Hatching order and size-dependent mortality in relation to brood sex ratio composition in chinstrap penguins

Juan A. Fargallo, a Vicente Polo, a Liesbeth de Neve, a José Martín, a José A. Dávila, b and Manuel Soler c
aDepartamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, José Gutierrez Abascal 2, 28006 Madrid, Spain, bInstituto de Investigación en Recursos Cinegéticos, Consejo Superior de Investigaciones Científicas-Universidad de Castilla-La Mancha, Ronda de Toledo s/n, E-13005 Ciudad Real, Spain, and cDepartamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

The differential environmental sensitivity of the sexes has strong implications in the evolutionary history of species as it can alter sexual size dimorphism, population sex ratios, and the faculty of parents to manipulate offspring sex in relation to environmental conditions. We studied sexual differences in hatching patterns and evaluated sex- and size-related mortality in relation to hatching order and brood sex ratios in the chinstrap penguin Pygoscelis antarctica, a moderately size-dimorphic species, with a modal clutch size of 2 eggs. We found that male, second-hatched, and large eggs showed shorter hatching periods than female, first-hatched, and small eggs. We also found a male-biased mortality of nestlings in the colony. However, male mortality patterns differed depending on the brood sex ratio composition. Mortality of male chicks in all-male broods was higher than in mixed broods and higher than female mortality in all-female broods. Contrary, females from mixed brood showed higher mortality than their male nest mates and higher too than females in all-female broods. Second-hatched chicks also suffered from higher mortality than first-hatched chicks. Our results indicate that both the superior competitive capacity and the higher energy demand of the larger sex constitute 2 causal factors explaining patterns of sex-biased mortality. Both factors occur in the same species and in different situations of sibling competition shaped by brood sex ratio composition. This study constitutes a good example of how patterns of sex-related mortality can vary depending on nest environmental circumstances. Furthermore, our study suggests that hatching period can be a mechanism underlying sexual differences in the embryonic period of birds.

Key words: egg size, hatching asynchrony, hatching period, nestling survival, Pygoscelis antarctica. [Behav Ecol 17:772–778 (2006)]

The ability to compete with siblings and to face adverse environmental conditions affect body and health condition during early life and may thereby have profound effects on the survival and reproductive value of an individual (Clutton-Brock 1991). Individual skills to do well out of sibling rivalry or adverse conditions can be sex dependent. Postnatal sex-related vulnerability to nest environment has been frequently described in avian species (e.g., Clutton-Brock et al. 1983; Bortolotti 1986; Anderson et al. 1993; Potti and Merino 1996; Fargallo et al. 2002; Velando 2002; Tschirren et al. 2003; Kalmbach et al. 2005). However, the interaction between size and sex has been a confounding factor in many studies, generating contradictory results. It is expected that sexual differences in size involve sexual differences in energetic requirements, leading to the idea that the larger sex is more vulnerable to adverse conditions due to higher energy demands. This “energy demand” hypothesis has been suggested when researchers found male-biased vulnerability in sexual size-dimorphic species (Clutton-Brock et al. 1985; Roskraft and Slagsvold 1985; Müller, Kalmbach, et al. 2005) or female-biased vulnerability in species with reversed dimorphism (Torres and Drummond 1997; Velando 2002; Laaksonen et al. 2004; Kalmbach et al. 2005). However, other studies have reported higher mortality of smaller sex under food restrictions (Bortolotti 1986; Dijkstra et al. 1990; Anderson et al. 1993; Oddie 2000; Hipkiss et al. 2002). In this case, authors have proposed the “competitive capacity” hypothesis that posits the competitive superiority in sibling rivalry of the larger sex, reaching closer toward the parent, occupying favored feeding positions, or pushing smaller nest mates away from food deliveries, in both siblicidal and nonsiblicidal species (Bortolotti 1986; Anderson et al. 1993; Oddie 2000; Fargallo et al. 2003). Irrespective of size, another idea suggests that inherent characteristics in sex phenotype, such as the high levels of testosterone in males, estrogens in females, or other sexual characters can determine differential vulnerability. This “sex phenotype” hypothesis has been proposed to explain why males are generally less favored in the development of the immune function or they are more susceptible to parasite infection (Olsen and Kovacs 1996; Potti and Merino 1996; Fargallo et al. 2002; Müller et al. 2003; Tschirren et al. 2005). Although the opposite has been observed in Alpine swifts, Apus melba, where males were more vulnerable to parasitism than females (Bize et al. 2005).

