

# Effect of initial asymmetry in Magellanic penguin chick's performance. A cross-fostering experiment.

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## Abstract

When chicks in a brood hatch asynchronously, the first to hatch gets fed sooner, creating a hierarchy of asymmetries in the brood. In species that suffer from brood reduction, this asymmetry can facilitate the death of one chick during periods of low food availability. The aim of this study was to analyze the effect of initial asymmetries on the growth and survival of Magellanic penguin *Spheniscus magellanicus* chicks, after disentangling the effects of parental condition, during four breeding seasons. We manipulated chicks' asymmetries within the brood by performing a cross-fostering experiment, creating broods with different weight ratios in a colony located in Isla Quiroga, Santa Cruz, Argentina. We found that weight ratio determines the asymmetry within the brood throughout the entire breeding season, and that final asymmetry also depends on the study season. Chicks that hatch last have a greater chance of survival when the weight ratio with their older sibling is closer to 1. Parental body condition affects chick growth but not asymmetry. To conclude, parents do not reverse the effect of initial asymmetry in post-hatching stages, even during breeding seasons of high reproductive success.

## Introduction

Chicks in a brood can hatch asynchronously (Lack 1947, 1954; Clark and Wilson 1981; Stoleson and Beissinger 1995; Sockman et al. 2006). In some species, this hatching asynchrony is related to asymmetries within the brood during the early stage of chick growth (Boersma and Stokes 1995). Adults are able to feed the first-hatched chick before the sibling's hatch, creating a hierarchy of asymmetries within the brood. Some authors have proposed that the hierarchies are an adaptation that facilitates mortality of the last-hatched chick by competition among siblings in years in which food resources are insufficient for rearing the whole brood (Forbes and Ankney 1987; Price et. al, 1996; Ostreiher, 1997; Parker et al. 2002). So, under poor food conditions, chicks of symmetrical broods (similar sized) receive the same amount of food, insufficient though, reducing nesting success. In contrast, the larger chicks of asymmetrical broods receive more food than their smaller sibling, causing the early death of the latter but the remaining chicks receive enough food to survive. In seasons with high food supply, parents feed all the chicks equally, and there is no brood reduction despite de asymmetry (Temme and Charnov 1987). Thus, females lay the number of eggs that they could raise in conditions of high food availability, and then reduce the clutch size in adverse conditions (Mock 1984, Magrath 1990).

Several studies on seabirds have attempted to test the effects of initial asymmetry within the brood (Seddon and Van Heezik 1991; Boersma and Stokes 1995; Giudici et al. 2017; Wagner and Boersma 2019). However, all the previous studies, even those on the same species, include a single breeding season or, if more than one season is covered, they all have similar favorable environmental conditions. Seddon and Van Heezik (1991), using a breeding season on Jackass penguin (*Spheniscus demersus*), found that nestlings in more asynchronous broods (i.e. more asymmetrical broods) starved to death more frequently than in more symmetrical broods. Giudici et al. (2017) on imperial cormorant (*Phalacrocorax articeps*), found that the breeding success was independent of the asymmetry and the hatching asynchrony favored the early brood

reduction. Boersma and Stokes (1995), in a non-manipulative study on Magellanic penguin (*Spheniscus magellanicus*), found that in asymmetrical broods, heavier chicks were more likely to fledge than its sibling. Parental regulation of asymmetries may be due to food delivery preferences and different strategies have been reported, such as (a) parents may prefer to feed the larger chick (Smith et al. 2005); (b) females prefer to feed the smallest chick, but the males do not (Ploger and Medeiros 2004); (c) parents have no preference (Wagner and Boersma 2019); and (d) it was also found that parental favoritism changes over the reproductive season (Shizuka and Lyon 2013). In Magellanic penguin, Wagner and Boersma (2019), during three season of high breeding success, found that in broods with two chicks, none of the chicks received more food than its sibling. Thus, the effect of asymmetry within the brood may be masked by other factors (e.g. variability among different breeding seasons, effects inside the brood and the chick's stage period). Indeed, in this same species, Blanco et al. (1996) found that parents feed preferentially larger chicks.

The Magellanic penguin (*Spheniscus magellanicus*) is a seabird with facultative brood reduction (Lamey 1990). This species has highly variable fledging success among breeding seasons and colonies due to differences in the quality and quantity of food obtained by the adults to feed their chicks (Boersma et al. 1990; Barrionuevo et al. 2018; Ciancio et al. 2018). Starvation is the most common cause of chick death (Boersma and Stokes 1995, Frere et al. 1998). This species lay two eggs that hatch with an asynchrony of 1.6 days (range: -1 to 4 days) (Boersma et al. 1990; Barrionuevo 2015). In this species, studies of food distribution within the clutch are contradictory.,

This study intended to provide evidence of whether the initial asymmetry has adaptive significance in brood reduction, or whether it is a consequence of other processes or restrictions, such as physiological ones that generate hatching asynchrony and therefore an initial asymmetry. The aim of this study was to determine the effect of initial asymmetry (IA) in Magellanic penguin brood's performance by means of a cross-fostering experiment that allows to establish several initial asymmetries. This would provide understanding of how the initial asymmetry is related to the dynamics of the asymmetries within the brood throughout the season, and to the growth and survival of the chicks within the brood, disentangled from parental body condition. This work addresses four consecutive reproductive seasons with different conditions of food availability (and fledging success). We hypothesized that: 1) The asymmetry within the clutch during the nestling period is a combination of the IA and the food availability; 2) the season and the IA affect chick survival and growth.

