

The effect of hatching date on parental care, chick growth, and chick mortality in the chinstrap penguin *Pygoscelis antarctica*

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(With 2 figures in the text)

We studied the effect of hatching date on breeding performance (chick growth and mortality) and phenology (crèching and fledging ages) of the chinstrap penguin during three years. The year affected every variable considered, probably due to pack-ice persistence and food availability differences between years. Hatching date had slight or no effect on mortality and early growth, but was negatively correlated with crèching age, which, in turn, was positively related to final size. The decision to leave the chicks unguarded does not seem to be based on the condition of the chicks, but on that of adults. Fledging age was negatively correlated with hatching date, and this effect was more marked in the year with poor growth performance. Given the short time available for breeding in Antarctica, there must be conflicting pressures between investing in feeding chicks and advancing the period of premoult resource storage, this explaining the strong relationship between hatching dates and subsequent phenological events (crèching and fledging). In this kind of study, it may be important to remove the effect of inter-year variation before assessing the possible effects of other variables.

Introduction

Birds breeding in polar regions experience short breeding seasons. Some penguin species breeding in Antarctica have to compress a complete breeding cycle in a period of barely three months. Selection for early breeding must thus have been very strong in these species, balanced, of course, by countervailing selection for not breeding so early that adverse conditions preclude successful incubation. Any delay in the commencement of breeding may retard the onset of moult, with possible negative consequences. Late breeders may be young or inexperienced individuals (Ainley, LeResche & Sladen, 1983; but see Williams, 1990). Negative effects of late breeding on breeding success have been reported in studies of Adélie *Pygoscelis adeliae* (Taylor, 1962; Spurr, 1975) and gentoo *P. papua* penguins (Bost & Jouventin, 1991), but not in others (Davis & McCaffrey, 1986; Williams, 1990). Breeding performance of Antarctic penguins shows high year-to-year variability (e.g. Williams, 1990; Bost & Jouventin, 1991), so, before assessing the effect of laying date on breeding success, it must be important to remove the variance explained by interannual variation, a fact not always considered in this kind of study. Also,

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crèching and fledging ages have been shown to be variable between years (Williams, 1990), and to depend on hatching date (Taylor, 1962).

In the present study, we have focused on the variation in the breeding biology of the chinstrap penguin *Pygoscelis antarctica*, the least studied of the Antarctic penguins. Hatching dates, crèching ages and fledging ages have been recorded during three years, and chick growth and mortality have been quantified in a chinstrap rookery on Deception Island, South Shetlands. The aim has been to explore interannual variability in these parameters and to detect year-independent associations between hatching date and chick growth, patterns of parental care, and breeding success.

Methods

The study was conducted at the Vapour Col chinstrap rookery (20,000 breeding pairs) on Deception Island, South Shetlands (63°00'S, 60°40'W) during the austral summers of 1991/92, 1992/93, and 1993/94 (hereafter 1991, 1992, and 1993, respectively). In the first breeding season, we undertook an intensive study of chick growth and mortality on a small sample of families, while in the next two years we concentrated on fewer sequential measurements, so that the number of nests surveyed could be substantially increased. At the end of incubation, we marked 30 nests in 1991, 99 nests in 1992, and 75 nests in 1993 with numbered sticks. Marked nests were part of a large colony in 1991 (> 500 nests), while in the other 2 years we studied the same colony of 150 pairs. Both colonies were separated by 1500 m. Nests occupied different locations with respect to the colony edge. Only nests with the modal clutch size of 2 eggs were included. Adults were banded with metal flipper bands (standard 34 × 17 mm penguin bands produced by Lambournes Ltd., Solihull, UK). The presence of banded individuals in the study colony in 1993 was noted. To study the interannual constancy in hatching date and crèching age, we used the same paired individuals breeding in the years 1992 and 1993.

