Polar Biol (1994) 14: 21-30

ORIGINAL PAPER

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Hatching asynchrony, sibling hierarchies and brood reduction in the Chinstrap penguin *Pygoscelis antarctica*

Received: 15 September 1992 / Accepted: 24 May 1993

Abstract We studied patterns of chick growth and mortality in relation to egg size and hatching asynchrony during two breeding seasons (1991 and 1992) in a colony of chinstrap penguins sited in the Vapour Col rookery, Deception Island, South Shetlands. Intraclutch variability in egg size was slight and not related to chick asymmetry at hatching. Hatching was asynchronous in 78% (1991) and 69% (1992) of the clutches, asynchrony ranging from 1 to 4 days (on average 0.9 in 1991 and 1.0 days in 1992). Chicks resulting from one-egg clutches grew better than chicks in families of two in 1991. In 1992, single chicks grew to the same size and mass at 46 days of age as chicks of broods of two, suggesting food limitation in 1991 but not in 1992. In 1991, asymmetry between siblings in mass and flipper length was significantly greater in asynchronous than in synchronous families during the initial guard stage, but these differences disappeared during the later crèche phase. In 1992, asymmetry in body mass increased with hatching asynchrony and decreased with age. Only the effect of age was significant for flipper length and culmen. Asymmetries at 15 days were similar in both years, but significantly lower in 1992 than in 1991 at 46 days of age. There were relatively frequent reversals of size hierarchies during both phases of chick growth in the two years, reversals being more common in 1991 than in 1992 for small chicks. In 1991, survivors of brood reduction grew significantly worse than chicks in non-reduced broods. In both years, chicks of synchronous broods attained similarly large sizes before fledging as both A and B chicks of asynchronous broods. In 1991, chick mortality rate increased during the guard stage due to parental desertions, decreased during the transition to crèches (occurs at a mean age of 29 days) and returned to high constant levels during the crèche stage, when it is mostly due to starvation (in total 66% of hatched chicks survived to fledging). In contrast, in 1992, mortality was relatively high immediately after hatching and almost absent for chicks older than 3 weeks (87% of chicks survived to fledging). Mortality affected similarly one- and two-chick families. In 1991, asynchronous families suffered a significantly greater probability of brood reduction than synchronous families, but this probability was not significantly related to degree of asymmetry between siblings. No association between asynchrony and mortality was found in 1992. These results show that there is food limitation in this population during the crèche phase in some years, that asynchronous hatching does not facilitate early brood reduction and that it does not ensure stable size hierarchies between siblings. Brood reduction due to starvation is not associated to prior asymmetry and does not facilitate the survival or improve the growth of the surviving chick. Asynchronous hatching may be a consequence of thermal constraints on embryo development inducing incubation of eggs as soon as they are laid.

Introduction

Food supply can limit growth and chick survival in penguins (Taylor and Roberts 1962; Ainley and Schlatter 1972; Boersma 1976, 1991; Cooper 1977; Williams 1980). Williams and Cooper (1984) have suggested that both egg-size differences and hatching asynchrony can

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facilitate brood reduction in penguins, which show both facultative brood reduction and obligate chick loss (Lamey 1990). Hatching asynchrony in altricial birds has been proposed as a strategy to favour the creation of size hierarchies between siblings which can facilitate brood reduction in cases of food shortage (Lack 1947, 1954; Ricklefs 1965; Howe 1976, 1978; O'Connor 1978; Mock 1984). In the context of this hypothesis, egg-size differences have been considered as a means of adjusting the asymmetries resulting from hatching asynchrony (Howe 1976, 1978; Slagsvold et al. 1984). Other adaptive explanations for hatching asynchrony have also been proposed (Magrath 1990; Amundsen and Slagsvold 1991).

Despite extensive descriptive literature on penguin breeding biology, few studies have been specifically undertaken to explore the importance of competitive asymmetries for differential chick survival (but see Boersma 1991; Seddon and Van Heezik 1991; Williams and Croxall 1991). In his review of brood reduction in penguins, Lamey (1990) noted that according to the scarce information available, Chinstrap penguins *Pygoscelis antarctica* represented an intriguing contrast to the two other members of the genus, the Adélie *P. adeliae* and the Gentoo penguin *P. papua*. Chinstrap penguins apparently lack both asynchronous hatching and the asymmetries between eggs or chicks that might facilitate brood reduction. However, he suggested that further field data were needed to confirm this suggestion.

In this study we analyze the relationship between egg size asymmetry, hatching asynchrony, sibling size hierarchies and chick mortality in the Chinstrap Penguin. If food was a limiting factor affecting chick growth and survival, we should expect growth asymmetries between siblings due to competition or parental preference (Cooper 1977; Taylor and Roberts 1962; Boersma 1991). We would also predict that single chicks might grow faster than those of two-chick broods (Cooper 1977; Taylor and Roberts 1962; Ainley and Schlatter 1972; Boersma 1991). If food limitation is present and asynchronous hatching or egg size differences produce initial asymmetries between siblings, we would expect a relationship between sibling asymmetries and differential chick survival. This assumes that hatching asynchrony or resource apportionment between eggs function as brood reduction mechanisms. These predictions were tested observationally in a chinstrap rookery in the South Shetlands during two contrasting breeding seasons. Patterns of chick growth and development and chick mortality were compared between seasons to ascertain reproductive success and infer relative food availability for the chicks. We would predict that mechanisms favouring brood reduction would operate more clearly in the less favourable year.