## Methods

### *Study area and species*

Isla Quiroga, Santa Cruz, Argentina (47°45'S, 65deg53'W) is an island situated 80 m from the coast, in the Ria Deseado (river inlet). It hosts a Magellanic penguin colony of about 1500 breeding pairs (Millones et al. 2022). Magellanic penguins have a seasonal breeding schedule (Barrionuevo & Frere 2014). Both parents share parental care (Boersma et al. 1990). Chicks hatch with a weight ratio of 94% (i.e., the weight of the second chick at birth is 94% of the weight of its sibling on the same day) ranging from 80% - 102% (Marchisio unpubl.). The proportion of high/low quality prey in the diet is important to nestling survival and growth (Barrionuevo et al. 2018). Chick diet is based on fish and squid (Frere et al. 1996). However, the proportion of these prey items is more similar to the father's diet than to the mother's because both parents consume the same prey but in different proportions (Ciancio et al. 2018), and chick growth is more closely related to the father's condition than to mother's (Barrionuevo et al. 2018). At Isla Quiroga, Magellanic penguin breeding success (0.9 fledglings/nest, according to a 13-year study (Frere et al. unpubl.)) is higher than in other colonies (0.53 fledgling/nest at Cabo Virgenes (Frere et al. 1998), 0.61 fledgling/nest at Punta Tombo (Boersma et al. 2013)).

### *Field methodology*

We worked for four consecutive breeding seasons (2018: 150 nests; 2019: 97 nests; 2020: 160 nests; 2021: 160 nests). In early October, at the very beginning of the breeding season, we randomly selected nests with either a male or a couple and marked them with flagging tape. We checked them daily and when an egg was laid, we numbered it. We repeat the same procedure for second egg.

To assess parental body condition (BC), we captured females on the day they laid the second egg, and males when they returned to the nest to take their first incubation shift. We measured the following: weight (+ 25 g; using a spring scale), length of foot (+ 1 mm; using a ruler) from the bend in the tarsus to the end of the middle toenail, length of flipper (+ 1 mm; using a ruler) from the joint between humerus and radius-ulna to the tip of the flipper, bill length (culmen, from the point where the upper mandible emerges from the forehead feathers to its tip; + 0.1 mm) and bill depth (up to the nostrils; + 0.1 mm) using a Vernier caliper. A body-size index was calculated as the first component extracted from a principal component analysis (PCA) of all the measurements (one index was calculated for males and another for females, since this species has slight sexual dimorphism, the males being larger than the females (Gandini et al. 1992)). Residuals of body weight and size index regression were used as indices of body condition (BCI, FBCI for females and MBCI for males) (Yorio et al. 2001).

Thirty-five days after the first egg was laid, we checked nests daily to determine the hatching date of both eggs. On the hatching day, we marked the chicks with a waterproof pen, weighed them using a spring scale (+ 1 g) and measured foot length, flipper length, bill length and bill depth with a caliper (+ 0.1 mm). After the second egg hatched, we weighed chicks every three days. We assumed a chick fledged if it was alive at 60 days old.

### *Cross-fostering experiment*

When both eggs of the brood hatch, the marked nests were randomly classified into two categories: ‘control brood’ or ‘manipulated brood’. Control nests were only used to check that the cross-fostering was not affecting nestling survival. In those nests, we only did the procedure described in the “field methodology” section.

In the “manipulated broods”, when the second egg hatched, we weighed chicks and then exchanged the chicks among the nests to obtain broods with three initial conditions: 1) both chicks of the same weight (i.e., the second chick’s weight was 98% - 102% of the weight of the first chick), 2) a second chick smaller than the first chick, covering the natural difference range of the colony (80% - 97% weight difference), and 3) the more extreme values (80% - 65% weight difference). Therefore, this method established clutches with different initial weight asymmetries. We calculated a weight ratio (WR) per brood with the weight asymmetries of the chicks:

$$WR = \frac{\text{Weight of second chick}}{\text{Weight of first chick}}$$

We used this relativized measure (WR) instead of the asymmetry (2nd chick weight-1stchick weight), so we can have a standardized measure of the relation of the chicks throughout of the breeding season. Initial weight ratio (IWR) is the WR at the day of the relocation of the chicks. Thus, IWR ~1 corresponds to “manipulated broods” with the initial condition of second chicks having similar weight to firsts chick. Also, we made sure that no chick was placed in a brood with a biological sibling.

### *Data analysis*

#### *Validation of the cross-fostering manipulation and annual breeding success*

To assess the effect of cross-fostering manipulation, we fitted generalized linear model (GLM) with the function ‘glm’ using the “Poisson” family and ‘log’ like link function. We used the number of chicks alive per brood at the end of the season as breeding success of each brood as the response variable and the predictive variables: treatment (control and manipulated), study season (2018, 2019, 2020 and 2021) and the interaction between both. The nest ID was a random variable. In all other analyses that follow we only used the “manipulated broods”.

#### *Weight ratio at different stages*

To evaluate hypothesis 1, i.e., to assess the effect of IWR and the breeding season on the observed WR across different chicks ages, we fitted four linear models (LM). We run one LM for four different chick's ages (5 days old, 15 days old, 25 days old and 50 days old, for the latter we used an average of the last four weight records due to the high daily variability of weight at this age). The response variable was the WR observed within the brood for each age. The predictor variables were IWR, female body condition index, male body condition index, the study season (2018, 2019, 2020 and 2021, except for the age of 50 days where we excluded the 2019 season due to lack of broods with two chicks), and the double interactions possible. In all cases we used broods with two live chicks for the evaluated age.

