et al. 2000), with the population increasing slightly over the study period (Clarke et al. 2003). This site has been monitored annually since the 1990/91 split-year breeding season as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (SC-CCAMLR 1997).

Nest census data

Data for Adélie penguin phenology in this study included dates for clutch initiation (CID), chick hatch, chick crèche and nest failure. Here, we present the results from data collected from 1991/92 through to 2003/04 to ensure data consistency. During this period, CIDs were available in all years, chick crèche dates were available in all years except in 1994/95 because of high chick failure and in 1995/96 due to logistic difficulties. Nest fail dates were available for all years.

Clutch initiation, chick hatch and crèche dates specifically refer to the first egg laid, first chick hatched and first chick crèched in each of the monitored nests. Nest fail dates refer to the date when the entire nest failed (both chicks had died). A nest that had at least one chick crèched was considered to be successful (for determining the probability of a chick

crèching). Nest observations were conducted daily from when the first egg was laid in the colony (mid-November) until the first chick hatched and then twice daily from then until all chicks had crèched (early February). This involved checking nests in the study sub-colonies for the presence of an adult and the presence of eggs and chicks. Incubation length for each of the observed nests was calculated as the number of days between the CID and the first egg hatch. Guard length for each monitored nest was calculated as the period from the date of the first egg hatch to the date when the first chick crèched.

CIDs and nest fail dates of birds of known age

To examine the possibility that CIDs or nest fail dates were related to bird age, we examined nest attendance and nest census data for a small subset of birds of known age and sex. Up to 300 Adélie penguin chicks were tagged annually from 1990/91 on Béchervaise Island, with electronic identification devices implanted subcutaneously (Clarke & Kerry 1998). High chick mortality in 1994/95 meant that no chicks were tagged, nor were chicks tagged in 2003/04 due to logistics. The annual detection of tagged birds at nests as part of the nest surveys described above commenced in 1991/92. The tags were glass-coated passive transponders (TIRIS, Texas Instruments), which were supplied in sterilised cartridges and can theoretically last a bird's lifetime. Implanting details are described by Kerry et al. (1993b). Long-handled tag readers were used to detect tags at a distance of about 10 to 20 cm from the bird. Bird sex was ascribed either through cloacal examination or by presence at a nest between 23 and 29 November, corresponding to the time when predominantly breeding males are present, and 11 to 18 December, when predominantly breeding females are present (Kerry et al. 1993a).

Breeding success

To determine annual overall population level breeding success, island-wide nest and chick counts were conducted on, or within a few days of, 2 December and 30 January, respectively. Overall breeding success was defined as the total number of chicks crèched on the island divided by the number of nests that were occupied in each year. Breeding success was calculated for all 13 years from 1991/92 through to 2003/04.

Environmental variables

Windchill

To understand how the windchill profile relates to Adélie penguin breeding phenology, we calculated daily mean, minimum and maximum values from September through to March using data from 1991/92 to 2003/04. Windchill temperatures were determined from the ambient air temperature, wind speed and the relative humidity recorded at Mawson Station (data obtained from the Australian Bureau of Meteorology). Windchill was calculated as follows:

$$AT = T_a + 0.33e - 0.70ws - 4.00 \quad (1)$$

where T_a is the dry bulb temperature (°C), e is the water vapour pressure (hPa), and ws is the wind-speed (m s^{-1}) at 10 m elevation following the Australian Bureau of Meteorology's formula (www.bom.gov.au/info/thermal_stress/). The water vapour pressure was determined from:

$$e = \frac{rh}{100} \cdot 0.6105 \cdot \exp\left(\frac{17.27 \cdot T_a}{237.7 + T_a}\right) \quad (2)$$

where rh is the relative humidity (%).

The number of snow days from 1991/92 to 2003/04 was determined from data obtained from the Australian Bureau of Meteorology for Mawson Station. Because weather observations were made every 6 h, we defined a snow day as one where any of the observations within each day had a continuous moderate or heavy fall of snowflakes or heavy drifting or blowing snow.

Near-shore sea ice extent

Sea ice extent was calculated in the region bounded to the south by the Antarctic coastline, to the north by latitude 66.75°S, and to the east and west by longitudes 60°E and 65°E. These bounds encompass the most northerly limit of fast-ice (ice that remains attached to the continent) during the early chick-rearing period and the longitudinal range over which Adélie penguins breeding at Béchervaise Island concentrate their foraging activities at sea (Clarke et al. 2006). This region was used in an earlier study demonstrating the effects of sea ice on Adélie penguin breeding success (Emmerson & Southwell 2008). We term this region and the ice contained within it as the near-shore region and near-shore sea ice, respectively.

The average near-shore sea ice cover was calculated over the 3 wk period from 25 December to 15

January, when adults were guarding chicks. The region comprises predominantly fast-ice during the early chick-rearing period (guard stage) and is a combination of fast-ice and pack-ice during the latter part of the chick-rearing period (crèche stage). Sea ice data were obtained from SMMR-SSM/I passive microwave data from the National Snow and Ice Data Center (NSIDC, <http://nsidc.org/data/nsidc-0051.html>) (Cavalieri et al. 1996), using tools for their extraction available through the Australian Antarctic Division Data Centre. Data represent the total ice cover within the defined region with >15% sea ice concentration. Grid cell size for satellite imagery was 25×25 km.

Data analysis

Reproductive outcomes in relation to early and late laying

To determine whether there was an advantage for reproductive outcomes related to the timing of clutch initiation, we used logistic regression models (family = binomial) to determine the probability of a chick crèching from each nest in relation to the CID for each year. A nest was considered to have crèched chicks if it had 1 or 2 chicks reach the crèche stage. We developed a global model across years using the absolute CID (the calendar date on which clutch initiation occurred) and a relative model across years (where each individual nest's CID was expressed relative to the mean CID for each year). The deviation values calculated for the relative model provide a standardised measure of the extent to which the CID tracked the mean population response over time (Reed et al. 2009). We determined whether there was an advantage of early or late laying (linear model) compared with an intermediate (quadratic model) date for optimal egg lay for the annual, global, and relative models. Linear and quadratic logistic regression models were compared with ANOVA, using a chi-squared test to determine the significance of the change in deviance between the 2 models. The most supported model out of the linear and quadratic models was then compared to the null model.