Methods

The study was conducted at the Vapour Col chinstrap rookery (20000 breeding pairs) on Deception Island, South Shetlands (63°00′ S, 60°40′ W) during the austral summers of 1991/92 and 1992/93 (hereafter 1991 and 1992 respectively). Both seasons were different with respect to indications of food availability close to the rookery. In 1992, we frequently observed whales and large aggregations of petrels and penguins feeding close to the shore. This was not so in 1991. In the first breeding season, we undertook an intensive study of chick growth on a smaller sample of families, while in 1992 we concentrated on a reduced number of sequential measurements but increased substantially the number of nests. Both study seasons provided the opportunity of testing yearly consistency in asynchrony-asymmetry-survival patterns in relation to inferred variability in food availability.

At the end of incubation, we marked 51 nests in 1991 and 120 nests in 1992 with numbered sticks on parts of larger colonies (more than 500 pairs in 1991, 150 pairs in 1992), including nests which differed in locations with respect to the colony edge. In 1991, nests were randomly selected with respect to clutch size (thus including nests with one egg). In 1992, we included only nests with two eggs (the modal clutch size in this species) to reduce sources of variability in reproductive success.

We tried to visit nests daily before hatching of the chicks. In 1991, we measured egg length and maximum width to the nearest 0.1 mm with digital calipers. Egg volume was calculated according to the formula: Vol. = 0.5 (length × width^2) (Reid 1965; Lishman 1985). Eggs were numbered with an indelible felt marker. The order of laying of eggs was unknown, as we arrived to the study area after completion of laying.

In 1991, chicks were weighed and measured (flipper length and culmen) on the first visit after hatching (chicks partly contained in the eggshell were not measured). If one day had elapsed since the last visit, the chick was considered to have hatched on the day on which it was found fully hatched (day 1 for chicks). Thus, chick age was estimated with a precision of one day. If more than one day (2–3 days) had elapsed since the last visit, chick age was estimated by comparing mass and measurements with those of chicks of known age. If the second chick (B-chick) had not hatched completely (fully or almost out of the egg) on the visit when the A-chick was found to have hatched, hatching was considered to be asynchronous. In some cases asynchrony could not be determined due to our absence from the colony on the days when both chicks hatched. Asynchrony was estimated in 16 cases with a precision of one day, and for 32 nests we were only able to know if hatching had been synchronous or not. In the case of hatching asynchrony, both siblings were weighed and measured on the first visit with both chicks fully hatched (day 1 for broods). In 1992, we ascribed hatching to the first date on which the chick was observed fully or partially out of the egg (cracks and holes in eggs and pipping not considered). 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 (number of days after hatching); flipper = 30.3 + 3.9 × age, r = 0.999 based on data from 1991. Asynchrony was estimated with a precision of one day in 55 nests.

In 1991, siblings were marked on the head with an indelible felt pen for individual recognition, and weighed and measured at weekly intervals until the age of one month (at brood ages or mean age of siblings of 7, 14, 21 and 28 days). At that age, crèches begin to form, making it difficult to follow individual chicks without creating major disturbances in the colony. Therefore, chicks were banded with numbered metal flipper bands when 28 days old (standard 34 x 17 mm penguin bands produced by Lambournes Ltd., England, Solihull) and later weighed and measured during two round-ups of all banded chicks. The age of the different broods on these two occasions varied due to the nonselective character of the capture method. Therefore, we have used the mean brood age of all banded chicks during these round-ups (47.4 ± 2.4 days, $n = 29$ broods, range $= 43$–52 and 57.7 ± 2.2 days, $n = 9$ broods, range $= 54$–60 days) in data analysis. When comparing different groups of chicks for those two ages, we have checked for brood age differences between groups before the analyses, without finding statistical differences in average age. In 1992, individually known chicks (initial markings with felt pens and banding with 28 days of age) were weighed and measured at exactly 15 and approximately 46 (45.9 ± 1.8 days, range $= 42$–48, $n = 108$ broods) days of age, making these measurements comparable with those taken at 14 and 47 days in 1991 (the ages will be referred to as 15 and 46 days hereafter).

When analyzing chick growth in 1991, we have not used growth curve analysis due to the great number of regression parameters (3) in relation with the low number of sequential measurements (6–7 for each chick), and to the absence of a clear asymptote for mass and culmen. Chicks leave for the sea with values below adult values (Volkman and Trivelpiece 1980), so the asymptote estimate would be biased. In comparisons between broods, we have used measurements of chicks for the different ages, without applying any growth function. In intrabrood comparisons, we have used the linear period of growth between chick ages 7 and 28 to determine the regression coefficient (b) as growth rate (correlation r-values exceed 0.95 in all cases during this period). In both 1991 and 1992, we have used as an index of growth asymmetry between siblings the absolute difference in measurements or mass divided by the brood mean and expressed as percentage. Due 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. In both years, we were unable to find some crèche-age chicks due to band loss, so these families have been excluded from growth and survival analyses for those ages.

Chick mortality was recorded as: desertion by guarding parent, brood reduction due to starvation, or predation by skuas *Catharacta skua*. Chicks of crèche age lying dead in the colony or its surroundings without signals of predation by skuas were considered to have starved. We checked carefully the surroundings of the study colonies for dead marked 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 monitored chick mortality during the guard stage in a distant part of the colony which was only visited at weekly intervals (49 nests). Disturbance to the adults in this control area was reduced to a minimum. The aim was to detect possible effects of our frequent visits on chick mortality patterns in the study nests. No significant effect of our disturbance in the study area was noted on egg or chick survival ($\chi^2 = 1.61$, $P = 0.20$ for eggs, $\chi^2 = 1.00$, $P = 0.32$ for chicks, 1 d.f. in both cases).

Statistical tests are indicated in the text when applied. We tried to perform parametric tests, except in cases when the normality and homoscedasticity assumptions were not fulfilled. All tests are two-tailed. Probability values below 0.05 are termed significant.