### *Chick mortality analysis*

To evaluate the first part of the hypothesis 2, we ran a mixed effects COX model ('coxme' package, Therneau 2022) using the chick age when died or 60 age when the checking finished as the response variable. The predictable variables were study season (2018, 2019, 2020 and 2021), IWR, hatching order (HO) (1<sup>st</sup> or 2<sup>nd</sup>), female body condition index, male body condition index, the double interaction between all variables and the triple interaction among IWR, HO and the study season. The brood ID as a random variable.

### *Chick growth*

We fitted individual chick growth (weight) curves using a Gompertz growth curve (Barrionuevo 2015). This fitting, curve has three parameters: asymptotic value (a) (maximum weight [g]), rate of change (b) (growth rate [g \* day<sup>-1</sup>]) and inflection point (c) (days until maximum rate [days]).

To assess the second part of the hypothesis 2, we ran a non-linear mixed model (NLMM). The response variable was chick weight (g) throughout the breeding season (all measures taking during nests checks). The predictor variables were IWR, hatching order (HO), the season under study (2018, 2019, 2020 and 2021), female body condition index, male body condition index, the double interaction between all the variables and the triple interaction among IWR, HO and the study season. In all cases, nest ID and chick ID were independents random variables. We only used broods with two surviving chicks at the end of each season. The 2019 season was excluded from the analysis due to the lack of clutches with two chicks at the end of the season.

All analyses were performed in R software version. 4.2.0 (<[www.r-project.org](http://www.r-project.org)>). For the first analysis, validation of the cross-fostering manipulation, we used the function 'glm' with the "Poisson" family and 'log' like link function and "Chisq test" was used to compare the different models. For the linear models we used the 'lme4' package and for the non-linear models we used the 'nlme' package. For mortality analysis we used the 'coxme' package (Therneau 2022). When necessary, we tested for random effects by comparing the model with and without the random factor with a likelihood ratio test (Zuur et al. 2009). We used a backwards selection procedure for the non-linear models, removing the terms one by one in decreasing order of complexity (interactions first) and according to a decreasing P value. After this, we compared models with and without the eliminated variable to the 'ANOVA' function and selected the model with the lowest AIC (Akaike information criterion) (Crawley 2012).

## **Results**

### *Validation of the cross-fostering manipulation and annual breeding success*

There was no relationship between treatments (control broods and treatment broods) and reproductive success (dev = -1.001,  $p = 0.751$ ), so cross-fostering did not affect brood success. The interaction between season and treatment, was not significant (dev = -0.108,  $p = 0.991$ ) (Table S1).

We found differences in reproductive success among the study seasons. The season 2019 ( $0.18 \pm 0.30$  chicks/brood) had the lowest breeding success, followed by 2018 ( $0.48 \pm 0.62$  chicks/broods) and 2021 ( $0.97 \pm 0.76$  chicks/broods), and season 2020 with the highest ( $1.37 \pm 0.8$  chicks/brood) (dev = -101.352,  $p < 0.001$ ).

### *Weight ratio at different stages*

We cross-fostered 308 broods (80 in 2018, 60 in 2019, 80 in 2020 and 88 in 2021). In those broods, the mean IWR (initial weight ratio=weight 2<sup>nd</sup>/1<sup>st</sup> chick) generated was similar among seasons:  $0.74 \pm 0.23$  in 2018;  $0.88 \pm 0.25$  in 2019;  $0.76 \pm 0.26$  in 2020; and  $0.79 \pm 0.25$  in 2021.

The WR evaluated at different ages depended only on the IWR at early ages (5 days old, 15 days old, 25 days old and 50 days old). At the end of the nestling period (50 days old), in addition to the IWR, it also depended on the study season (Table 1). The WR between siblings was larger with increasing the IWR (Table 1). At 50 days old, the WR was also larger in season 2018 than seasons 2020 and 2021, but there was no difference between 2020 and 2021 (Table 1, Figure 1). The other study variables, parental body conditions and interactions, did not have a significant effect (Table S2).

### *Chick mortality analysis*

Nestling mortality depended on the interaction between IWR, HO and study season (Table 2).

Comparison of the different reproductive seasons showed that there was differential mortality between the two chicks only during the 2018 season (Table 2) (i.e., Second chicks from broods with higher IWR (i.e., broods with more symmetrical chicks) had higher mortality than those from broods with lower IWR (i.e., more asymmetrical broods) in the season 2018 compared with seasons 2019, 2020 and 2021 (Table 2)). Male and female parental BCI were not significant (Table S3).

### *Chick growth*

Regarding chick growth, the asymptotic estimated weight depended on the interaction between IWR and the study season, and the interaction between HO and the study season (Table 3). During 2020, chicks from broods with a higher IWR (i.e., more symmetrical broods) had greater asymptotic estimated weight than chicks from broods with a lower IWR (i.e., more asymmetrical broods) (Table 3). Growth rate depended on the interaction between MBCI and the season, the interaction between MBCI and HO, and the interaction between IWR and HO (Table 3). During 2020, males with higher BCI had chicks with a lower growth rate than males with a lower BCI, comparing with 2018. Similarly, second chicks from broods with males with a higher BCI had a lower growth rate than chicks from broods with males with a lower BCI. On the other hand, second chicks from broods with a higher IWR (i.e., more symmetrical broods) had a lower growth rate than chicks from broods with a lower IWR (more asymmetrical broods) (Table 3). The other variables evaluated were not significant (Table S4).

## **Discussion**

Our results suggest that initial weight ratio between siblings (IWR) determined the asymmetry present in the clutch throughout the reproductive season. The effect of the IWR in the WR at late stages of the chick rearing period was not the same for all breeding seasons. The effect of the IWR on nestling survival was not the same for all seasons. IWR was stronger during the intermediate/low breeding season where IWR affected nestling fate more than in the other seasons. Parental body condition, especially the physical condition of the male, only had a season dependent effect where more symmetrical broods had heavier chicks in the season of high breeding success. On the other hand, parental body condition, only had an effect on chick's growth.