Due to the difficulty in calculating the percent deviance of models with a binary response variable, we examined model fit by calculating the total proportion of nests that had chicks crèching during each 3 d period over the entire clutch initiation period and compared them with both the global and relative model predictions. We presented these graphically

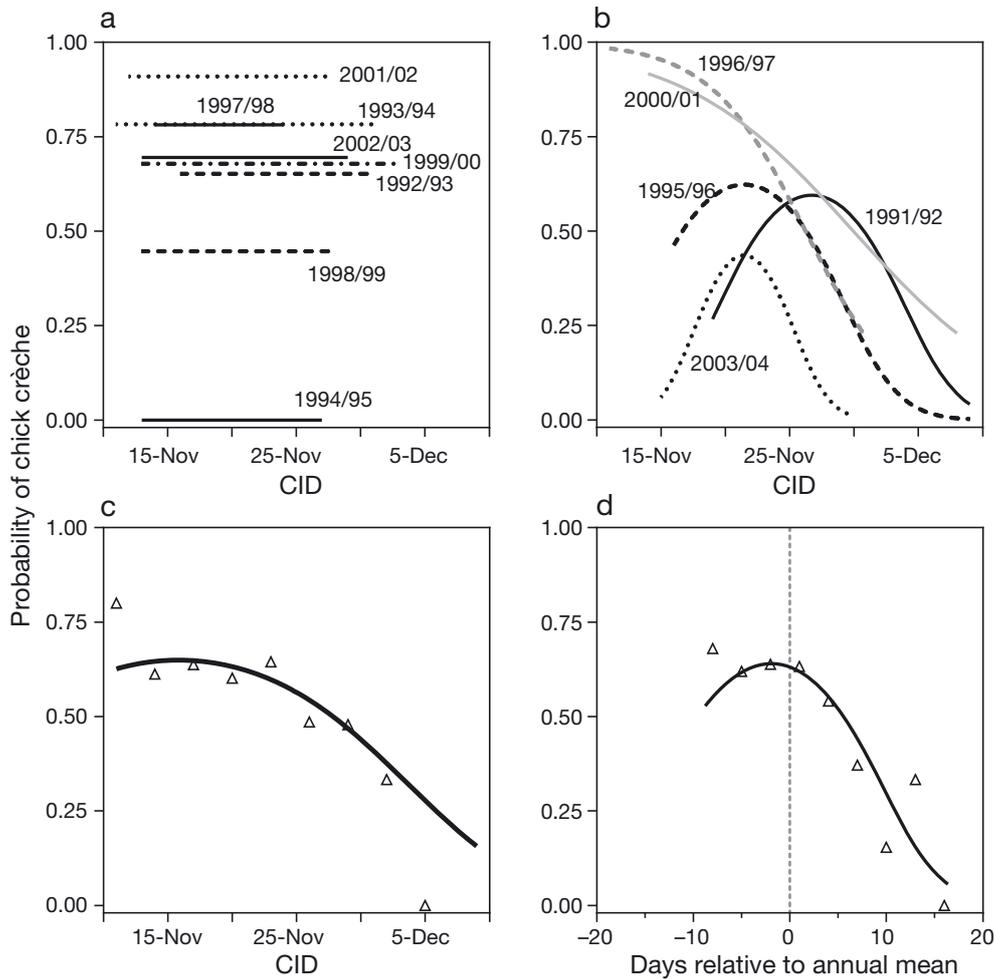


Fig. 1. Probability of a chick hatching per nest in (a) years where the timing of clutch initiation had no impact on reproductive success, (b) years with either an advantage for early egg laying or a disadvantage for either early or late egg laying. Model predictions for (c) the global model across years and (d) the relative model across years for each nest's clutch initiation (CID) relative to the mean for each year. Δ : proportion of chicks reaching crèche over 3 d periods in relation to CID based on real data. Note that 1998/99, 1994/95, and 2003/04 had extensive sea ice near the colony, which resulted in high and widespread chick failure across the colony. Probability of chick crèche was not based on logistic models for 1994/95 because models failed to converge

(Fig. 1c,d). Values close to the model predictions indicate good model fit.

Age and sex effects on CIDs and reproductive outcomes

Length of incubation and guard periods in relation to CID and hatch date

We performed linear regressions to assess whether the length of the incubation period was related to the CID and whether the length of the guard period was related to the hatch date. Specifically, we tested whether early laid nests had shorter or longer incubation periods and whether earlier hatched nests had shorter or longer guard periods. In each case, we developed a model for each year as well as a global model that pooled values across years.

To determine whether the success of early breeding birds was related to their age, whereby older, more experienced birds may breed earlier and be more successful, we examined the relationship between age and the timing of clutch initiation, and nest fail dates for females and males. We calculated the age of known-sex birds that had been tagged as chicks and that had appeared on our monitored nests. Because the number of birds that were of known age and sex was small (48 males and 37 females over 9 yr, i.e. 2 to 11 birds of known age/known sex in each year), we pooled data across years. We used a linear mixed-effects model (LME) that included bird age and sex

and their interaction term as factors, penguin ID as a categorical random factor, and relative CID and nest fail dates as response variables. Relative CIDs and nest fail dates were calculated as the difference between each nest's CID and the average for that year across all nests. Variance components were estimated with maximum likelihood to compare models with different fixed-effects structures (Crawley 2002). We also conducted linear regressions between the nest fail dates and the CID for each year to determine whether the earliest or latest nesting birds failed early or not.