We tried to visit nests daily before hatching of the chicks. When chicks hatched between visits which were more than one day apart, we estimated hatching dates from a regression model of flipper length (mm) on age ((no. of days after hatching): flipper = 30.3 + 3.9 × age, $r = 0.999$). As hatching is normally asynchronous in this species (modal asynchrony = 1 day, Moreno *et al.*, 1994), we used the date of the first chick to hatch as the hatching date of the brood. Siblings were marked at hatching below the flipper with an indelible felt pen for individual recognition, and weighed and measured at 14–15 days of age. On periodic visits after that age (daily whenever possible), we recorded if chicks were accompanied by a guarding parent or if they had been left alone. The difference between the first date on which chicks were seen without their parent and hatching date will be hereafter called the crèching age of the family. Before the formation of crèches, chicks were banded with numbered metal flipper bands. Capturing each chick at a specific age in crèches involves daily visits during a prolonged period, with the attending disruption due to chick localization and capture. To avoid this type of disturbance, all banded chicks were weighed and measured during a few round-ups at dates selected to try to catch as many of them as possible at the age of 45 days. The age of the different broods differed due to the non-selective capture method. Sample size was thus reduced to those broods in which average chick age ranged between 43 and 48 days. This age was referred to as 45 days. There was no significant difference between years in the mean age of the chicks captured in crèches ($P > 0.1$).

When analysing chick growth, we have not used growth curve analysis because of the low number of sequential measurements (ages of 15 and 45 days). Instead, the increment in measurements was divided by the number of days elapsed as a rough estimate of growth rate before 15 days of age, when growth rate is nearly linear. To estimate growth after crèching, we have considered chick mass and flipper length at 45 days of age (there was no correlation between mass or flipper length and age for the range of 43–48 days, $P > 0.1$). Owing to our absence from the rookery on certain days during the fledging period, the presence/absence of some chicks could not be ascertained with enough precision to allow estimation of fledging dates. Fledging age refers to the oldest age at which a certain banded chick was observed in the study colony.

TABLE I

Breeding parameters of chinstrap penguins at Deception Island during three consecutive reproductive seasons. \bar{x} : mean; S.E.: standard error; n : sample size. Values under the same line are not significantly different ($P > 0.05$ in Tukey HSD *a posteriori* tests). Date 1 = December 1

| | 1991 | | | 1992 | | | 1993 | | |
|-------------------------------|-----------|-------|-----|-----------|-------|-----|-----------|-------|-----|
| | \bar{x} | S.E. | n | \bar{x} | S.E. | n | \bar{x} | S.E. | n |
| Hatching date | 24.6 | 0.45 | 30 | 22.3 | 0.24 | 99 | 24.2 | 0.33 | 75 |
| Guard phase growth rates | | | | | | | | | |
| Mass (g/day) | 52.9 | 2.46 | 30 | 68.9 | 0.84 | 99 | 66.2 | 0.99 | 66 |
| Flipper length (mm/day) | 5.9 | 0.13 | 30 | 6.6 | 0.05 | 99 | 6.1 | 0.06 | 66 |
| Crèching age (days) | 27.9 | 0.72 | 30 | 35.0 | 0.32 | 99 | 30.3 | 0.36 | 75 |
| Body mass (g) at age 45 | 2453.9 | 82.39 | 19 | 3201.0 | 32.67 | 84 | 3372.4 | 73.81 | 31 |
| Flipper length (mm) at age 45 | 182.2 | 2.13 | 19 | 191.5 | 0.61 | 84 | 191.6 | 0.86 | 31 |
| Chicks per nest at age 45 | 1.5 | 0.11 | 30 | 1.6 | 0.06 | 99 | 1.87 | 0.04 | 75 |
| Fledging age (days) | 57.4 | 1.19 | 7 | 53.1 | 0.28 | 29 | 55.0 | 0.58 | 13 |

The mortality of marked or banded chicks due to parental desertion, starvation, or skua (*Catharacta skua*) predation (Moreno *et al.*, 1994) was recorded on each visit. The surroundings of the study colonies were carefully searched for dead chicks. According to our experience, skuas consume chicks of crèche age close to the natal colonies and always leave skeletons and flippers untouched. In 1991, we checked the effects on chick mortality of our frequent visits to the studied nests in a distant part of the colony which was only visited at weekly intervals. No significant effect of our disturbance on chick survival was noted (Moreno *et al.*, 1994). Chick survival was square root transformed for parametric analyses.