When manipulating IWR within a brood by generating broods with first and second chicks with the same weight (symmetrical broods) and broods with first chicks larger than second chicks (asymmetrical broods), we found that the WR at different stages of the chick rearing period had positive dependence on the IWR until the end of the season.

The latter was not found for the same species from a different colony, in which the initial asymmetry (IA) had an effect only during the early stage of chick rearing, and the effect wore off towards the end of the season (Boersma and Stokes 1995). On the other hand, it has been reported that in the Magellanic penguin, at mid/late stages of the rearing period, the parents deliver a similar amount of food to the chicks, so it is expected that the differences in weight between siblings will be diluted (Wagner and Boersma 2019). Blanco et al. (1996) reported that the largest chick received more food. The difference between these two

studies, which were conducted in the same colony, may be due to the fact that Wagner and Boersma (2019) only used seasons with high breeding success. Second chick survival was affected by IWR within the brood only during the season of mid/low breeding success, and not during the seasons with high or extremely low breeding success. This was expected since, for the same colony, Barrionuevo (2015) found that in a season with low breeding success, there was no difference between chicks according to hatching order, and both chicks were equally likely to die. Similarly, in seasons with high breeding success, differential mortality is not expected because the amount of food available is sufficient to rear both chicks, in agreement with Temme and Charnov (1987), where no brood reduction is expected. During the 2018 season, we found that second chicks had a higher survival rate when they came from more symmetrical clutches. This agrees with Davis and McCffrey (1986), who reported for the Adélie penguin (*Pygoscelis adeliae*) that the distribution of food within the brood is dependent on the competition between siblings. Thus, since there is no great difference in size between siblings, food is not monopolized by the largest chick.

Regarding chick growth, we found that chicks from more symmetrical broods had high weight at independence during the season with high breeding success, compared to seasons with mid/high and mid/low breeding success. Corroborating our hypothesis, due to the high availability of food during the 2020 season, the parents deliver more food to the entire brood. This is contrary to the report by Boersma and Stokes (1995), who found no relationship between IWR and the weight of the chicks at the end of the reproductive season. On the other hand, it has been reported for Magellanic penguins that the asymmetry between siblings does not influence the amount of food received by the chicks in highly successful breeding seasons (Wagner and Boersma 2019).

In this species, body condition of males may cause effects between siblings (Marchisio et al. 2021). We found that improving males body condition leads to a detriment in the growth rate of chicks on the season of high breeding success. This was not expected since for the same colony it was found that male body condition affects the food received by chicks (Ciancio et al. 2018). What we have found in our study, may be due to the fact that at the end of this season (season of higher breeding success) chicks that come from broods with males with larger condition begin the moulting early, which generates a weight drop.

## Conclusion

This study corroborated the hypothesis that initial weight ratio has an effect throughout the entire reproductive season of the Magellanic penguin. In seasons of medium/low reproductive success, having initial weight ratio closer to 1 (i.e.: in more sim broods) gives the second chick a survival advantage by preventing food monopolization by the older sibling. Once asymmetry is established within the brood, the parents do not interfere with it, and these asymmetries and the conditions of food availability determine the survival of the chicks in a brood. The mechanism by which the parents could intervene in the survival within the brood would be through the establishment of an initial asymmetry, following which the rivalry between siblings would act on their destiny. In addition, the condition of the parents is important for chick growth, but not for survival.

## References

- Barrionuevo, M. (2015). Inversión parental en el Pingüino de Magallanes (*Spheniscus magellanicus*): asincronía de eclosión, causas próximas y últimas (Doctoral dissertation, Universidad de Buenos Aires. Facultad de Ciencias Exactas y Naturales).
- Barrionuevo, M. and Frere, E. 2014. Parental investment in eggs and its effect on nestling growth and survival in Magellanic penguins. *Emu-Austral Ornithol* . 114: 259–267.
- Barrionuevo, M., & Frere, E. (2016). Egg temperature and initial brood patch area determine hatching asynchrony in Magellanic penguin *Spheniscus magellanicus* . *Journal of Avian Biology* , 47(1), 16-25.
- Barrionuevo, M., Ciancio, J., Marchisio, N., & Frere, E. (2018). Parental body condition and high energy value of fish determine nestling success in Magellanic penguin (*Spheniscus magellanicus*). *Marine Biology* , 165(6), 1-16.