Potential environmental drivers of reproductive outcomes

We examined the intra- and inter-annual changes in snow days and windchill to determine whether laying eggs early or having early hatching chicks resulted in the eggs or chicks experiencing different conditions compared to eggs laid and chicks hatched later in the breeding season. Given that the timing of clutch initiation was shown to be important for reproductive outcomes in some years, we wanted to determine whether snow days or windchill were potential environmental drivers of the differences in reproductive outcomes and to understand the changes in environmental conditions that the penguins experienced, particularly for the earliest and latest breeders in each year.

We calculated the number of snow days within 2 wk periods for each year from September to March in 1991/92 through to 2003/04 and determined the mean, minimum, and maximum values to create a profile of snow days throughout the penguins' breeding season. Likewise, we calculated the mean, minimum, and maximum daily windchill within 2 wk periods during the same period to create a temperature profile. Both the snow days and windchill temperatures were overlaid with the dates for the breeding phenology for this population presented in Emmerson et al. (2011).

We calculated the 15 d windchill temperatures based on the clutch initiation and first egg hatch dates for each nest in each year to quantify its inter-annual variability. Windchill temperatures were averaged over the first 15 d of incubation (when the temperature is likely to be at its most extreme from the time that each egg is laid) and the first 15 d after each chick hatched (i.e. the time frame for the development of homeothermy in chicks; Déglétagne et al. 2013) for each of the monitored nests. Data were analysed with 1-way ANOVAs and post-hoc Tukey's

multiple comparisons tests. The 15 d period at the start of incubation and hatch seemed a reasonable way to assess temperature effects in a consistent way.

We constructed separate LMEs to examine whether windchill temperatures and the number of snow days differed for eggs laid early or late or for chicks that hatched early or late within a breeding season. Windchill was calculated for each nest as the average value over the first 15 d from the date of egg lay or chick hatch, and the number of snow days was calculated as the total number of days with snowfall over the same 15 d period. Early nests were taken as the dates of the first 25 nests in each year, and late nests were the dates of the last 25 nests in each year. We performed a backward model-selection procedure with the systematic deletion of each of the fixed effects terms starting with the higher-order interaction terms. The significance of each term after removal was examined with likelihood ratio tests until no further deletions were warranted. The full model included period (early or late), stage (incubation or guard), the interaction between the two, and year as a random categorical variable.

Statistical analyses were conducted in R v.3.3.1 (R Development Core Team 2006) and GraphPad Prism (v.6.02), with a significance level of $p < 0.05$. The mixed effects models were fitted using the *lme* function in the *nlme* library (Pinheiro et al. 2015).

RESULTS

Reproductive outcomes in relation to early and late laying

In 7 of the 12 years examined with logistic regression models, there was no relationship between the timing of clutch initiation and the probability of a chick crèching (Fig. 1a, Table 1). In 6 of these years, a given nest had between 60 and 90% chance of having a chick crèche irrespective of the CID. In 2 years (1998/99 and 1994/95), this probability was $< 50\%$, with sea ice being at its greatest extent in this 13 yr period in 1994/95 (note that in 1994/95, logistic regression models did not converge because there were insufficient nests that had chicks reaching crèche stage). In 5 years, there was a clear relationship between reproductive success and the timing of clutch initiation (Fig. 1b, Table 1), with 2 years (1996/97 and 2000/01) showing an advantage for laying eggs early. In those 2 years, the probability of a chick crèching from nests with eggs was close to 100% for eggs laid in mid-November; nests with

clutches initiated as late as December were unlikely to produce crèched chicks. In 3 of the years (1991/92, 1995/96, and 2003/04), there was a disadvantage for early or late egg laying. One of those years (2003/04) had extensive fast-ice adjacent the breeding colony. In the other 2 years, laying eggs in December resulted in a low crèching probability. It is noteworthy that in the 7 years when reproductive outcomes were not related to the timing of clutch initiation (Fig. 1a), there were very few eggs laid as late as December.

The probability of a chick crèching was related to the CID through a quadratic relationship, both when pooled across years (Fig. 1c, Table 1) and when considered with the CID as a relative date (Fig. 1d, Table 1). There was a clear disadvantage for late laying in both the global and relative models. Model predictions for the global and relative models indicate a high agreement between the proportion of nests with a chick crèching for each 3 d period and model predictions (Fig. 1c,d), although the fit deviated more for earlier CIDs when the models predicted a reduction in reproductive outcomes. In both cases, reproductive success was higher than would be expected, based on the quadratic model for the year with the earliest CID.

Length of incubation and guard periods in relation to CID

The association between CID and incubation length and between hatch date and guard length varied between years (Table 2). CIDs explained 4 to 37% of the variance in incubation length, with a statistically significant association in 9 of the 13 years and negative correlations in all years except one (1993/94) (Table 2). There was a stronger association between the guard length and the hatch dates, with 20 to 84% of the variance in guard length explained by hatch dates (Table 2). This was statistically significant in 10 of the 11 years and negatively correlated in all years. The associations between CID and incubation length and between hatch and guard length were also statistically significant for the global model.