Statistical analyses employed were Pearson correlations, and one-way ANOVAs, ANCOVAs and 2-way ANCOVAs, after checking for normality and homoscedasticity. When not presented, interactions between covariates and factors were not significant.

Results

Hatching date, pooling years, ranged from 15–31 December (median date: 22 December). Hatching dates significantly differed among years (ANOVA, $F_{2,201} = 15.69$, $P < 0.001$, 13.5% of the variation accounted for by year; Table I), mainly due to the early hatching dates in 1992 (Table I). Therefore, in the subsequent analyses, we test the effect of hatching date on the remaining dependent variables controlling for the effect of year.

Hatching dates of the same 37 pairs breeding consecutively in 1992 and 1993 were highly correlated ($r = 0.58$, $P < 0.001$). The same result was obtained for crèching age for the same years ($r = 0.44$, $P = 0.008$), but the correlation disappeared when removing the effect of hatching date on crèching age ($r = 0.24$, $P = 0.17$).

Mass growth rate in the guard phase was affected by year ($F_{2,191} = 32.38$, $P < 0.001$, 25.3% of the variation accounted for by year; Table I), but not by hatching date (ANCOVA, $F_{1,191} = 0.04$, $P = 0.84$). Flipper length growth rate was also significantly affected by year ($F_{2,191} = 18.54$, $P < 0.001$, 15.9% of the variation accounted for by year; Table I), and was negatively correlated with hatching date ($F_{1,191} = 5.23$, $P = 0.02$, standardized regression coefficient = -0.15 ; year by hatching date interaction: $F_{2,189} = 2.99$, $P = 0.06$).

TABLE II

ANCOVA of crèching age on year, with hatching date, chick mass, and flipper length growth rates during the guard phase as covariates

| | F | d.f. | P |
|-------------------------------|-------|-------|---------|
| Year | 37.58 | 2,189 | < 0.001 |
| Covariates | 21.34 | 3,189 | < 0.001 |
| Hatching date | 60.99 | 1,189 | < 0.001 |
| Mass growth rate | 1.06 | 1,189 | 0.304 |
| Flipper length growth rate | 0.24 | 1,189 | 0.625 |
| Interaction year × Covariates | 1.57 | 6,183 | 0.158 |

Crèching age different among years (Tables I and II; 22.9% of the variation accounted for by year), and was strongly and negatively correlated with hatching date (standardized regression coefficient = -0.41 ; Fig. 1), but it was not significantly related to mass and flipper length growth rates during the guard phase (Table II). The slopes of the regressions of crèching age on hatching date did not differ significantly among years (Fig. 1, $F_{2,198} = 1.41$, $P = 0.25$). Body mass at age 45 (Table I) significantly differed among years ($F_{2,130} = 33.16$, $P < 0.001$, 34.4% of the variation accounted for by year), and was positively related to crèching age ($F_{1,130} = 10.25$, $P = 0.002$; standardized regression coefficient = 0.32 ; year by crèching age interaction: $F_{2,128} = 0.11$, $P = 0.90$), but not with hatching date ($F_{1,130} = 2.62$, $P = 0.11$). Flipper length at the same age (Table I) also significantly differed among years ($F_{2,130} = 9.49$, $P < 0.001$, 9.1% of the variation accounted for by year), but was neither correlated with hatching date nor with crèching age ($F_{1,130} = 0.18$, $P = 0.68$ and $F_{1,130} = 2.74$, $P = 0.10$, respectively).