- Blanco, D. E., Yorio, P., & Boersma, P. D. (1996). Feeding behavior, size asymmetry, and food distribution in Magellanic penguin (*Spheniscus magellanicus*) chicks. *The Auk*, 113(2), 496-498.
- Boersma, P. D., Stokes, D. L., Yorio, P. M., Davis, L., & Darby, J. (1990). Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. *Penguin biology*, 7, 15-44.
- Boersma, P. D., & Stokes, D. L. (1995). Mortality patterns, hatching asynchrony, and size asymmetry in Magellanic Penguin *Spheniscus magellanicus* chicks. *The penguins: ecology and management*. Surrey Beatty and Sons, Chipping Norton, NSW, Australia, 3-25.
- Boersma, P. D., Garcia-Borboroglu, P., Frere, E., Kane, O. J., Pozzi, L. M., Putz, K., Raya Rey, A., Rebstock, G. A., Simeone, A., Smith, J. R., Yorio, P. and Van Buren, A. 2013. Magellanic penguins *Spheniscus magellanicus*. In: Boersma, P. D. and Borboroglu, P. (eds), *Penguins: natural history and conservation*. Univ. of Washington Press, pp. 233–263.
- Braasch, A., & Becker, P. H. (2019). Maternal investment in last-laid eggs does not compensate for hatching asynchrony in a seabird. *Oecologia*, 190(1), 47-58.
- Ciancio, J. E., Yorio, P., Wilson, R., & Frere, E. (2018). Food provisioning in Magellanic penguins as inferred from stable isotope ratios. *Rapid Communications in Mass Spectrometry*, 32(6), 489-494.
- Clark, A. B., & Wilson, D. S. (1981). Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *The Quarterly Review of Biology*, 56(3), 253-277.
- Crawley, M. J. (2012). The R book. *John Wiley & Sons*.
- Davis, L. S., & McCaffrey, F. T. (1986). Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). *The Auk*, 103(2), 379-388.
- Forbes, M. R., & Ankney, C. D. (1987). Hatching asynchrony and food allocation within broods of Pied-billed Grebes, *Podilymbus podiceps*. *Canadian Journal of Zoology*, 65(12), 2872-2877.
- Frere, E., Gandini, P. A., & Boersma, D. P. (1996). Aspectos particulares de la biología de reproducción y tendencia poblacional del pingüino de Magallanes (*Spheniscus magellanicus*) en la colonia de Cabo Virgenes, Santa Cruz, Argentina.
- Frere, E., Gandini, P., & Boersma, D. (1998). The breeding ecology of Magellanic Penguins at Cabo Virgenes, Argentina: What factors determine reproductive success?. *Colonial Waterbirds*, 205-210.
- Gandini, P. A., Frere, E., & Holik, T. M. (1992). Implicancias de las diferencias en el tamaño corporal entre colonias para el uso de medidas morfométricas como método de sexado en *Spheniscus magellanicus*. *El Hornero*, 13(03), 211-213.
- Giudici, P. I., Quintana, F., & Svalgelj, W. S. (2017). The role of hatching asynchrony in a seabird species exhibiting obligate brood reduction. *Waterbirds*, 40(3), 221-232.
- Lack, D. (1947). The significance of clutch-size. *Ibis*, 89(2), 302-352.
- Lack, D. (1954). The natural regulation of animal numbers. *The Natural Regulation of Animal Numbers*.
- Lamey, T. C. (1990). Hatch asynchrony and brood reduction in penguins. In *Penguin biology* (pp. 399-416). Academic Press San Diego.
- MAGRATH, R. D. (1990). Hatching asynchrony in altricial birds. *Biological Reviews*, 65(4), 587-622.
- Mock, D. W. (1984). Siblicidal aggression and resource monopolization in birds. *Science*, 225(4663), 731-733.
- Marchisio, N., Barrionuevo, M., & Frere, E. (2021). Compensatory effect of egg size dimorphism on hatching asynchrony in Magellanic penguin. *Journal of Avian Biology*, 52(10).

- Millones, A., Morgenthaler, A., Gandini, P., & Frere, E. (2022). Population Numbers of the Magellanic Penguin along Its Central-Southern Distribution in Argentina: An Update after 25 Years. *Waterbirds* , 44(4), 499-508.
- Ostreiher, R. (1997). Food division in the Arabian babbler nest: adult choice or nestling competition?. *Behavioral Ecology* , 8(2), 233-238.
- Parker, G. A., Royle, N. J., & Hartley, I. R. (2002). Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society of London . Series B: Biological Sciences*, 357(1419), 295-307.
- Ploger, B. J., & Medeiros, M. J. (2004). Unequal food distribution among great egret *Ardea alba* nestlings: parental choice or sibling aggression?. *Journal of Avian Biology* , 35(5), 399-404.
- PRICE, K., HARVEY, H., & Ydenberg, R. O. N. (1996). Begging tactics of nestling yellow-headed black-birds, *Xanthocephalus xanthocephalus* , in relation to need. *Animal Behaviour* , 51(2), 421-435.
- Reid, W. V., & Boersma, P. D. (1990). Parental quality and selection on egg size in the Magellanic Penguin. *Evolution* , 44(7), 1780-1786.
- Seddon, P. J., & Heezik, Y. V. (1991). Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *The Auk* , 108(3), 548-555.
- Shizuka, D., & Lyon, B. E. (2013). Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism. *Ecology Letters* , 16(3), 315-322.
- Smith, T. E., Leonard, M. L., & Smith, B. D. (2005). Provisioning rules and chick competition in asynchronously hatching common terns (*Sterna hirundo* ). *Behavioral Ecology and Sociobiology* , 58(5), 456-465.
- Sockman, K. W., Sharp, P. J., & Schwabl, H. (2006). Orchestration of avian reproductive effort: an integration of the ultimate and proximate bases for flexibility in clutch size, incubation behaviour, and yolk androgen deposition. *Biological Reviews* , 81(4), 629-666.
- Stoleson, S. H., & Beissinger, S. R. (1995). Hatching asynchrony and the onset of incubation in birds, revisited. In *Current ornithology* (pp. 191-270). *Springer* , Boston, MA.
- Temme, D. H., & Charnov, E. L. (1987). Brood size adjustment in birds: economical tracking in a temporally varying environment. *Journal of Theoretical Biology* , 126(2), 137-147.
- Therneau, T. (2022). Mixed Effects Cox Models.
- Wagner, E. L., & Boersma, P. D. (2019). Food allocation and feeding behaviours of Magellanic penguin, *Spheniscus magellanicus* , adults and chicks. *Animal Behaviour* , 148, 161-168.
- Yorio, P., Borboroglu, P. G., Potti, J., & Moreno, J. (2001). Breeding biology of magellanic penguins *Spheniscus magellanicus* at golfo San Jorge, Patagonia, Argentina. *Marine Ornithology* , 29, 75-79.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (Vol. 574). New York: *Springer* .