Table 1. Results from quadratic and linear logistic regression models of the probability of a chick crèching from each nest in relation to the date of clutch initiation (CID). Models presented for each year, a global model across years and a relative model across years. The relative model included dates for each nest relative to the mean for each year. Results indicate ANOVA pairwise model comparisons for linear, quadratic and null models. χ^2 tests were used to determine model significance between pairs of models, with the final column indicating the most supported model. n is the number of nests for each year, with significance indicated by *. Data from 1994/95 was not assessed because there were too few chicks crèching, resulting in lack of model convergence. Blank cells indicate that pairwise model comparisons were not required

Year	n	quad vs. lin (χ^2 , p)	lin vs. null (χ^2 , p)	quad vs. null (χ^2 , p)	Supported model
1991/92	134	5.7, 0.017*		6.5, 0.040*	Quadratic
1992/93	161	0.8, 0.372	1.9, 0.173		Null
1993/94	166	1.0, 0.318	2.0, 0.156		Null
1994/95	144	—	—	—	—
1995/96	121	8.7, 0.013*		4.3, 0.038*	Quadratic
1996/97	123	1.9, 0.174	14.1, 0.0002*		Linear
1997/98	96	0.7, 0.396	0.1, 0.735		Null
1998/99	132	2.1, 0.150	1.0, 0.328		Null
1999/00	115	4.2, 0.041*		4.5, 0.108	Null
2000/01	69	0.1, 0.753	5.8, 0.016*		Linear
2001/02	129	<0.001, 0.99	1.6, 0.213		Null
2002/03	141	2.7, 0.101	0.03, 0.856		Null
2003/04	102	6.0, 0.015*		8.8, 0.012*	Quadratic
Global	1633	5.0, 0.025*		26.7, <0.001*	Quadratic
Relative	1633	11.8, 0.001*		24.8, <0.001*	Quadratic

Age and sex effects on CIDs and reproductive outcomes

We found no evidence that the relative CID across years was related to the age of either the females or

Table 2. Linear regression results between CIDs and incubation length and hatch dates and guard length. Linear regressions were conducted for each year and for a global model across years with significance indicated by *. Blank cells indicate that data are not available in those years

Year	Incubation			Guard		
	r	p	n	r	p	n
1991/92	-0.37	<0.001*	101	-0.23	0.03*	87
1992/93	-0.37	<0.001*	118	-0.69	<0.001*	105
1993/94	0.22	<0.001*	161	-0.84	<0.001*	152
1994/95	-0.16	0.07	120			
1995/96	-0.17	0.07	110			
1996/97	-0.11	0.25	106	-0.65	<0.001*	125
1997/98	-0.36	<0.001*	82	-0.32	<0.001*	83
1998/99	-0.04	0.70	110	-0.61	<0.001*	59
1999/00	-0.30	<0.001*	98	-0.42	<0.001*	82
2000/01	-0.36	<0.001*	56	-0.72	<0.001*	92
2001/02	-0.32	<0.001*	108	-0.68	<0.001*	101
2002/03	-0.18	0.04*	127	-0.61	<0.001*	98
2003/04	-0.26	0.02*	79	-0.20	0.28	32
Global	-0.19	<0.001*	1376	-0.41	<0.001*	1016