At present, we are far from solid conclusions defining a general rule for sex-linked sensitivity to environmental conditions. Probably, more than one hypothesis can act in the same species at different levels depending on the environmental circumstances or the degree of sexual size dimorphism. For example, it is predictable that in sexually size-dimorphic species the response of an individual of a given sex to the environment can be different depending on the number of individuals of the same sex sharing the nest.
In this sense, another aspect of interest is the possibility of parents to intercede for one or another offspring sex. Hatching asynchrony has been considered, through some of the great variety of hypotheses proposed, a mechanism by which parents may create within-brood size hierarchies to favor an adequate dynamic of sibling competition. This permits females to produce an optimal brood composition and to distribute resources among the offspring of a brood to maximize fitness (e.g., Forbes et al. 2002; Laaksonen 2004). The pattern of hatching has been traditionally explained by the timing of incubation in relation to the laying sequence. Thus, by manipulating incubation, females can create the required pattern of hatching (e.g., Drent 1975; Clark and Wilson 1981; Viega and Viñuela 1993). However, even if essential to understand the potential function of hatching asynchrony, most studies have ovulated other proximate mechanisms and the role that the sex may play in hatching asynchrony (see Stoleson and Beissinger 1995; Cook and Monaghan 2004).

The sex allocation theory predicts that parents able to recognize sex-biased environmental sensitivity of offspring and to adjust their resources accordingly should be favored by natural selection (Trivers and Willard 1975; Chutton-Brock 1991). In this sense, sex differences in the embryonic period (Blanco, Martínez-Padilla, Dávila, et al. 2003; Cook and Monaghan 2004), egg size (Anderson et al. 1997; Cordero et al. 2000, 2001; Blanco, Martínez-Padilla, Serrano, et al. 2003), laying sequence (Cordero et al. 2001; Velando et al. 2002 and references therein), hatching order (Dzus et al. 1996; Blanco et al. 2002), or androgen levels deposited in the egg (see Gil 2003; Müller, Groothuis, et al. 2005) have been suggested as possible sources of variation that mothers could manage to produce an optimal structure of hatching or to create a dynamic of sibling competition adjusted to the vulnerability of offspring sex.

The aim of the present study is to explore sexual differences in hatching patterns and to evaluate how these differences affect sex-related vulnerability in the chinstrap penguin Pygoscelis antarctica. The chinstrap penguin is a semi-altricial species with moderate sexual size dimorphism. The modal clutch size in 2-egg broods consists of 2 chicks (Viñuela et al. 1996). The primary sex ratio shows a Mendelian segregation of sex chromosomes (Fargallo et al. 2004), for which all-female, mixed-sex, and all-male broods are represented in 25%, 50%, and 25% frequencies, respectively. Starvation and predation by skuas (Catharacta spp.) when starvation are the main causes of penguin chick mortality (Young 1994), also in chinstrap penguins (Moreno et al. 1994, 1999). We explored sexual differences in hatching order and hatching period in relation to hatching asynchrony in mixed broods. Furthermore, we studied the effect of brood sex ratio composition (all-female, mixed, all-male broods) on sexual differences in mortality. If the energy demand hypothesis works in this species, we would expect a higher overall mortality in all-male broods compared with all-female broods. On the other hand, if the “competitive advantage” hypothesis is true, then males in mixed broods will be more likely to survive than males in all-male broods. Similarly, females will survive better in all-female broods compared with mixed broods. Finally if the sex phenotype hypothesis is the prevalent mechanism, we should expect higher vulnerability of the same sex irrespective of the brood sex ratio.

METHODS

Study area and procedures

The study was conducted during the austral summer of 2002–2003 at the Vapour Col penguin rookery in Deception Island, South Shetlands archipelago (63°00′S; 60°40′W). We arrived in the rookery at the middle-end incubation period (5 December) of chinstrap penguins. As the quality of eggs and breeding performance can vary in relation to the nest position and subcolony size (Barboza et al. 1997; De Neve et al. 2006), we randomly selected 22 subcolonies of different size (from 24 to 1250 nests) in which we randomly selected 10 nests along an axis extended from one border to the opposite border of the subcolony (n = 220). A subcolony was defined as an aggregation of nests separated from other subcolonies by ground not used for nesting (De Neve et al. 2006).