Results

Egg size and hatching pattern

In 1991, most clutches included in the study (78%, $n = 51$) contained two eggs, the rest only one egg. The mean egg volume ($\pm$ SD) was 90.1 ± 6.9 cm^3 ($n = 51$ clutches) with a median of 89.9 and a range of 74.6–105.8 cm^3 (smaller than the value of 92 cm^3 reported for Signy Island by Lishman 1985: t-test for comparison of an expected mean with the mean of our data series: $t_{50} = 1.97$, $P = 0.05$). Egg size did not differ significantly between clutches of one and two eggs ($t_{49} = 0.66$, $P = 0.51$; egg size in two-egg clutches was averaged). In 1991, eggs hatched in the colony around December 25 (day 10.0 ± 2.5, range 5–16, $n = 46$ nests, day 1 = December 16). In 1992, eggs hatched significantly earlier, around December 23 (day 7.9 ± 2.5, range 1–16, $n = 117$ nests, $t_{161} = 4.90$, $P < 0.001$). Hatching dates did not differ between one- and two-egg clutches in 1991 ($t_{44} = 0.24$, $P = 0.81$; hatching dates for clutches of two were averaged). In 1991, there was no significant correlation between hatching date and egg volume, either for all clutches ($r_{46} = 0.23$, $P = 0.124$) or for two-egg clutches ($r_{35} = 0.30$, $P = 0.07$).

Hatching was asynchronous in most clutches where hatching of both eggs could be adequately followed both in 1991 (78%, $n = 32$) and in 1992 (69.1%, $n = 55$). These percentages are statistically indistinguishable ($\chi^2_1 = 0.83$, $P = 0.36$). Average asynchrony in 1991 was 0.94 ± 0.93 days (range 0–3, $n = 16$ nests where asynchrony was exactly determined), being 0.96 ± 0.84 days in 1992 (range 0–4, $n = 55$ clutches with asynchrony exactly determined). Hatching asynchrony did not differ between years ($t_{69} = 0.11$, $P = 0.91$). Eggs of asynchronous and synchronous clutches did not differ significantly in size (data for 1991: 91.1 ± 8.1 cm^3, $n = 25$ versus 86.8 ± 5.2 cm^3, $n = 7$ resp.; $t_{30} = 1.32$, $P = 0.19$). Hatching date of asynchronous and synchronous clutches was similar both in 1991 (day 5.1 ± 2.2, $n = 25$ versus day 4.2 ± 2.9, $n = 7$ resp.; $t_{30} = 0.89$, $P = 0.38$) and in 1992 (day 3.4 ± 1.4, $n = 38$ versus 3.8 ± 1.6, $n = 17$ resp.; $t_{53} = 0.90$, $P = 0.372$), using average dates for the two eggs in each clutch.

Intra-clutch variability in egg size measured in cm^3 or as percentage difference of the mean of both eggs (EDI, Lamey 1990: 100 × (absolute diff./mean)) did not differ significantly between asynchronous and synchronous clutches in 1991 ($t_{30} = 0.79$, $P = 0.43$ and $t_{30} = 0.68$, $P = 0.50$ resp.). The mean EDI was 4.4% with respect to volume. To examine the different components of egg size variability, we conducted a nested ANOVA with synchrony/asynchrony, nest and eggs within clutch as effects. More than 77% of the variation in egg size was due to differences between nests ($F_{30,63} = 10.40$, $P < 0.001$), with only marginal importance for synchrony (5.9%; $F_{1,63} = 1.76$, $P = 0.19$), and within-nest variation (error component: 16.5% of variation). In half of the asynchronous clutches, the largest egg was the first to hatch and in the other half the smallest egg was the first to hatch.

Growth patterns

Chicks were significantly larger and heavier in 1992 than in 1991 with both 15 and 46 days of age (Table 1). In 1991, chicks from one-egg clutches became significantly

Table 1 Differences in biometry between years for chicks of 15 and 46 days of age. Means of broods have been averaged. Results of t-tests comparing both years are presented (*x* = mean; *sd* = standard deviation; *n* = sample size)

	1991 x	sd	*n*	1992 x	sd	*n*	t	*P*
Age = 15 days								
Culmen (mm)	20.3	1.7	33	21.8	1.4	88	5.05	< 0.001
Flipper length (mm)	81.6	9.4	33	97.8	8.6	88	9.01	< 0.001
Mass (g)	726.7	183.4	33	1017.2	127.6	87	9.80	< 0.001
Age = 46 days								
Culmen (mm)	33.8	3.6	29	39.6	2.3	61	9.30	< 0.001
Flipper length (mm)	181.4	16.6	29	192.4	5.9	61	4.63	< 0.001
Mass (g)	2444.9	419.7	29	3226.8	283.7	61	10.41	< 0.001

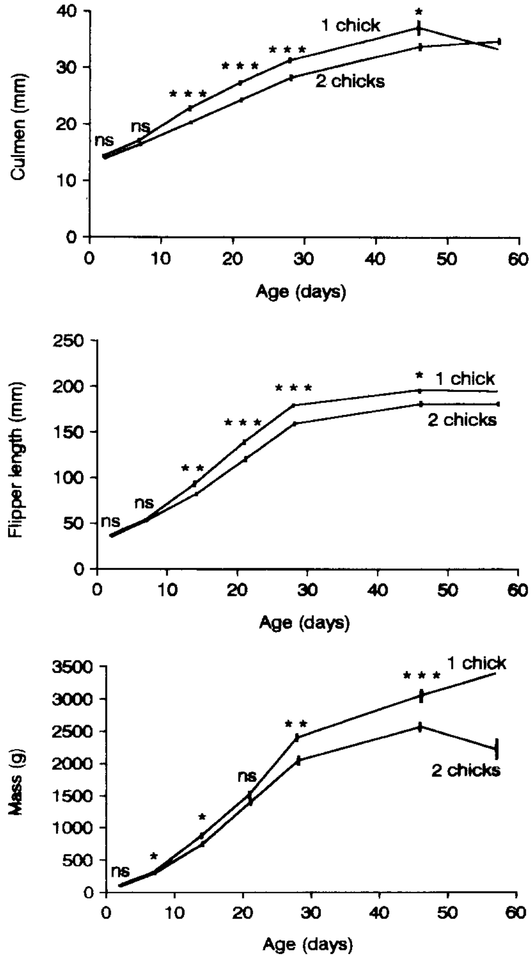

Fig. 1 Growth of chicks from one-egg clutches and chicks in broods of two with respect to culmen, flipper length and mass in 1991. Bars represent ± SE. Results of t-tests for each age are presented (ns: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). The mean age of transition between the guard and crèche phases in this year was 29 days