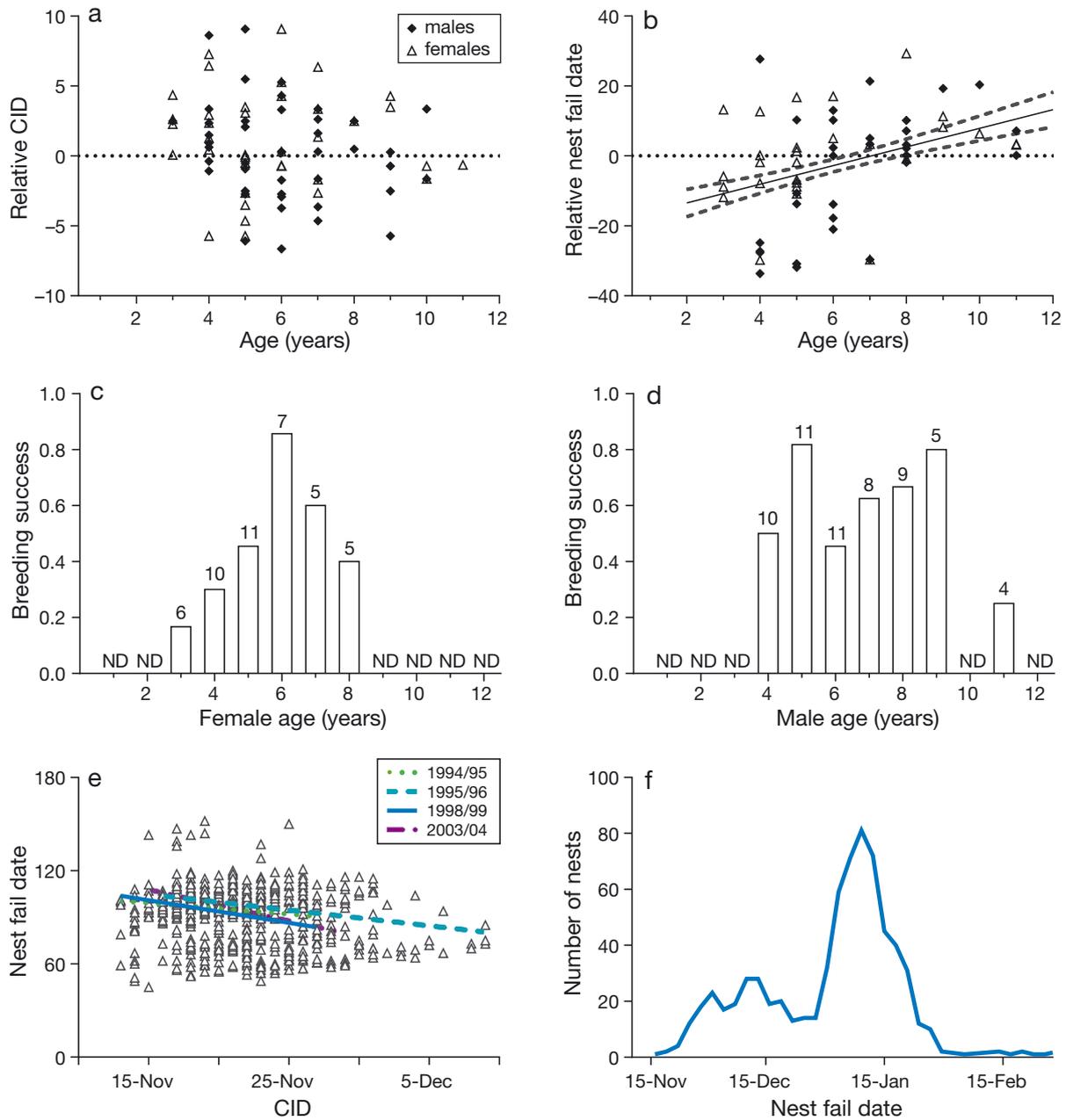


Fig. 2. Relative (a) CIDs and (b) nest fail dates in relation to individual penguin age and sex (line of best fit and standard errors from LME model); mean breeding success in relation to age for (c) females and (d) males (sample size indicated above bars); mean (e) nest fail date in relation to CIDs for all years (line of best fit shown for years with statistically significant linear regression); and (f) distribution of nest fail dates across years. ND: insufficient data

the males (likelihood ratio test: $L = 0.44$, $p = 0.51$ [interaction term], $L = 0.43$, $p = 0.51$ [sex term], $L = 2.30$, $p = 0.13$ [age term]; Fig. 2a). However, for both sexes, the older birds had later relative nest fail dates (likelihood ratio test: $L = 2.20$, $p = 0.14$ [interaction term], $L = 1.76$, $p = 0.18$ [sex term], $L = 10.35$, $p = 0.001$ [age term]; Fig. 2b). In this case, for every year older, nests failed on average 2.7 ± 0.81 d.

Females aged around 6 yr had greater

reproductive success than older or younger birds (Fig. 2c), bearing in mind that we had no data available for birds older than 8 yr to include in this analysis. In contrast, there was no obvious peak for the reproductive success in relation to male age (Fig. 2d).

In 4 of the 13 years (1994/95, 1995/96, 1998/99, and 2003/04), the nest fail dates were statistically significantly earlier for the nests with a later CID (linear regression: 1994/95: $r^2 = 0.03$, $F = 4.112$, $df = 142$, $p =$

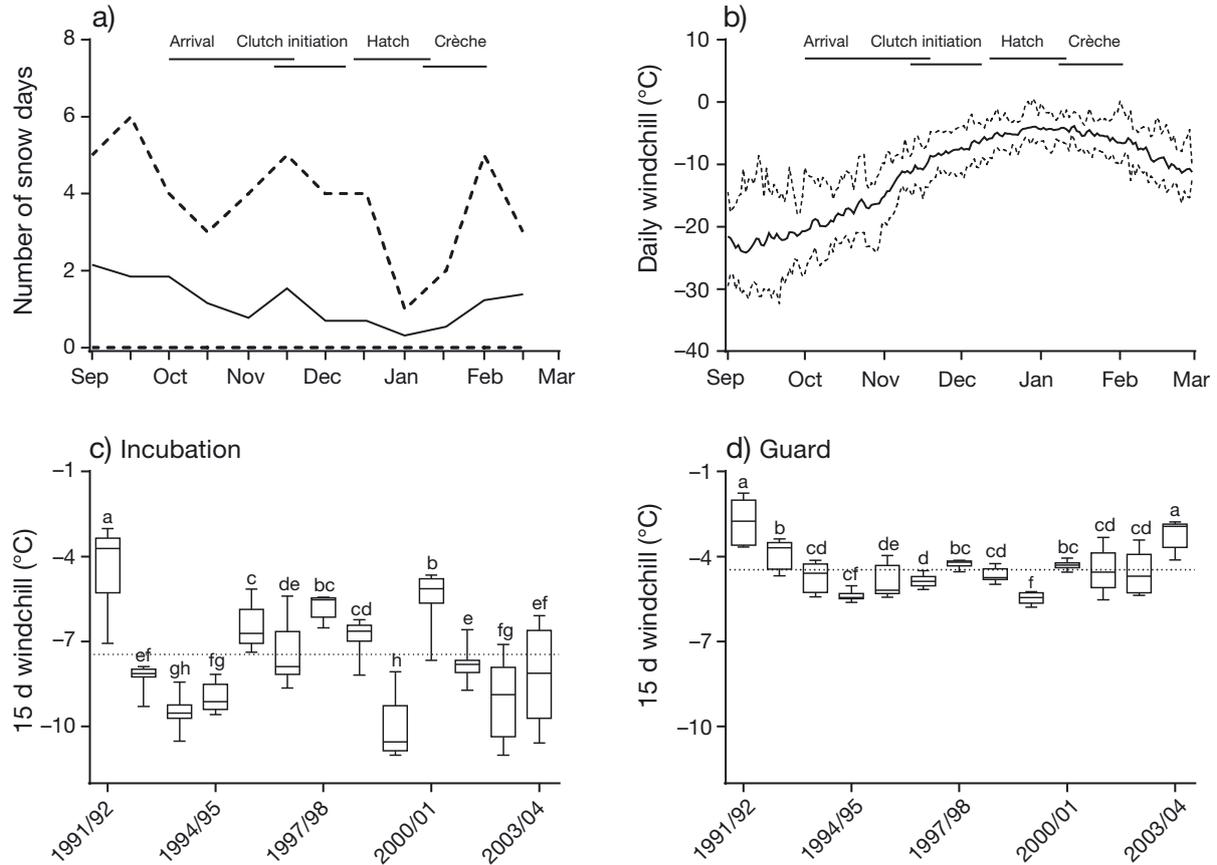


Fig. 3. Intra-annual changes in relation to the breeding phenology for this population as presented by Emmerson et al. (2011) for (a) snow days during each fortnight around the breeding season, (b) daily windchill temperatures during each month around the breeding season; the intra- and inter-annual variability in the mean windchill temperature during the first 15 d of (b) incubation and (c) guard for each nest. Boxes show 25th, 50th and 75th percentiles with whiskers extending to maximum and minimum values. Letters denote significant differences based on Tukey's post-hoc comparisons at $p = 0.05$ significant level. Solid lines in (a) and (b) indicate mean values across years, and dashed lines indicate minimum and maximum values. Dotted lines in (c) and (d) indicate mean values over the 13 yr period from 1991/92 to 2003/04