Only 2-egg nests, the modal clutch size, were considered. The eggs were marked with indelible ink and measured to estimate egg volume (1/6π × length × breadth^2). We also measured flipper length of trapped parents (214 females and 212 males) as an estimation of body size. Nests were checked every 2 days until the first-hatched egg was observed in the colony (17 December), then each nest was daily checked until the hatchlings were blood sampled. Birds initiate the hatching process by making a little hole or a scratch in the eggshell. This process is usually called pipping. Chinstrap penguin eggs can remain at this stage from less than 1 day to 4 days before they complete the hatching process. We defined the hatching period as the interval of time (days) passed between the onset of pipping and hatching. Hatching asynchrony was defined as the difference in days (range from 0 to 4 days) between the hatching dates of the first and second eggs. We considered as synchronous nests those showing a hatching asynchrony lower than 1 day, and the rest of nests were considered asynchronous nests. At the pipping stage, the chicks were marked with indelible ink in the hatching tooth in order to know the egg origin of each nestling. Intrachlutch variation in egg volume was calculated as the percentage difference of the mean of both eggs (100[absolute difference/mean]; de León et al. 2001).

A drop of blood (20–50 μl) was collected from each nestling within 2 days of hatching by foot-vein puncture and stored in ethanol. Chinstrap penguins do not remove dead chicks from the nest (personal observation), which allowed us to collect a sample of muscular tissue from chicks that died before blood sampling and also from unhatched embryos to determine sex. The sex of the chicks was determined from blood and muscle samples with molecular methods as described by Griffiths and Tiwari (1995) applied on chinstrap penguins (Fargallo et al. 2004). However, we were not able to extract DNA from some of the dead chicks due to the bad conditions of these samples. In 16 of the 22 subcolonies, we followed up every 5 days all hatched chicks (n = 249) until they reached 25 days of age in order to estimate mortality during this period and sexual size dimorphism at this age. The chicks were marked with colored ink on the head until they were banded on the flipper with numbered metal rings. When the last measures of chicks were taken, we removed the rings to avoid their potential detrimental costs after independence (Jackson and Wilson 2002). Eggs and bill measurements were taken with a sliding caliper to the nearest 0.01 cm, flipper length with a metal rule to the nearest 1 mm, and body mass with a Pesola spring balance to the nearest 50 g.

Ninety-four (21.4%) of 440 eggs did not reach hatching. Twenty-six of these (27.7%) were due to nest abandonment, 22 (25.4%) were predated, and 46 (48.9%) did not hatch. Only 10 (24.4%) of the unhatched eggs contained dead embryos. Both eggs hatched in 142 nests. The sex of both chicks and hatching asynchrony could be determined in 130 nests. Hatching order and hatching period of both eggs were recorded in 108 nests (89 asynchronous and 19 synchronous). Of these latter, mortality and body condition of both chicks...
until 25 days of age could be surveyed in 92 nests (82 asynchronous and 10 synchronous).

**Statistical analyses**

Analyses were performed using SAS statistical software (SAS 2001 Institute Inc., Cary, North Carolina). To analyze egg volume and chick body measurements, we used general linear mixed models (GLMM, Littell et al. 1996) with normal error distribution. In the models, the egg/chick was considered as the unit, and the nest was included as a random factor to avoid pseudoreplication. Hatching order (first- vs. second-hatched egg) and chick mortality (dead vs. alive chicks) were analyzed in generalized linear mixed models (GLIMMIX, Littell et al. 1996) with binomial error distribution in which the egg/chick was considered as the unit and the nest was included in the model as a random factor. Hatching asynchrony showed a Poisson distribution ($\chi^2 = 4.83, P = 0.18$); thus this variable was analyzed using generalized linear models (GLIM) adjusted to a log link function and Poisson error. Hatching period did not follow a normal distribution (Shapiro–Wilk, $W = 0.8, P < 0.01$), for which residuals from GLMM models where hatching period was included as response variable were checked for normal distribution. As explanatory variables of the models, we included the covariates hatching date of the egg and flipper length of both parents. Hatching order, brood sex ratio (0, 1, or 2 males), hatching success (hatched vs. unhatched), hatching asynchrony (synchronous vs. asynchronous), and/or chick sex were considered as fixed factors in the different models.