## Tables

Table 1: To evaluate the instant weight ratio at different stages of the chick rearing period of Magellanic penguin, we ran four linear models using instant weight ratio (the asymmetry between chicks at the age of evaluation) as the response variable, and initial weight ratio, season, MBCI, FBCI, and doble interaction between all variables as predictor variable. Only significant results are shown. For the age 50 days, we used an average of the last three weights recorded, due to high daily variability in chick weight. We excluded



from the analysis the season 2019 for ages 25 days and 50 days because there were not enough broods with two live chicks at these ages.

First Chick's age	Predictable variable	Estimate	Std. Error	z-value	p-value
5 days	Intercept	0.076	0.058	1.300	0.194
	Initial Asymmetry	0.916	0.070	12.996	<2E-16
15 days	Intercept	0.245	0.149	1.613	0.107
	Initial Asymmetry	0.785	0.176	4.385	1.E-05
25 days	Intercept	0.272	0.142	1.861	0.063
	Initial Asymmetry	0.936	0.168	5.426	1.0E-07
50 days	Intercept	0.731	0.300	2.398	0.016
	Initial Asymmetry	0.707	0.229	3.007	0.003
	2018 - 2020	-0.473	0.206	2.241	0.025
	2018 - 2021	-0.407	0.204	1.949	0.051
	Intercept	0.471	0.193	2.384	0.003
	2021 - 2020	-0.066	0.131	0.487	0.626

Table 2: To evaluate the mortality of Magellanic penguin chicks, we ran a COX mixed model, using chick mortality. The predictable variables were IWR, HO, season, FBCI, MBCI, the double interaction between all variables and the triple interaction among IWR, HO and season. The nest ID was used as a random variable. Only significant variables are shown. The table shows the predictor variables, the variables with which they are contrasted, the coefficient with its standard deviation, the hazard (exp (Coefficient)), the Z-value and the p-value for each case. See Table S2 for the non-significant variables.

Contrast	Predictable variable	Coefficient	S.E. Coefficient	exp(Coefficient)	z-value	p-value
2018 - HO1	<b>2019 X HO2 X IWR</b>	<b>-2.082</b>	<b>0.902</b>	<b>0.125</b>	<b>-2.31</b>	<b>0.021</b>
	<b>2020 X HO2 X IWR</b>	<b>-4.136</b>	<b>1.338</b>	<b>0.016</b>	<b>-3.09</b>	<b>0.002</b>
	<b>2021 X HO2 X IWR</b>	<b>-2.370</b>	<b>0.909</b>	<b>0.093</b>	<b>-2.61</b>	<b>0.009</b>
2019 - HO1	2020 X HO2 X IWR	-2.054	1.612	0.128	-1.27	0.200
	2021 X HO2 X IWR	-0.288	1.280	0.749	-0.22	0.820
2020 - HO1	2021 X HO2 X IWR	1.766	1.617	5.846	1.09	0.270

Table 3: Non-Linear Mixed Model to assess growth in weight of Magellanic Penguin chicks, using IWR, hatching order (HO), study season, FBCI, MBCI, the double interaction among all variables and the triple interaction among IWR, HO and study season as predictor variables. The individual ID was the random variable. We only used broods with two siblings at the end of the season. The 2019 season was not used due to a lack of broods with two chicks by the end of the season. Only the significant variables are shown.

Parameter	Predictor variable	Value	S.E. value	d.f.	t-value	p-value
<i>a (Estimated asymptotic weight)</i>	Intercept (2018, HO1)	2117.792	414.238	2398	5.113	<0.001
	<b>IWR X 2020</b>	<b>1264.662</b>	<b>590.223</b>	<b>2398</b>	<b>2.143</b>	<b>0.032</b>
	IWR X 2021	-74.796	565.374	2398	-0.132	0.894
	<b>HO2 X 2020</b>	<b>-659.498</b>	<b>332.129</b>	<b>2398</b>	<b>-1.986</b>	<b>0.047</b>

Parameter	Predictor variable	Value	S.E. value	d.f.	<i>t</i> -value	<i>p</i> -value
<i>b</i> ( <i>Growth rate</i> )	<b>HO2 X 2021</b>	<b>-729.972</b>	<b>339.712</b>	<b>2398</b>	<b>-2.149</b>	<b>0.032</b>
	Intercept (2020, HO1)	2628.567	274.953	2398	9.560	<0.001
	<b>IWR X 2021</b>	<b>1339.458</b>	<b>444.738</b>	2398	<b>3.012</b>	<b>0.003</b>
	HO2 X 2021	-70.474	225.088	<b>2398</b>	-0.313	0.754
	<b>Intercept (2018, HO1)</b>	<b>12.613</b>	<b>1.910</b>	<b>2398</b>	<b>6.602</b>	<0.001
	<b>MBCI x 2020</b>	<b>-4.569</b>	<b>2.100</b>	<b>2398</b>	<b>-2.175</b>	<b>0.029</b>
	MBCI x 2021	-2.330	2.069	2398	-1.126	0.260
	<b>MBCI X HO2</b>	<b>-4.864</b>	<b>1.502</b>	2398	<b>-3.237</b>	<b>0.001</b>
	<b>IWR X HO2</b>	<b>-5.906</b>	<b>2.573</b>	<b>2398</b>	<b>-2.295</b>	<b>0.022</b>
	Intercept (2020, HO1)	10.077	1.517	<b>2398</b>	6.642	<0.001
	MBCI x 2021	2.240	1.144	<b>2398</b>	1.957	0.050