heavier and larger than chicks in families of two after the first week (Fig. 1), and these differences were maintained throughout development (sample sizes just before fledging are too small for statistical analyses due to mortality or colony abandonment). In 1992, single chicks (due to absence of hatching of its sibling or earlier brood reduction) were significantly larger but not heavier at 15 days of age than chicks in families of two (Table 2). At 46 days of age, no differences in biometry between single chicks and those in two-chick families were found (Table 2). These results suggest that there was food limitation in 1991, but not in 1992.

Hatching asynchrony and growth asymmetry in siblings

In 1991, asymmetry in linear measurements and mass between siblings was greater throughout development in asynchronous families (asynchrony $\geq$ 1 day) than in synchronous ones (Fig. 2). These differences between type of broods were significant during the guard phase for flipper length and mass, but became nonsignificant during the crèche phase (Fig. 2). They were nonsignificant throughout for culmen (Fig. 2).

In 1992, when we were able to estimate hatching asynchrony for a large sample of nests, asymmetry in body mass increased significantly with hatching asynchrony and decreased with age (Fig. 3 and Table 3). The trend with age was common to all measures (Fig. 3), while the effect of hatching asynchrony was not significant for flipper length and culmen (Table 3). The interaction between asynchrony and age was significant for body mass (Table 3), showing that the older the chicks the lower the differences in asymmetry with respect to degree of hatching asynchrony (as in 1991 for the two categories of asynchrony, Fig. 2). The interaction between these two factors was not significant for flipper length and culmen (Table 3). A separate test for each age category of the ordered trend in asymmetry with hatching asynchrony (one-way trend analyses of variance), reveals that asymmetries in all measurements increase with hatching asynchrony at 15 days of age (culmen: $F_{1,84} = 14.10$, $P < 0.001$; flipper: $F_{17,92} = 17.92$ $P < 0.001$; mass: $F_{1,83} = 34.43$, $P < 0.001$). At the age of 46 days, there is only statistical association between asymmetry in culmen and

Table 2 Comparison of sizes and masses (means ± SD) of single chicks and chicks in broods of two (means of siblings) at 15 and 46 days of age in 1992. Single chicks resulted from clutches of two where one egg did not hatch or to brood reduction. Sample sizes refer to families. Results of t-tests comparing brood sizes are presented

	One chick	Two chicks	t	*P*
15 days	$n = 25$	$n = 88$		
Culmen (mm)	22.52 ± 1.64	21.80 ± 1.35	2.25	0.027
Flipper length (mm)	106.9 ± 10.2	97.8 ± 8.6	4.48	0.000
Mass (g)	1078.2 ± 170.5	1017.2 ± 127.6	1.95	0.054
46 days	$n = 28$	$n = 61$		
Culmen (mm)	40.26 ± 2.79	39.61 ± 2.26	1.18	0.240
Flipper length (mm)	191.2 ± 6.1	192.4 ± 5.9	0.87	0.390
Mass (g)	3167.9 ± 305.3	3226.8 ± 283.7	0.89	0.380

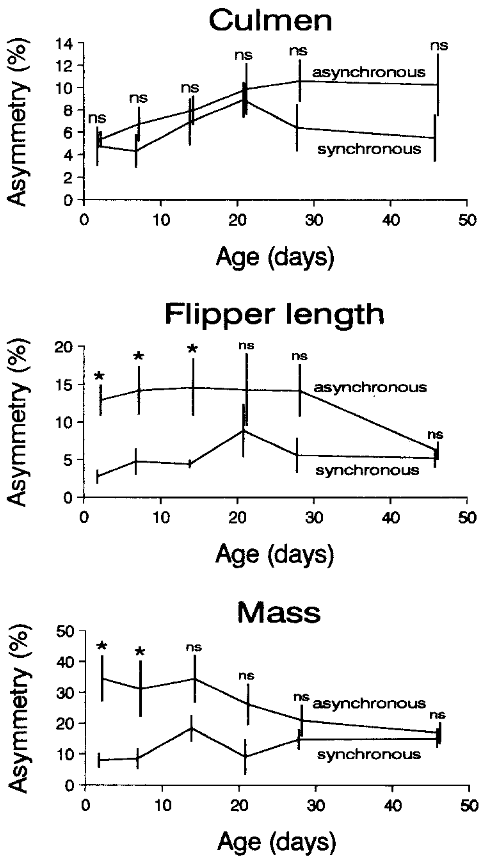

Fig. 2 Comparison between sibling asymmetry for culmen, flipper length and mass in asynchronously and synchronously hatched broods at different ages in 1991. Asymmetry is expressed as 100 × (absolute difference between siblings/mean of siblings). Bars represent ± S.E.. Tests refer to t-tests on arcsin-transformed data (symbols as in Fig. 1). The small sample of complete broods measured at the approximate age of 58 days makes inclusion of these data in the statistical analysis unfeasible. Chicks were left unguarded at a mean age of 29 (22–36) days in this year. Acronyms as in Fig. 1