Some of the explanatory variables could covariate; thus we fitted their effects to the observed data following forward and backward stepwise procedures, testing the significance of each variable one by one, and adding (forward) or removing (backward) only the variable that resulted in the largest increase in model fit. The result is the most adequate model for explaining the variability in the response variable that coincided in both forward and backward processes. We used the Akaike’s Information Criterion (AIC; Akaike 1973) to determine the model that fitted better the data, when 2 alternative models resulted. When we compared the proportion of chick mortality within a sex in different brood types, we used generalized linear models with logit link function and binomial distribution (PROC GENMOD, SAS 2001). Mean values $\pm$ standard errors are given. To maintain a better clarity of the results, only $P$ values are given from nonsignificant outcomes.

**RESULTS**

**Egg volume, sex, and hatching period**

Egg volume did not differ between hatched and unhatched eggs (GLMM, $P = 0.54$). Considering only hatched eggs, we did not find any effect of sex, hatching date, or parent flipper lengths on egg volume (GLMM, all $P > 0.41$).

Hatching period was significantly explained by sex, egg volume, and hatching date (Table 1). Larger eggs and eggs hatched earlier in the season showed shorter hatching periods. Males also showed shorter hatching periods than females (Figure 1). Parent flipper lengths and hatching asynchrony (synchronous vs. asynchronous) were not significant (GLMM, all $P > 0.22$). Residuals from the model showed a normal distribution (Shapiro–Wilk, $W = 0.98, P = 0.23$). Considering only asynchronous nests, hatching period was significantly affected by sex, egg volume, and hatching order (Table 1). Second-hatched eggs showed longer hatching periods than first-hatched eggs. Parent flipper lengths, hatching date, and the interactions between sex $\times$ hatching order and sex $\times$ egg volume were not significant (GLMM, all $P > 0.14$).

**Hatching order and hatching asynchrony**

Controlling for hatching period, we did not find sexual differences in hatching order (GLIMMIX, hatching period: $F_{1,80} = 13.84, P < 0.001$; sex: $F_{1,80} = 0.07, P = 0.79$).

Hatching asynchrony was less than 1 day in 31 (24%) nests, 1 day in 60 (46%) nests, 2 days in 26 (20%) nests, 3 days in 11 (8%), and 4 days in 2 (2%). Hatching asynchrony was only explained by the intraclutch variation in egg volume (GLIM, $F_{1,129} = 11.27, P = 0.001$). Clutches with higher egg volume variation showed higher hatching asynchrony. Parent flipper lengths, hatching date, and brood sex ratio did not show significant effects (GLIM, all $P > 0.31$). Considering only asynchronous nests, hatching asynchrony was likewise explained by the intraclutch variation in egg volume (GLIM, $F_{1,88} = 4.69, P = 0.033$). The rest of the variables did not show significant effects (GLIM, all $P > 0.11$). Nevertheless, when also including the egg size and hatching period of first- and second-hatched eggs in the model, the effect of the intraclutch variation in egg volume disappeared (GLIM, $P = 0.10$), and hatching asynchrony became significantly explained by the hatching period of the second-hatched egg (GLIM, $F_{1,88} = 10.52, P = 0.002$). No other variables remained in the model. Because the hatching period was larger in females, hatching asynchrony increased significantly when the second-hatched egg was a female (GLIM, $F_{1,88} = 4.16, P = 0.044$). The sex of the first egg did not affect hatching asynchrony (GLIM, $P = 0.98$).