Figure

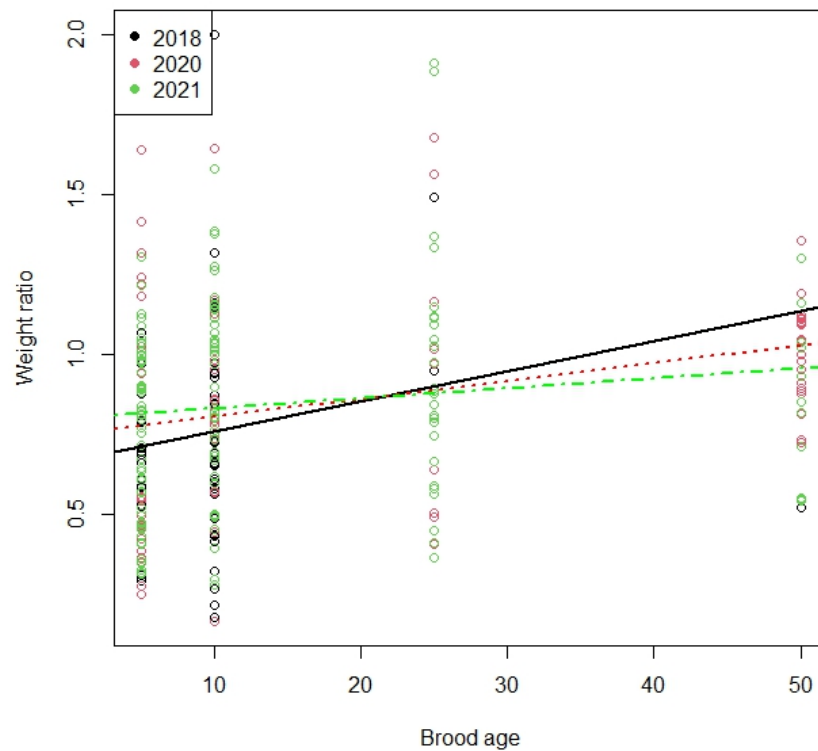


Figure legends

Figure 1: Weight ratio (second chick's weight / first chick's weight) within the brood at different brood ages for all study seasons. A tendency line for each season is shown. Circle colors and line types represent the season (black circles and solid line for 2018; red circles and dotted line for 2020, and green circles and dash-dotted line for 2021). The season 2019 was removed from this figure due to the lack of broods with two chicks at 50 days old.

### Supplementary Online Material

Table S1: Generalized Linear Model for the breeding success for different treatments (control and manipulated broods), for each season, and the interaction between the season and the treatment. All variables and comparisons are shown. Significant variables are shown in bold.

Predictable variable	Estimate	Standard error	z-value	p-value
Intercept	-0.588	0.258	-2.277	0.023
Treatment (manipulated)	-0.105	0.304	-0.347	0.729
<b>Season2019(2018)</b>	<b>-0.860</b>	<b>0.278</b>	<b>-3.091</b>	<b>0.002</b>
<b>Season2020(2018)</b>	<b>0.903</b>	<b>0.306</b>	<b>2.950</b>	<b>0.003</b>
<b>Season2021(2018)</b>	<b>0.659</b>	<b>0.318</b>	<b>2.073</b>	<b>0.038</b>
Treatment x 2019(2018)	0.047	0.613	0.076	0.939
Treatment x 2020(2018)	0.109	0.358	0.303	0.762
Treatment x 2021(2018)	0.045	0.372	0.122	0.903
Intercept	-1.482	0.447	-3.313	<0.001

Predictable variable	Estimate	Standard error	z-value	p-value
Treatment (manipulated)	-0.059	0.532	-0.111	0.912
<b>Season2020(2019)</b>	<b>1.797</b>	<b>0.476</b>	<b>3.771</b>	<b>&lt;0.001</b>
<b>Season2021(2019)</b>	<b>1.553</b>	<b>0.484</b>	<b>3.207</b>	<b>&lt;0.001</b>
Treatment x 2020(2019)	0.062	0.565	0.110	0.912
Treatment x 2021(2019)	-0.001	0.574	-0.002	0.998
Intercept	0.315	0.164	1.917	0.055
Treatment (manipulated)	0.003	0.190	0.018	0.986
<b>Season2021(2020)</b>	<b>-0.291</b>	<b>0.124</b>	<b>-2.355</b>	<b>0.019</b>
Treatment x 2021(2020)	-0.064	0.286	-0.222	0.824

**Table S2 :** To evaluate the instant weight ratio at different stages of the chick rearing period of Magellanic penguin, we ran four linear models using instant weight ratio (the asymmetry between chicks at the age of evaluation) as the response variable, and initial weight ratio, season, MBCI, FBCI, and doble interaction between all variables as predictor variable. Only non-significant results are shown. For the age 50 days, we used an average of the last three weights recorded, due to high daily variability in chick weight. We excluded from the analysis the season 2019 for ages 25 days and 50 days because there were not enough broods with two live chicks at these ages.