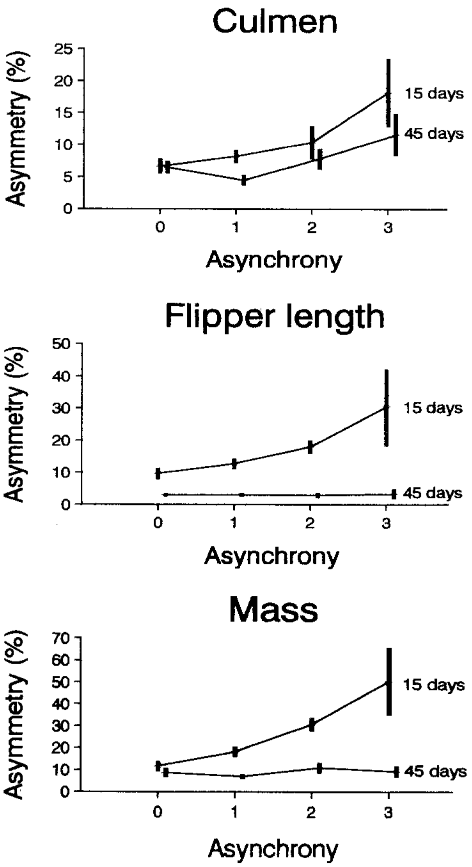

Fig. 3 Relationships of sibling asymmetry in culmen, flipper length and body mass with hatching asynchrony in days for two chick ages (15 and 46 days) in 1992. Trends for flipper length and mass at 45 days were not statistically significant (see text). Asymmetry measured as in Fig. 2. Bars represent ± S.E.

hatching asynchrony (culmen: $F_{1,57} = 5.87$, $P = 0.019$; flipper: $F_{1,57} = 0.04$, $P = 0.842$; mass: $F_{1,57} = 0.19$, $P = 0.67$). Thus, the association between hatching asynchrony and sibling asymmetry vanished between 15 and 46 days of age.

Asymmetry at the age of 15 days did not differ significantly between the two study years for any biometrical variable (culmen: $t_{120} = 1.33$, $P = 0.185$; flipper length: $t_{120} = 0.95$, $P = 0.344$; mass: $t_{120} = 1.72$, $P = 0.087$). However, asymmetries at 46 days of age were significantly lower in 1992 than in 1991 (culmen: $t_{77} = 2.51$, $P = 0.014$; flipper length: $t_{77} = 2.31$,

Table 3 Results of analyses of variance for repeated measures with one grouping (hatching asynchrony) and one within group (age) factor, testing the effects of degree of hatching asynchrony (0, 1, 2 and ≥ 3 days) and chick age (15 and 46 days) on asymmetry in culmen, flipper length and body mass. Data for 1992

	d.f.	F	*P*
Culmen			
Asynchrony	3,55	2.43	0.075
Age	1,55	6.21	0.016
Interaction	3,55	2.00	0.124
Flipper length			
Asynchrony	3,55	2.62	0.060
Age	1,55	63.79	0.000
Interaction	3,55	2.62	0.060
Mass			
Asynchrony	3,55	7.93	0.000
Age	1,55	45.49	0.000
Interaction	3,55	6.34	0.001

$P = 0.023$; mass: $t_{77} = 3.03$, $P = 0.003$; compare Figs. 2 and 3 for interannual differences in asymmetry). These results indicate that asymmetries decrease during growth to a further extent in a "good" year than in a "less good" year.

In 1991, reversals in size hierarchies were relatively frequent in asynchronous broods before day 15, especially for mass and flipper length (Table 4). They were equally frequent between 15 and 46 days of age (tests comparing both growing periods: culmen: $\chi_1^2 = 0.44$, $P = 0.51$; flipper length: $\chi_1^2 = 2.49$, $P = 0.11$; mass: $\chi_1^2 = 1.15$, $P = 0.28$). In 1992, reversals during the first two weeks were significantly less common than in 1991 (Table 4). The frequency of reversals in this year increased significantly during the period 15–46 days (culmen: $\chi_1^2 = 7.22$, $P = 0.007$; flipper length: $\chi_1^2 = 12.13$, $P = 0.001$; mass: $\chi_1^2 = 8.55$, $P = 0.003$; Table 4). This led to a nonsignificant difference between years in the frequency of reversals for this period (Table 4). The cumulative number of reversals in size hierarchies between hatching and day 46 of age was similarly high in both years (Table 4). These results indicate that reversals are a common phenomenon, and that they were if anything more common during the "less good" year for breeding.

In 1991, we have compared within broods the linear regression coefficients of mass on chick age for the first and second chicks to hatch in asynchronous broods to determine if hatching order affected growth. No significant difference was found (Wilcoxon matched-pairs test, $Z = 1.60$, $P = 0.109$, $n = 16$). No linear regressions are possible in 1992, but we can compare the growth rates of the A and B chicks between 15 and 46 days of age. The B chicks grew significantly faster than the A chicks with respect to flipper length (3.3 ± 0.4 vs. 2.9 ± 0.4 mm/day, Wilcoxon matched-pairs test: $Z = 4.53$, $P < 0.001$, $n = 42$) and mass (77.3 ± 13.7 vs. 70.2 ± 11.6 g/day, Wilcoxon matched-pairs test: $Z = 3.31$, $P < 0.001$). This was not so for culmen (0.58 + 0.07 vs. 0.56 + 0.07 mm/day, Wilcoxon matched-pairs test: $Z = 1.37$, $P = 0.17$). This result agrees with the maintenance of asymmetries for culmen in 1991 (Fig. 3) and with the absence of interaction between hatching asynchrony and age.