**Sexual size dimorphism and body condition of chicks**

At 25 days of age, chick size (flipper length) was significantly affected by sex and egg volume (Table 2). At this age, males...
were already 4% larger than females (males = 167.7 ± 1.0 mm, n = 99; females = 161.1 ± 1.0 mm, n = 85). Chicks coming from larger eggs showed larger flipper lengths. Parent flipper lengths, hatching date, hatching period, hatching asynchrony (synchronous vs. asynchronous), brood sex ratio, and the interaction sex × egg volume had no significant effects (GLMM, all F > 0.11). Body mass of chicks was similarly significantly explained by sex and egg volume and also by hatching date (GLMM, sex: F₁,81 = 9.55, P = 0.003; egg volume: F₁,81 = 10.35, P = 0.002; hatching date: F₁,81 = 7.78, P = 0.007). Chicks from larger eggs and hatched earlier in the season were heavier. Males were 6% heavier than females (males = 2105 ± 24 g, n = 99; females = 1982 ± 26 g, n = 85). Parent flipper lengths, hatching period, brood sex ratio, and hatching asynchrony did not affect significantly body mass of chicks (GLMM, all F > 0.31). Body mass was corrected by flipper length (covariate) to have an estimation of body condition. In this case, body mass was significantly affected by egg volume, hatching date, and chick flipper length (Table 2). The rest of the variables, including sex and the interaction sex × egg volume were not significant (GLMM, all P > 0.50). To know the effect of hatching order on chick body condition, we worked only with asynchronous nests. No differences were found between first- and second-hatched chicks, and the interactions sex × egg volume and sex × hatching order were not significant (GLMM, all P > 0.39).

**Table 2**

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**Chick mortality**

Mortality was only explained by brood sex ratio and hatching period (GLIMMIX, brood sex ratio: F₂,90 = 4.71, P = 0.011; hatching period: F₁,90 = 8.33, P = 0.005). Parent flipper lengths, egg volume, hatching date, and hatching asynchrony (asynchronous vs. synchronous) had no significant effects (GLIMMIX, all P > 0.16). Mortality increased with brood sex ratio; all-male broods showed the highest mortality rate. In addition, chicks were more prone to die when their hatching periods were longer. However, because hatching period was affected by sex (see above), we repeated the previous analysis excluding hatching period to see if there existed then a sex-biased nestling mortality that would have been masked by the correlated hatching period. Indeed, male chicks were generally more prone to die (GLIMMIX, sex: F₁,90 = 6.26, P = 0.014; brood sex ratio: F₂,90 = 6.96, P = 0.002). Parent flipper lengths, egg volume, hatching date, and hatching asynchrony (asynchronous vs. synchronous) had no significant effects (GLIMMIX, P > 0.20). Furthermore, we wanted to see if hatching order (also defining hatching period, see above) also affected mortality. But because this information was only available in asynchronous broods, we excluded synchronous broods from the following model. In asynchronous broods, the effect of hatching period disappeared, and chick mortality was significantly explained by sex, hatching order, and brood sex ratio (Table 3). Egg volume and hatching date explained some of the variance of chick mortality although the effect was not significant. The model with both variables fitted better the data (AIC = 967.1) than without them (AIC = 1093.0). Parental body measurements, hatching asynchrony, and hatching period did not correlate significantly with chick mortality (GLIMMIX, all P > 0.19).

**Table 3**

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**Chick mortality and body condition in each brood type**

We evaluated the effect of hatching order on chick mortality in asynchronous nests (18 all female, 39 mixed, and 25 all male) and additionally of sex and its interaction with hatching order in mixed broods (Figure 2). Because egg size and hatching date previously were included in the model that best explained chick mortality model, these were also considered in the following analyses.

In all-female nests, chick mortality was not significantly affected by hatching order (Figure 2), hatching date, or egg volume (GLIMMIX, all P > 0.56). In all-male nests, mortality was correlated with hatching date and was higher, although only marginally significant, in second-hatched chicks (GLIMMIX, hatching date: F₁,25 = 5.83, P = 0.025; hatching order: F₁,25 = 4.06, P = 0.056; Figure 2). Egg volume had no significant effect (GLIMMIX, P = 0.33). Interestingly, chick mortality in mixed broods was biased toward females and was also higher for second-hatched chicks (GLIMMIX, sex: F₁,37 = 14.63, P < 0.001; hatching order: F₁,37 = 28.64, P < 0.001; Figure 2). Hatching date, the interaction between sex and hatching order, and egg volume did not affect significantly chick mortality (GLIMMIX, both P > 0.46).