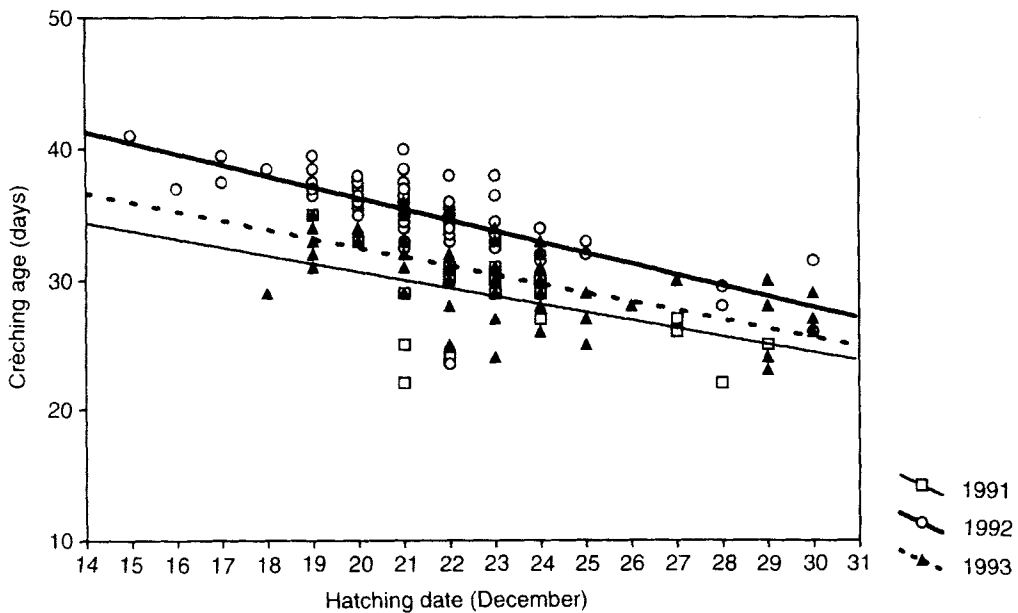


FIG. 1. Variation of crèching age (ca) with hatching date (hd) in three different years. Regression equations for the three years are: 1991: $ca = 43.1 - 0.62 \times hd$, $R^2 = 0.26$, $n = 30$, $P = 0.004$; 1992: $ca = 53.0 - 0.83 \times hd$, $R^2 = 0.56$, $n = 99$, $P < 0.001$; 1993: $ca = 46.3 - 0.69 \times hd$, $R^2 = 0.39$, $n = 75$, $P < 0.001$.