In 1991, survivors of brood reduction surviving alone for more than 14 days ($n = 9$) reached significantly smaller sizes and masses at age 46 days than chicks in broods of two (means of both chicks) which had suffered no reduction ($n = 15$) (flipper: 178.1 ± 10.4 vs. 188.3 ± 6.8, $t = 2.91$, $P = 0.008$; culmen: 32.2 ± 3.76 vs. 35.6 ± 5, $t = 2.83$, $P = 0.01$; mass: 2325 ± 375 vs. 2599 ± 290, $t = 2.01$, $P = 0.057$). In 1992, single chicks reached similar sizes at 46 days of age than chicks in broods of two (Table 2). In both years, chicks of synchronous broods (means of both chicks) reached the same size and mass at 46 days of age than the A chicks of asynchronous broods (Table 5). However, the B chicks of asynchronous broods had significantly shorter bills than chicks of synchronous broods in both years (Table 5).

Chick mortality patterns

To analyze patterns of chick mortality in the two years, we will only include nests with two eggs, as no one-egg clutches were included in the study in 1992. In 1991, chick mortality increased throughout the guard phase

Table 4 Number of reversals for the two years in size and mass hierarchies between siblings (reversals/totals) in asynchronous broods between hatching and 15 days and between 15 and 46 days of age and cumulative number of reversals from hatching to 46 days of age

	Culmen			Flipper length			Mass		
	1991		1992	1991		1992	1991		1992
1–15	5/18	*	4/49	11/18	***	5/49	11/18	***	4/48
15–46	4/10	NS	10/32	3/10	NS	14/32	4/10	NS	11/32
1–46	5/10	NS	11/32	5/10	NS	16/32	2/10	NS	13/32

The level of significance of χ^2 tests for differences between years is presented between the tested values (NS: $P > 0.05$; *: $P < 0.05$; ***: $P < 0.001$)

Table 5 Comparison of mass and size (means ± SD) at 46 days of age of synchronously hatched chicks (means for each brood) with the first (A) and second (B) chicks of asynchronously hatched broods. Only for culmen were there statistically significant differences between chicks of synchronous and B chicks of asynchronous broods in 1991 ($t_{13} = 2.45$, $P = 0.03$) and 1992 ($t_{59} = 2.55$, $P = 0.01$)

	Mean of synchronous siblings	A chick in asynchronous broods	B chick
1991			
	$n = 5$	$n = 10$	$n = 10$
Culmen (mm)	36.7 ± 2.5	35.7 ± 2.1	33.3 ± 2.5
Flipper length (mm)	189.3 ± 8.8	187.1 ± 6.5	184.1 ± 10.0
Mass (g)	2732.5 ± 316.2	2490 ± 385.0	2490.0 ± 228.3
1992			
	$n = 19$	$n = 42$	$n = 42$
Culmen (mm)	40.51 ± 1.68	39.75 ± 2.61	38.64 ± 2.96
Flipper length (mm)	192.6 ± 5.0	192.0 ± 7.5	191.8 ± 7.2
Mass (g)	3205.3 ± 258.9	3244.6 ± 308.9	3228.6 ± 373.9

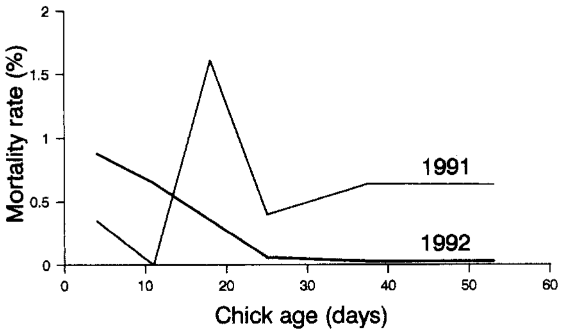

Fig. 4 Daily mortality rate with respect to chick age for both years of the study. Data points refer to measurement periods between two measurement ages. Mortality rates are percentages of chicks reaching initial age that die during a certain period. The mean age of transition between the guard and crèche phases was 29 days in 1991 and 35 days in 1992.

to reach a peak during the third week of life (Fig. 4). Mortality during the guard stage was mainly produced by nest desertion (9 chicks of 6 broods) due to prolonged absences of one parent. Only two cases of starvation were observed during the guard stage. Mortality decreased during the fourth week when crèches started to form (one case of starvation, Fig. 4). During the crèche stage, chick mortality again increased and then stabilized at a daily mortality rate of 0.6% (Fig. 4). In most cases mortality was associated to starvation (9 of 14 cases), as most fresh chick carcasses were found untouched before being scavenged by skuas. There were however three cases of predation by skuas. One or both chicks in broods of two might die during the crèche stage, but deaths of siblings were not simultaneous as in the guard phase.

In 1992, the pattern of mortality with respect to chick age was the opposite (Fig. 4). Most chicks died before 15 days of age (25 of 30 cases), and 7 of them died at hatching (no case of death at hatching was observed in 1991). The difference in mortality rate between years was significant for ages 1–15 days ($\chi^2 = 4.34$, $P = 0.04$), 16–46 days ($\chi^2 = 37.38$, $P < 0.001$), and more than 46 days ($\chi^2 = 14.83$, $P < 0.001$). While mortality was higher in 1992 for the first two weeks, it was much lower for subsequent age periods (Fig. 4). In total, 65.7% of hatched chicks survived to fledging age in 1991 while 87.2% did in 1992, which is a significantly higher percentage ($\chi^2 = 15.82$, $P < 0.001$).