0.0445; 1995/96: $r^2 = 0.18$, $F = 11.86$, $df = 53$, $p = 0.0011$; 1998/99: $r^2 = 0.05$, $F = 4.63$, $df = 85$, $p = 0.034$; 2003/04: $r^2 = 0.17$, $F = 11.66$, $df = 74$, $p = 0.001$; Fig. 2e). There was 1 main peak for nest fail dates (Fig. 2f), around 10 January, which coincided with the period just after peak chick hatch. The number of nests failing also increased to a lesser extent around 10 to 15 December, when the males were incubating eggs. Although the data presented in this case were pooled across years, they reflect a typical curve in any given year.

Potential environmental drivers of early and late laying success

There were typically few snow days, with an average of 2.4 moderate to heavy snow days per month (Fig. 3a). During each fortnight, there were zero to 6

snow days, with mid-September (pre-arrival) having the most snow days and early January (mid-hatch to early crèche) the least. Arrival and clutch initiation occur during a period when windchill temperatures are rapidly increasing (October to mid-November) (Fig. 3b). During arrival, mean windchill temperatures varied from an average value of -20.73 to -8.63°C . Peak windchill temperatures tended to occur when chicks were hatching and beginning to crèche (early December to mid-January), with windchill temperatures beginning to decrease partway through the crèche period. The warmest windchill temperatures were recorded during the hatch period, with mean windchill temperatures ranging from -5.85 to -3.97°C .

There were statistically significant inter-annual differences in windchill temperatures, during both the first 15 d of incubation and the first 15 d of the guard period for each nest (ANOVA $p < 0.01$),

although not between every year (Tukey's post-hoc comparisons tests $p < 0.05$) (Fig. 3c,d). Inter-annual variation in mean (± 1 SD) windchill temperature during the first 15 d of incubation for each nest varied from $-10.07 \pm 1.0^\circ\text{C}$ in the coldest incubation period (1999/00) to $-4.30 \pm 1.3^\circ\text{C}$ in the warmest incubation period (1991/92) (Fig. 3c). Mean inter-annual variation during the first 15 d of guard varied between $-5.46 \pm 0.2^\circ\text{C}$ (coldest: 1999/00) and $-2.84 \pm 0.8^\circ\text{C}$ (warmest: 1991/92) (Fig. 3d). Intra-annual windchill temperature variation in the first 15 d of incubation (1.08 to 4.50°C) was greater than the intra-annual variation during the first 15 d of the guard period (0.42 to 2.21°C), which is to be expected given the profile of the windchill temperature (which reaches a relatively stable peak during the guard period) (Fig. 3b).

Deletion tests from the full model of windchill in relation to the breeding stage (incubation or guard) and period (early or late egg lay or hatch) showed a significant interaction term between stage and period (likelihood ratio test: $L = 144.74$, $p < 0.0001$). In general, eggs that were laid earlier in the season were generally laid into a colder environment than those that were laid later (mean difference \pm SED = $1.2 \pm 0.14^\circ\text{C}$; Fig. 4a). However, in some years, the difference in windchill temperature between the early and late incubation periods was either small or absent (Fig. 4a). On average, there was no difference in ambient windchill temperature experienced by early and late hatching eggs (mean difference SED = $0.08 \pm 0.07^\circ\text{C}$; Fig. 4a). There was considerable variability in windchill temperatures between years (random effect year: intercept = 1.26, residual = 1.03) and in terms of the difference between early and late nests during egg lay and chick hatch stages.

Unlike the predictable seasonal pattern of increases in temperature, the number of snow days varied considerably, both within a breeding season and between years. As a result of this variation, eggs laid (and chicks hatched) earlier in the breeding season only experienced more snow days than eggs laid (and chicks hatched) later in the season in some