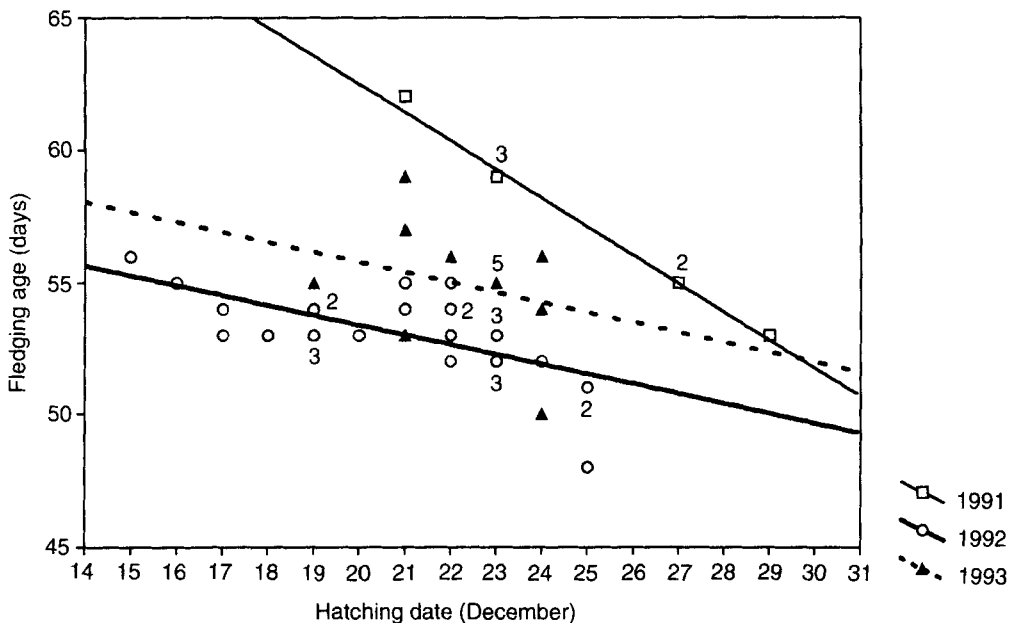


FIG. 2. Variation of fledging age (fa) with hatching date (hd) in three different years. Figures near dots show the number of overlapping points. Regression equations for the three years are: 1991: $fa = 83.8 - 1.07 \times hd$, $R^2 = 0.99$, $n = 7$, $P < 0.001$; 1992: $fa = 60.9 - 0.38 \times hd$, $R^2 = 0.46$, $n = 29$, $P < 0.001$; 1993: $fa = 63.4 - 0.38 \times hd$, $R^2 = 0.10$, $n = 13$, $P = 0.287$.

Chick survival until the age of 45 days (Table I) differed significantly between years ($F_{2,198} = 7.61$, $P = 0.001$, 7.1% of the variation accounted for by year), being higher in 1993 than in the other two years (Table I). Hatching date did not significantly vary with chick survival ($F_{1,200} = 0.09$, $P = 0.76$).

Fledging age varied significantly between years ($F_{2,43} = 15.29$, $P < 0.001$, 47.1% of the variation accounted for by year), and was negatively correlated with hatching date ($F_{1,43} = 36.24$, $P < 0.001$; Fig. 2) and crèching age ($F_{1,43} = 4.09$, $P = 0.049$), the effect due to hatching date being stronger as shown by the standardized regression coefficients (hatching date = -0.78 , crèching age = -0.26). The interactions between year and each covariate were significant (hatching date: $F_{2,43} = 5.34$, $P = 0.008$; crèching age $F_{2,43} = 4.75$, $P = 0.014$), showing that the effects of hatching date and crèching age on fledging age varied between years (Fig. 2). For the same hatching date, chicks in 1991 fledged at older ages than in the other two years, fledging age decreasing with hatching date at a higher rate in 1991.

Discussion

Hatching dates in our population were, to our knowledge, the earliest recorded for the species (Lishman, 1985: 8–24 January in a more northerly location; Trivelpiece, Trivelpiece & Volkman, 1987: 22 December–3 January at a similar latitude; Conroy, Darling & Smith, 1975: first hatching on 26 December in a more northerly location). These early hatching dates indicate early laying dates that may be related to the special features of our study area, as it is a volcanic island.

Also, the Vapour Col rookery is located near the main geological fracture system of the island. The ground of the rookery showed thermal anomalies with temperatures as high as 12°C at 10 cm below ground (J. L. Díez, pers. comm.). One of the main factors determining the start of breeding in pygoscelid penguins is the timing of appearance of snow/ice-free ground (Williams, 1990), and this could occur especially early in our rookery.

Almost every long-term study on breeding performance of gentoo and Adélie penguins has reported important year-to-year variation in laying dates, chick growth, or breeding success (Williams, 1990; Williams & Croxall, 1991; Bost & Jouventin, 1991). Annual variation of laying/hatching dates in pygoscelid penguins has been related to two different factors (e.g. Trivelpiece *et al.*, 1987): (1) persistence of pack ice: long spring-summer persistence of pack ice may delay the arrival to the rookeries and consequently laying dates; (2) food availability: in years of low food availability the penguins may need longer time to store pre-laying reserves. In our study, 1991 was clearly a 'bad' year, with late hatching and poor breeding performance, while in the following two years there was a good breeding performance with respect to chick growth, despite the difference in hatching dates. In 1991, there was a longer persistence and greater abundance of pack ice on the sea than in the other two years (pers. obs.). Pack ice persistence has been shown to have a strongly detrimental effect on breeding success in this species (Conroy *et al.*, 1975; Volkman, Presler & Trivelpiece, 1980; Fraser *et al.*, 1992; Croxall, 1992). Hatching dates during 1993 were as late as during 1991, but 1993 was a year of good breeding performance. Probably a combination of both factors have been acting during our three-year study period: long persistence of ice and low food availability during 1991 (similar to results reported by Croxall, 1992), but only long persistence of ice (or snow cover) not related to low food availability during 1993 (delayed laying not related to poor breeding success as shown in several studies: Williams, 1990; Williams & Croxall, 1991; Bost & Jouventin, 1991).