First Chick's age	Predictable variable	F-value	p-value
5 days	FBCI	0.067	0.796
	MBCI	1.994	0.160
	Season	1.105	0.349
	FBCI X Season	0.435	0.727
	MBCI X Season	0.794	0.499
	FBCI X IWR	0.169	0.681
	MBCI X Season	0.143	0.705
	IWR X Season	0.307	0.302
15 days	FBCI	0.021	0.886
	MBCI	1.253	0.266
	Season	1.050	0.375
	FBCI X Season	0.759	0.471
	MBCI X Season	0.150	0.929
	FBCI X IWR	0.024	0.876
	MBCI X Season	1.628	0.206
	IWR X Season	0.168	0.917
25 days	FBCI	0.115	0.735
	MBCI	0.493	0.486
	Season	0.854	0.452
	FBCI X Season	0.794	0.416
	MBCI X Season	1.630	0.163
	FBCI X IWR	0.037	0.846
	MBCI X Season	0.146	0.704
	IWR X Season	1.043	0.385
50 days	FBCI	0.116	0.735
	MBCI	0.493	0.486
	FBCI X Season	0.794	0.461
	MBCI X Season	0.368	0.223
	FBCI X IWR	0.038	0.847
	MBCI X Season	0.146	0.704

First Chick's age	Predictable variable	<i>F</i> -value	<i>p</i> -value
	IWR X Season	1.043	0.385

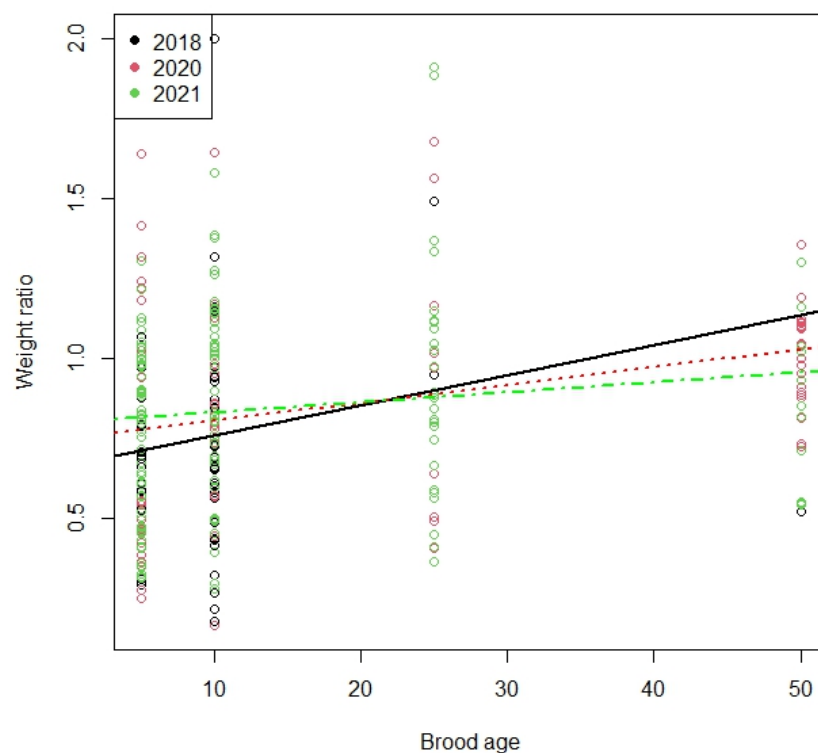
**Table S3 :** To evaluate the mortality of Magellanic penguin chicks, we ran a COX mixed model, using chick mortality. The predictable variables were IWR, HO, season, FBCI, MBCI, the double interaction between all variables and the triple interaction among IWR, HO and season. The nest ID was used as a random variable. The table shows the predictor variables, the Z-value and the p-value for each case. Only variables not used in Table 3 are shown.

Predictable variable	<i>z</i> -value	<i>p</i> -value
MBCI	0.30	0.770
FBCI	-0.15	0.880
HO	3.72	0.000
IWR	1.20	0.230
season	1.66	0.097
MBCI * HO	-1.17	0.240
MBCI * IWR	-0.19	0.850
MBCI * season	-0.36	0.720
FBCI * HO	0.38	0.700
FBCI * IWR	-0.11	0.910
FBCI * season	0.49	0.630
HO * IWR	-3.03	0.003
HO * season	-0.53	0.600
IWR * season	-0.12	0.900

**Table S4:** Non-Linear Mixed Model to assess growth in weight of Magellanic Penguin chicks, using IWR, hatching order (HO), study season, FBCI, MBCI, the double interaction among all variables and the triple interaction among IWR, HO and study season as predictor variables. The individual ID was the random variable. We only used broods with two siblings at the end of the season. The 2019 season was not used due to a lack of broods with two chicks by the end of the season. Only the non-significant variables are shown.

Parameter	Predictor variable	<i>L</i> -ratio	<i>p</i> -value
<i>a</i>	FBCI	1.949	0.163
	MBCI	2.563	0.162
	IWR	0.546	0.785
	HO	0.186	0.069
	season	0.785	0.662
	MBCI * IWR	2.153	0.360
	MBCI * season	1.395	0.497
	MBCI * HO	2.030	0.132
	FBCI * IWR	2.052	0.152
	FBCI * season	2.365	0.306
	FBCI * HO	1.818	0.177
	IWR * HO	1.338	0.247
	IWR * HO * season	0.767	0.681
<i>b</i>	FBCI	2.461	0.116
	MBCI	1.679	0.432
	IWR	3.731	0.155

Parameter	Predictor variable	<i>L</i> -ratio	<i>p</i> -value
c	HO	4.156	0.093
	season	1.986	0.163
	MBCI * IWR	3.092	0.786
	MBCI * season	2.576	0.109
	MBCI * HO	1.365	0.253
	FBCI * IWR	0.068	0.794
	FBCI * season	3.731	0.155
	FBCI * HO	0.087	0.767
	IWR * HO	2.450	0.076
	IWR * HO * season	2.431	0.297
	FBCI	1.338	0.247
	MBCI	3.362	0.123
	IWR	2.153	0.360
	HO	0.503	0.430
	season	0.186	0.069
	MBCI * IWR	2.903	0.088
	FBCI * IWR	0.178	0.672
	FBCI * season	3.731	0.155
	FBCI * HO	2.431	0.297
	IWR * season	0.044	0.978
	HO * season	0.503	0.430
	IWR * HO * season	1.679	0.432



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