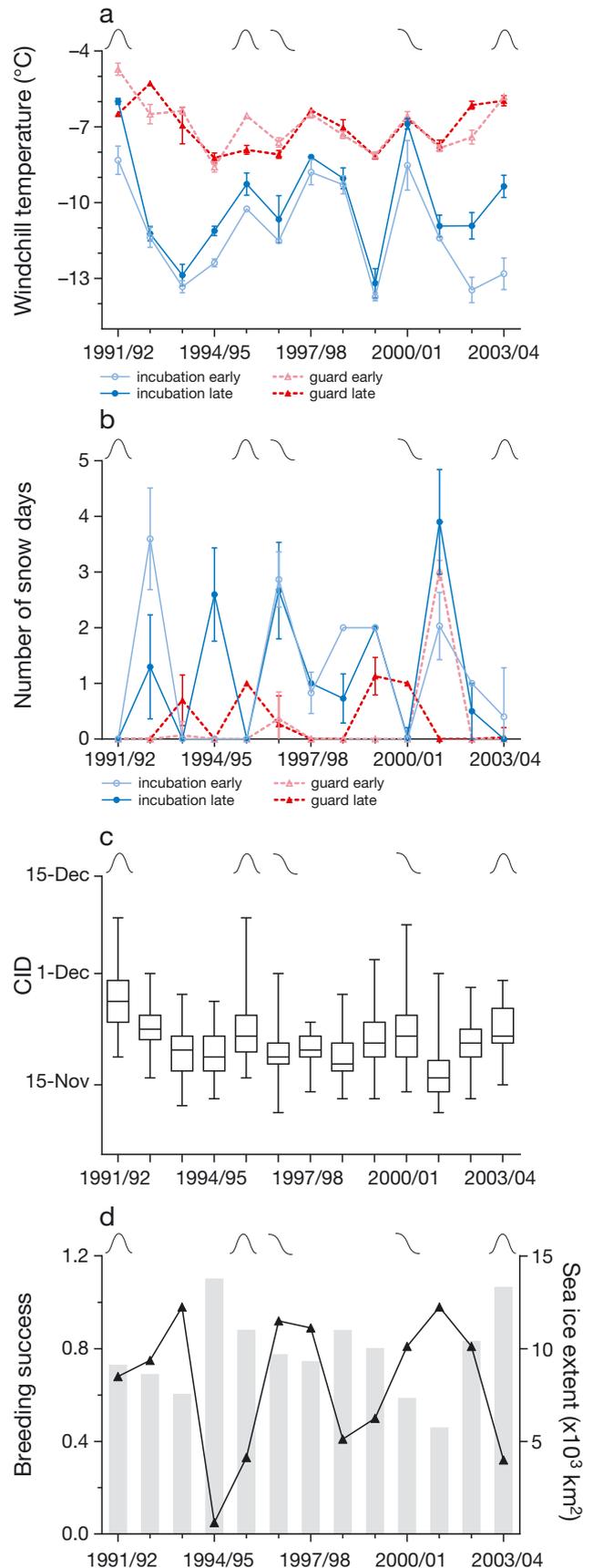


Fig. 4. Inter- and intra-annual variability in the difference in the (a) windchill temperatures and (b) number of snow days experienced by the early and late laying or hatching nests; (c) CIDs (adapted from Emmerson et al. 2011); and (d) inter-annual variation in near-shore sea ice extent (bars) and breeding success (line and solid triangles). Small curves at the top of each panel reflect whether there was an advantage of laying early or on an intermediate date as presented in Fig. 1

years (Fig. 4b). Deletion tests from the full model showed no significant effect of the interaction term (stage \times period: likelihood ratio test: $L = 0.04$, $p = 0.53$), or breeding stage (incubation or guard; likelihood ratio test: $L = 0.38$, $p = 0.54$) but retained period (early or late; likelihood ratio test: $L = 362.15$, $p < 0.0001$) with a significant difference between the number of snow days for early and late hatching nests (mean difference \pm SED = 0.84 ± 0.05 d). There was a large degree of variability in the number of snow days throughout a breeding season and between years (random effects: intercept = 0.64, residual = 0.82).

The years in which the timing of clutch initiation was important for reproductive outcomes (1991/92, 1995/96, 1996/97, 2000/01, and 2003/04) were not aligned with years that had particularly early or late CIDs (Figs. 1b & 4c). Likewise, most of these years were not particularly cold during the first 15 d of incubation or guard (Figs. 3c,d & 4a), nor did they have more or less snow days during the incubation or guard (Fig. 4b). Two of the years in which reproductive success was highest for individuals with an intermediate date for clutch initiation (1995/96 and 2003/04) had extensive sea ice, and hence, the population had low breeding success overall (Fig. 4d). There were insufficient nests with crèching chicks to examine the relationship between reproductive outcomes and timing of CID in 1994/95, which had the most extensive sea ice recorded at Béchervaise Island and was a year with total reproductive failure by the end of the breeding season. The 3 other years (1991/92, 1996/97, and 2000/01) in which timing of clutch initiation was associated with reproductive outcomes had neither high nor low overall breeding success across the population (Figs. 1b & 4d).

DISCUSSION

In this multi-year study, we found that although early breeding for Adélie penguins was advantageous in only 2 years at Béchervaise Island in east Antarctica, late breeding was always disadvantageous. While the benefits of earlier breeding are well known for many seabird species, the confounding cues and constraints from the highly seasonal environment combined with any potential age effects on reproductive success made it unclear whether this advantage would also hold for the Antarctic-breeding Adélie penguin and whether any advantage would be consistent across years. As with studies of common guillemots *Uria aalga* breeding on the

Southeast Farallon Island (Reed et al. 2009), there was an overall reproductive advantage for individuals that bred within ~ 1 wk of the mean CID each year (Fig. 1). However, when considering each year in isolation, that pattern was not always present, and it was difficult to determine why the timing of CID was important for reproductive success in some years but not in others. To some extent, this result is similar to that of the common guillemot, whereby the shape of the relationship varied among years (Reed et al. 2009). However, Reed et al. (2009) were able to clearly identify the conditions under which the timing of CID was important, and the shape of the curve matched the quality of the environment in each year. While our curves were similarly shaped (i.e. flat, advantage for early CID, or advantage for an intermediate CID) (Table 1, Fig. 1), unlike in the Reed et al. (2009) study, there were no governing conditions that we could identify which dictated the shape of this relationship.

Peak nest failure at Béchervaise Island occurred in mid-January (Fig. 2f), which is just after peak hatch. This fits in with the notion that the first 8 d after hatching is a time when the ectothermic chicks are especially vulnerable to unfavourable environmental conditions (Olmastroni et al. 2004), predation by skuas (Young 1994), and starvation if not fed shortly after hatching (Davis 1982). A secondary peak occurred around early to mid-December during the male incubation period. This result matches observations by Davis (1982), where the probability of egg loss was low during early incubation before reaching a peak at 22 to 24 d and again at 36 d. One would expect that if these nests failed primarily due to the tardiness of one partner in returning in time to relieve its mate (Davis 1982), then the older, more experienced birds would fare better as they are better coordinated as a pair (Weimerskirch 1990, Lewis et al. 2006).

In this study, the age of the parents did not influence the CIDs as much as could have been expected given previous studies (e.g. Brooke 1978, Polito et al. 2009, Goutte et al. 2010). However, this may be due to the limited number of known aged birds in our study and the fact that we had to pool data across years to increase the sample size for data analysis (Fig. 2). We found no evidence that the older birds laid eggs earlier. Females in this study reached a peak in reproductive output at 6 yr of age, and older birds had later failing nests. The later failing nests for the older birds could be due to their enhanced foraging abilities, which allow them to attain better condition to withstand a longer fast before nest abandon-

ment, or simply reflects their greater experience with the fasting and provisioning cycle. Our results suggest that the higher reproductive output of nests with earlier CIDs in some years is unlikely to be solely a function of bird age. The age/experience of both parents may also be important for reproductive success, because no matter how skilled one parent is, having a younger/less experienced mate may result in lower reproductive success than if the birds are of a similar age/experience. Unfortunately, we were unable to assess this with our data.