**Figure 2**

Mortality (percentage) related to hatching order of chinstrap penguin chicks in asynchronous nests with different brood sex ratio composition. Squares represent males and dots represent females.
Combining synchronous and asynchronous nests, we found sexual differences of mortality depending on the brood sex ratio composition (GLMM, both $\chi^2 > 12.26$, $P < 0.007$). Between-group contrasts showed that the frequency of chick mortality was significantly higher in all-male than in all-female broods ($\chi^2 = 8.88$, $P = 0.003$). Also, more males died in all-male than in mixed broods ($\chi^2 = 7.03$, $P = 0.008$). In the case of females, chick mortality was higher in mixed than in all-female broods ($\chi^2 = 3.73$, $P = 0.053$).

In relation to body size and condition, controlling for hatching date and egg volume, males from all-male broods did not differ in flipper length or body condition (body mass corrected by flipper length) from males of mixed broods (GLMM, both $P > 0.34$). Female chicks in mixed broods did not differ in body condition (GLMM, $P = 0.93$) but were smaller (flipper length), although not significantly so (GLMM, $F_{1,14} = 4.27$, $P = 0.058$), than female chicks in all-female broods.

**DISCUSSION**

**Hatching patterns**

We found that hatching period had an important role in defining the within-nest hatching patterns. Hatching period was affected by hatching order, sex, and egg size (volume). First-hatched eggs showed shorter hatching periods than second-hatched eggs in asynchronous nests. Possibly, this is a consequence of the less efficient incubation that second eggs receive when there is already a hatching in the nest. The presence of hatched chicks in a nest decreases the temperature of remaining pipped eggs and thereby reduces the metabolic rate of the embryo (Evans 1990; Ricklefs 1993). In our penguin colony, adults stop to incubate the eggs when the first-hatched chick reaches 4 days because the size of the chick prevents the adults from incubating (personal observation). If the second egg does not hatch in this 4-day period, probably it will never hatch. This observation coincides with the fact that the highest hatching asynchrony found was 4 days.

We found that males are more capacitated in some way to break the shell and hatch faster than females. Lipar and Ketterson (2000) reported in the red-winged blackbird *Agelaius phoeniceus* that the anabolic effect of yolk testosterone increases the development of the hatching muscle musculus complexus, conferring the chick a more efficient breaking through the eggshell. Although no sexual differences in the mass of the hatching muscle were observed in that study, male egg-embryos of birds likely possess or develop higher levels of testosterone during the embryonic period (Petrie et al. 2001), presumably allowing them to hatch more efficiently compared with their female nest mates.

Furthermore, also chicks coming from larger eggs hatched faster. In birds, chicks from large eggs result in better quality adults (Grant 1991; Amundsen 1995) and experience a faster growth and a higher probability of survival (Schifferli 1973; Williams 1994; Amundsen 1995). In our study, we did not find mortality to be significantly affected by egg volume, but, after taking into account the effect of sex, surviving chicks until 25 days of age were of larger size, weight, and of better body condition when they came from larger eggs. Given these persistent effects of egg size on chick quality, larger eggs probably contain higher amounts of essential egg compounds, such as fat (yolk) reserves, that allow the chicks to withstand more prolonged food restrictions (Ricklefs 1993). These higher storage of nutrients or energetic compounds in larger eggs, coming probably from parents of better quality, could also make the chicks more efficient in breaking the eggshell. In addition, the consistency of eggshell thickness can diminish as the egg size increases in pigmented eggs (Gosler et al. 2005). Although penguin eggs are unpigmented, this idea would be interesting to evaluate in future studies as it could account for differences in hatching period in relation to egg size.

Hatching asynchrony was only explained by the intraclutch variation in egg volume. This finding is in accordance with a previous study in the chinstrap penguin (de León et al. 2001). However, when also considering the hatching period, the effect of intraclutch variation of egg volume became just a tendency, and the degree of hatching asynchrony in the nest was explained by the hatching period of the second-hatched egg. This indicates that the combined effect of sex and size, which defines hatching period, explained hatching asynchrony in the nest. Larger eggs hatched faster; thus the intraclutch egg variation involved egg differences in hatching periods. In addition, males showed shorter hatching periods than females, for which hatching asynchrony also increased when second-hatched eggs were females. This would explain why the laying interval (varying from 0 to 5 days) in this species is not related to hatching asynchrony (de León et al. 2001), although the first-laid egg is also the first to hatch (de León et al. 2001). The effect of size and sex, at least, should be taken into account to find a correlation between these 2 variables.