In 1991, chick mortality did not differ between one-egg and two-egg nests (Kolmogorov-Smirnov test, $\chi^2 = 0.67$, $P = 0.41$), which leads to productivity of broods from two-egg clutches being significantly greater than for broods from one-egg clutches (1.35 versus 0.73 chicks). In that year, brood reduction was relatively rare during the guard phase in asynchronous broods, but relatively frequent during the crèche phase (difference between stages: Fisher's exact test: $\chi^2 = 12.61$, $P < 0.001$). This leads to a significant difference in the probability of brood reduction between both types of broods in 1991, as synchronous broods suffered no reduction (Fisher's exact tests: crèche $\chi^2 = 6.32$, $P = 0.019$; both phases $\chi^2 = 7.22$, $P = 0.007$). In 1992, there was no difference between synchronous and asynchronous broods in the frequency of brood reduction (3 of 30 synchronous families and 11 of 80 asynchronous broods suffered reduction at any stage, $\chi^2 = 0.364$, $P = 0.55$). In 1991, the order of hatching was known in 7 asynchronous broods which suffered reduction. In 5 of these, it was the B chick that died from starvation. In the other two broods, the A chick was found depredated by skuas. The overall probability of brood reduction was not related significantly to degree of asymmetry between chicks (broods suffering reduction were not more asymmetrical in the last instance of measurement than those not suffering reduction: Mann-Whitney U-test, $Z_{16} = 0.369$, $P = 0.712$). As most cases of brood reduction in 1992 occurred before 15 days of age, this analysis is not feasible for that year. In 1991, fledging occurred at 58.2 ± 3.3 days of age for a small sample of 6 chicks whose age of abandonment of the colony was exactly known. In 1992, chicks fledged with 52.5 ± 2.4 ($n = 43$) days, which is significantly earlier than in 1991 ($t_{47} = 4.09$, $P < 0.001$). The duration of the crèche stage was thus significantly reduced in 1992 compared with 1991 (18.0 ± 2.3, $n = 42$ vs. 32.5 ± 4.3 days, $n = 6$, $t_{46} = 8.07$, $P < 0.001$).

Discussion

Chinstrap penguins do not represent the intriguing contrast to the other pygoscelids as deduced by Lamey (1990) from the scarce detailed information available. Hatching asynchrony is as common as in other Pygoscelids (69–78% as compared to 56–66% in gentoos, Williams and Croxall 1991). The mean asynchrony of 1.0 days is only slightly lower than those reported for the other pygoscelids (1.4 in the Adélie and 1.6 in the Gentoo penguin, Lamey 1990), and favours the development of initial size hierarchies (28% difference in mass) between siblings as in gentoos (22.4–34.3%, Williams & Croxall 1991). Egg size differences in broods are similar to those reported for its congeners (4.4% as compared to 6.3% in the Adélie, Lamey 1990) and significantly different from the value reported for chinstraps on Signy Island by Lishman (1985) (1.2%; t-test for comparison of an expected mean with the mean of our data series: $t_{39} = 6.4$, $P = 0.001$). The low intraclutch variation in egg size makes egg-size manipulation an unlikely mechanism for the allocation of parental effort in this population. The same conclusion was reached for gentoos by Williams and Croxall (1991).

There are several pieces of evidence suggesting that food is a limiting factor on chick growth and survival in this population during the crèche phase (chicks older than 28 days) in certain years. In a "not so good" or "normal" year, single chicks grow faster throughout development than members of broods of two, and this difference appears more clear at the end of growth. In a "good" year, differences in growth between single chicks and two-brood chicks disappear during development, indicating that chick growth is not limited by food availability in certain situations. In other penguin species also, single chicks grow significantly better than young from two-chick broods (Taylor 1962; Taylor and Roberts 1962; Ainley and Schlatter 1972; Boersma 1991). Also, in a "normal" in contrast with a "good" year, there is a relatively large mortality of crèching chicks due to starvation. Chick mortality does not appear exceptional in this study compared with literature data (65.7–87.2% of hatched chicks survived to fledging age compared to reports for normal years on Signy: 84% in Conroy et al. 1975 and 60.8% in Lishman 1985). However, the distribution of mortality in the "normal" year differs from that reported for Adélies and for the Signy chinstrap population (Taylor 1962; Lishman 1985; Davis and McCaffrey 1986), where chick mortality is less important during the crèche than during the guard phase. Thus, the mean lifespan of lost chicks of 30.1 days in 1991 is significantly greater than that reported for a normal year on Signy (14.4 ± 9.6, $n = 41$, derived from Lishman 1985; t-test for comparison of an expected mean with a data series: $t_{64} = 4.4$, $P < 0.001$). In the "good" year, mortality occurred even earlier than in the study on Signy and is barely attributable to food limitation (more probably to the incidence of snowstorms at the end of incubation). The crèche stage is presumably the more energetically costly for parents due to greater chick needs (Green and Gales 1990), although both parents can simultaneously collect food for the chicks at this stage.

If starvation is frequent, we should expect it to be associated to efficient brood reduction. However, contrary to expectations from the brood reduction hypothesis (Lack 1954), chick starvation in a "normal" year strikes when parents have invested heavily in their broods. The same conclusion was reached for gentoos by Williams and Croxall (1991). Also, brood reduction precedes in 5 of 10 cases the death of the second chick, and thus does not apparently facilitate the survival of one of the chicks. Survivors from brood reduction grow worse than chicks of nonreduced broods. This is probably because the loss of one chick was due to poor parental care which also affected the growth of the survivor (see Taylor 1962 for a similar result in Adélies). Thus, brood reduction does not increase the future prospects of the surviving chick. The three cases of skua predation (two in the same family) happened in families where the surviving chick later died. In one case the chick was obviously starving when attacked. Predation cases are associated to indications of poor parental care. Thus in a "normal" year, chick mortality appears predominantly due to limitations acting on the feeding capacity of parents.