The timing of breeding has been found to influence breeding success in a number of seabird species, including western gulls *Larus occidentalis* (Sydeman et al. 1991), common terns *Sterna hirundo* (Arnold et al. 2004), and common guillemots *Uria aalge* (Lewis et al. 2006). Our results indicate that the Béchervaise Island Adélie penguins had higher reproductive success when their eggs were laid in mid-November, and eggs that were laid in early December were very likely to fail (Fig. 1). The arrival of the penguins at the colony early in the breeding season, when sea ice is at or near its maximum extent (Emmerson et al. 2011), must have been strongly selected for given the short length of the austral summer (Viñuela et al. 1996). Early breeding for this species needs to be balanced against arriving too early when the sea ice is extensive (Emmerson et al. 2011) and weather conditions are more likely to be adverse (Viñuela et al. 1996). In contrast, individuals that arrive or lay eggs too late may not be able to raise a viable chick as they may simply run out of time due to the need to complete moulting before the sea ice reforms (Ainley 2002).

Our study shows clearly that Adélie penguins breed in a temporally varying environment where aspects of the environment, like temperature, have a highly seasonal pattern, and others, such as snow fall, are less predictable (Fig. 3). The fact that Adélie penguins successfully breed in the harsh Antarctic environment across a reasonably wide latitudinal gradient is evidence that they can keep their eggs at temperatures suitable for embryonic development (Ainley 2002). However, relatively few studies have specifically examined the influence of temperature on incubation length for Adélie penguins. Our results indicate that birds which lay their eggs earliest within the breeding season at Béchervaise Island do so when the windchill temperature over the first 15 d can be up to 3.5°C colder than those which lay their eggs latest in the breeding season (Fig. 4a). Furthermore, there was a longer incubation period for the eggs in those nests, which may be related to the

colder windchill temperatures earlier in the breeding season. However, the confounding nature of a seasonal change in the environment, along with differences associated with the timing of egg lay, makes it difficult to tease out pure temporal correlation compared with a causal effect. It is also possible that colder conditions may have imposed additional thermoregulation costs (Chappell et al. 1989) or had an impact that would have been apparent in chick growth rates rather than their survival.

Declines in the length of the guard period as the breeding season progresses have been reported for Adélie penguins previously (e.g. Taylor 1962, Ainley 2002), and our results are consistent with this (Table 2). During the later stages of the guard period, chicks persistently beg for food (Young 1994) and the adults lose significant body condition (Clarke et al. 2006), which can influence when the chicks are left unguarded. However, chicks that are the first to crèche often end up on the edge of the breeding group, where they are vulnerable to attacks by skuas (Young 1994). The quality and condition of the provisioning adults and/or the condition of the chicks for several penguin species are thought to influence the length of the guard period and the effort that the parents put into provisioning their brood (Moreno et al. 1997, Penteriani et al. 2003, Ballard et al. 2010). In this regard, birds that lay earlier in the season may be higher quality parents, which are typically more efficient foragers (Lescroël et al. 2010) who can withstand longer periods of fasting and can therefore guard their chicks for longer (Viñuela et al. 1996).

Potential environmental drivers of early and late laying success

Adélie penguins are well adapted to the harsh environment in which they live, and, like other Antarctic seabirds, their specific breeding strategies are likely to have been moulded by their interactions with the Antarctic environment (Chastel et al. 1993). Whilst penguins are well equipped to deal with environmental challenges, including short-term events such as storms, longer-term events such as the late retreat of the sea ice can affect the body condition of the parents (Olmastroni et al. 2004) and breeding success (Emmerson & Southwell 2008). Due to the relatively synchronous breeding schedule of Adélie penguins, the entire population can experience relatively similar environmental conditions or a similar prey field, and hence, all nests across the breeding site can be affected simultaneously. For example, the

timing of clutch initiation was not associated with reproductive outcomes in the year when extensive sea ice remained around the colony, providing poor provisioning conditions (1994/95), or in years with overall high breeding success (1993/94 and 2001/02) (Figs. 1a & 4d).

It is likely that when conditions are extremely unsuitable or particularly favourable, the influence of the timing of clutch initiation or age and experience is less relevant than in other years. The variability between years in the importance of timing of breeding on reproductive outcomes in relation to environmental conditions is consistent with other seabird species (Reed et al. 2009). Our results show that the conditions that the penguins and their chicks experience can be quite different due to the timing of egg lay or hatch within a year, although it is unclear whether this difference is demographically important. It is clear from our results and previous studies that there are a number of factors, ranging from environmental conditions to food availability and the age/experience of the parents, that can all influence the survival of eggs and chicks. Additional information on snow persistence, snow depth or storm events, which can result in egg and/or chick loss (Olmastroni et al. 2004), may have also been informative in this case.

Our study has clearly shown that there were benefits for earlier reproduction in some years and disadvantages for breeding late. Furthermore, because late laying was disadvantageous, it could represent a squeeze point for Adélie penguins, especially considering the trend towards later laying reported for Adélie penguins breeding at Dumont d'Urville in East Antarctica (Barbraud & Weimerskirch 2006). Understanding whether the benefits of early laying or the disadvantages of late laying hold across the geographic range of breeding Adélie penguins will allow a better understanding of the potential impacts of shifts in the penguins breeding phenology on reproductive outcomes as well as the potential environmental influences on the timing of the various phases of their phenology throughout their breeding cycle.

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