If early breeding is advantageous, we would expect that consistently late breeding pairs would be of a lower 'quality' and thus show a poorer breeding performance than early pairs. That breeding dates are consistent for pairs is shown by the significant repeatability of hatching dates of the same pairs from year-to-year (also found in Adélie penguins, Spurr, 1975). Hatching date did not markedly affect early chick growth or mortality. This suggests that early and late pairs devote the same amount of resources to their chicks at the initial stages of chick care. The chicks of late pairs crèched at a younger age; early growth of chicks was not related to crèching age; and the chicks were left unguarded at an older age in the 'good' year (1992). These results suggest that: (1) the decision of leaving the chicks unguarded is taken by the adults and is not related to the growth or age of the chicks (Williams, 1990); (2) high 'quality' adults leave the chicks unguarded at older ages (Taylor, 1962); and (3) the decision to leave the chicks unguarded is probably based on the condition of the adults, those in better condition delaying the decision.

Final mass of the chicks (at 45 days of age) was positively correlated with crèching age, but not with hatching date. Also, late crèching chicks fledged earlier. So, although the time when both adults gathering food simultaneously was delayed for late crèching families, they attained a better growth performance. This indicates the existence of important 'quality' differences between late and early hatching pairs. Feeding conditions of chicks left unguarded is hazardous: they must find arriving adults in time or become involved in feeding chases with uncertain results (Bustamante, Cuervo & Moreno, 1992). Consequently, the feeding of chicks left unguarded earlier could be more irregular than that of chicks guarded by their parents. This could explain why the age at which the chicks are left unguarded may be more important in determining final growth rate than hatching date.

The chicks of late-hatching pairs fledged at younger ages (independently of the effects of year and crèching age), and this effect was more marked in the 'poor' year (1991). In a year of poor breeding performance (presumably associated with low food availability), chicks may require more time to attain fledging condition, but parents of late-hatched chicks may reduce investment at the end, thus inducing them to fledge at a similar age as in years of higher food availability. The advancement of fledging of late-hatched chicks can be explained in two ways. First, fledging is more synchronous than hatching or crèching. This may reflect a contagious 'social' effect, i.e. when the majority of chicks have departed from the colony, the rest may be induced to precipitate fledging, thus truncating the distribution of fledging dates. Secondly, it may reflect the restriction of breeding time in Antarctica. After fledging of their chicks, adult penguins must moult, and they must do it before the arrival of autumn. There must be conflicting pressures between feeding chicks and advancing the period of premoult reserve storage, and, consequently, a clear-cut limit to the extension of the breeding season. After a critical time (perhaps indicated by changes in daytime length), and given that penguins are long-lived birds with several opportunities to breed, they may stop the investment in the current brood to divert energy to moulting, thus favouring their own survival (Bost & Jouventin, 1991). This must be especially important for chinstrap penguins, as they are the pygoscelid with the latest laying dates (Trivelpiece *et al.*, 1987). The laying periods of gentoo and chinstrap penguins is reduced as latitude of breeding sites increases (Conroy *et al.*, 1975; Bost & Jouventin, 1990), this probably reflecting the shorter time available for breeding at higher latitudes. High 'quality' chinstrap penguins might start breeding as early as possible, but the factors limiting an earlier start of breeding remain to be explored (timing of availability of snow/ice-free nesting sites, avoiding competition with other pygoscelid species, or existence of handicaps for too early breeders).

There are contradictory results about the effect of laying/hatching dates on the breeding performance of pygoscelid penguins, some studies showing negative effects of late laying/hatching (Spurr, 1975; Bost & Jouventin, 1991), while others do not show any effects (Davis & McCaffrey, 1986; Williams, 1990). Our results show that late hatching has negative consequences for chicks, owing to being left unguarded and having to fledge at younger ages. Being left unguarded earlier implies slower growth, probably a reflection of parental quality. In future studies of breeding success, it may be important to remove the effect of interannual variation in breeding parameters.

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