Even if brood reduction is apparently inefficient, the question remains if it is favored by the size hierarchies established at hatching in conditions of food limitation, as predicted by the brood reduction hypothesis. Growth asymmetries established at hatching in asynchronous families are maintained during the guard phase, when parents can more easily regulate food distribution between siblings. However, they decrease after crèching and reach a level as low as in synchronous families before fledging. In contrast, the difference in culmen asymmetry between synchronous and asynchronous broods increases during the crèche stage. Chicks may redistribute resources devoted to anatomical growth before fledging in order to attain a sufficient size in important structures for survival. Flipper length and mass are probably more important characters for postfledging survival than bill size, which does not reach mature size at fledging (Volkman and Trivelpiece 1980). In a "good" year, asynchrony-dependent growth asymmetries have totally disappeared before the age of 46 days. During the guard phase, parental preferences do not augment the size differences due to age, as evidenced by the absence of significant differences in growth rate between first and second chicks. The reversals in size hierarchies occurring during this phase indicate that already at this stage, parents may not be able to maintain the chick rank determined through asynchronous hatching. If hatching asynchrony is an adaptation to favour brood reduction in conditions of food limitation, we should expect less frequent reversals with reduced food availability. Contrary to expectation, reversals are more frequent in the "normal" than in the "good" year during the guard stage. Reversals of rank during this phase are also common in gentoos (Williams and Croxall 1991).

In a "normal" year, in contrast to a "good" year, mortality due to starvation becomes common in asynchronous in contrast to synchronous broods after crèching. Although asynchrony is associated to brood reduction (in all cases of known hatching order it is the second chick that starves), the probability of brood reduction is not related to asymmetry of growth in asynchronous broods. This lack of relationship between asymmetry and future mortality, as well as the frequent reversals in hierarchies may be mediated through sibling competition in feeding chases during the crèche phase (Bustamante et al. 1992). The participation in chases may be subjected to variation unrelated to chick rank, and may mediate starvation mortality during food crises (Bustamante et al. 1992). Thus, hatching asynchrony does not determine asymmetries at the time when brood reduction occurs, and the rank in size at hatching is frequently reversed during growth. Also in gentoos, reversals in size rank at hatching are frequent and initial asymmetries do not predict asymmetries at 30 and 60 days of age (Williams and Croxall 1991). Also, A-chicks in asynchronous broods are not heavier and larger than chicks from synchronous broods before fledging, contradicting another prediction from the brood reduction hypothesis (Amundsen and Stokland 1988). In chinstraps as in gentoos (Williams and Croxall 1991), brood reduction is not only inefficient but apparently unrelated to hatching asynchrony.

Alternative hypotheses to explain hatching asynchrony like the 'peak load reduction hypothesis' (Hussell 1972), the 'hurry-up hypothesis' (Clark and Wilson 1981; Slagsvold 1986), the 'nest failure hypothesis' (Clark and Wilson 1981; Hussell 1985) or the 'sexual conflict hypothesis' (Slagsvold and Lifjeld 1989) do not apply to penguins, given their long development periods, the absence of clear seasonal trends in their food resources, the lack of important land predators and the equal sharing of breeding duties between the sexes (Seddon and Van Heezik 1991; Williams and Croxall 1991). Boersma (1991) has proposed that in Magellanic penguins *Spheniscus magellanicus*, asynchronous hatching is determined by nest relief intervals at hatching as a mechanism to maximize the chance that both chicks will be fed soon after hatching and before they lose much of their yolk reserves. In the present case, there is no increase in chick survival with asynchrony as in Magellanic penguins (Boersma 1991). The 'sibling rivalry reduction hypothesis' (Hahn 1981) proposes that sibling competition in equal-sized broods will lead to a reduced feeding efficiency. This waste of effort will lead to reduced growth and survival of chicks in synchronous compared with asynchronous broods, even when food is plentiful. There is no evidence for reduced growth in synchronous broods in our study. Seddon and Van Heezik (1991), following Amundsen and Stokland (1988), have extended this hypothesis to consider the effect of improved feeding efficiency not only on chick survival to fledging but also on mass-dependent postfledging survival. However, Williams and Croxall (1991) have not found a significant relationship between postfledging survival and fledging mass in gentoos. This possibility remains to be explored for chinstraps.

Williams and Croxall (1991) have suggested that asynchronous hatching in gentoos may not be adaptive in itself, but merely a consequence of selection for incubation starting before the clutch is complete. In cold temperate or polar environments, exposure to extreme low temperatures of recently laid eggs may induce parental incubation of eggs as soon as they are laid (Derksen 1977; Shaw 1985; Amundsen and Stokland 1988; Williams and Croxall 1991), to avoid a loss in egg viability (Webb 1987). However, the question remains why, in spite of such thermal constraints, some clutches still hatch synchronously. Given thermal constraints on embryo survival, asynchronous hatching could be the nonadaptive consequence of prolonged laying intervals for females in poorer condition. Penguins have comparatively long and variable laying intervals, which could be due to constraints acting on the mobilisation and deposition of mineral elements for the formation of the relatively heavy egg shell (Williams 1981) or on the allocation of nutrient reserves (Astheimer 1985). Prolonged laying intervals would induce females to begin incubation before the second egg is laid to avoid prolonged exposure and consequent loss of viability in the first egg (Arnold et al. 1987; Veiga 1992). Detailed studies of laying intervals and loss of egg viability in relation with hatching patterns and parental condition are needed in order to test this idea.

Acknowledgements The present study was supported by grant ANT91-1264 from the Spanish C.I.C.Y T. (Plan Nacional Antártico). Transport to and from the Island was offered by the Hespérides, Spanish Navy. We gratefully acknowledge the hospitality offered at the Spanish Base "Gabriel de Castilla" and at the Argentine Base on Deception Island during the two years. T. Williams, J. P. Veiga, T. Slagsvold and two anonymous referees contributed with their comments to improving previous versions of the MS.

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