In the chinstrap penguin, the degree of hatching asynchrony was not correlated with indicators of parental quality, such as hatching date, body condition, or health status (Moreno et al. 1994; de León et al. 2001; this study); was not more frequent in years with food scarcity (Moreno et al. 1994); and was not associated to survival or growth of penguin chicks (Moreno et al. 1994; this study). Results of the present and previous studies give no reasons to think that hatching asynchrony in chinstrap penguins is an outcome of parental quality.

**Sex/size-linked mortality**

Sexual differences in size were already detected at 25 days of age, in males having larger body size (flipper) and body mass compared with females. Body condition did not differ between the sexes at this age. Therefore, sexual size dimorphism could be an option to explain the male-biased mortality in this species, supporting the energy demand hypothesis. However, the pattern of male mortality was different depending on the brood sex ratio composition. The mortality of male chicks increased in all-male broods and diminished in mixed broods where actually more female than male chicks died. In addition, second-hatched females in mixed broods suffer from higher mortality than first-hatched females. Both results add support to the competitive advantage hypothesis. Together, these results allow us to reject the sex phenotype hypothesis accounting for sexual differences in mortality and also to think that 2 different mechanisms seem to operate in the same species during the same breeding season. Depending on nest conditions, the sexes responded differently to the same annual environmental conditions. The sex-linked mortality pattern observed in our study suggests that both the energy demand and the competitive capacity hypotheses act simultaneously. No intrasexual differences, however, were found in body condition between different brood types, although a trend was observed in the case of females. Probably mortality occurred at early phases of growth, promoting an efficient brood reduction (Lack 1954). If males, due to their larger size, need more food requirements than females, it is foreseeable to find more nestling starvation in nests where both chicks are males compared with all-female nests. In addition, if a large size also confers advantages in sibling
competition, it is predictable to find higher survival rates of males when their nest mates are females than when sharing the nest with other males. In contrast, females should die more frequently in mixed broods than in all-female broods, as it happens.

The foraging trip for chick feeding is a costly and risky activity for Antarctic penguins as parents have to forage frequently at long distances (Williams 1995) and have to avoid the constant presence of leopard seals Hydrurga leptonyx, a main penguin predator, on the colony coast (personal observation). Probably this is the reason why pygoscelids feed their young at most once a day and usually less often (Williams 1995; personal observation), implying that chicks of pygoscelid penguins consume infrequent but large meals relative to their body size (Prince and Harris 1988; Janes and Chappell 1995). In this scenario, any advantage in sibling competition, such as hatching first or being moderately larger, can be of vital importance for nestling survival. Furthermore, hatching order was a determining factor for survival in all-male broods but not so in all-female broods. These observations and the connection between hatching period and hatching order lead to the suggestion that males suffer from stronger pressures to hatch faster.

One possible confounding factor in the interpretation of our results could be that all-male broods were more frequently produced by low-quality parents inducing higher mortality rates in this brood type as a consequence of the lower capacity of parents to feed their chicks. However, previous studies in this species pointed out the opposite. More males seem to be produced by high-quality parents (Fargallo et al. 2004; JA Fargallo, V Polo, L de Neve, J Martín, JA Dávila, and M Soler, in preparation) as predicted by sex allocation theory (Trivers and Willard 1973).

In summary, our results suggest that hatching asynchrony in chinstrap penguins is greatly a consequence of proximate factors, such as within-nest differences in hatching periods and the sex of the second-hatched (laid) egg. Furthermore, our study suggests that hatching period can be a mechanism underlying sexual differences in the embryonic period as hatching period is implicit in the period covering from the onset of incubation and hatching. This information should be taken into account in future studies. Finally, our study constitutes a good example of how patterns of sex-related mortality can vary depending on nest environmental circumstances. Our results indicate that postnatal sex-biased vulnerability may vary in relation to brood sex ratio composition. Moreover, it seems that 2 different mechanisms, proposed up till now to explain interspecifically patterns of sex-biased mortality, probably acted in the same species and in the same breeding season.

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