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3 **An experimental approach to the Brood Reduction Hypothesis in Magellanic penguins**

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29 **Abstract**

30 In many bird species, eggs in a brood hatch within days of each other, leading to a size asymmetry in  
31 detriment of younger siblings. Hatching asynchrony is often thought of as an adaptive strategy, and the  
32 “Brood Reduction Hypothesis” is the most widely studied hypothesis in relation to this. This hypothesis states  
33 that when food resources are unpredictable, hatching asynchrony will allow the adjustment of the brood size  
34 maximizing fledging success and benefitting parents. The Magellanic Penguin (*Spheniscus magellanicus*) is  
35 an appropriate species to test this hypothesis because it has a 2-egg clutch that hatches over a 2-day interval  
36 with a broad range of variation (-1 to 4 days), it shows facultative brood reduction, and food abundance  
37 between breeding seasons is variable. We performed a manipulative study at Isla Quiroga, Argentina, during  
38 three breeding seasons (2010-2012) by forcing broods to hatch synchronously (0 days) or asynchronously (2  
39 or 4 days). Years were categorized as “bad” or “good” years based on estimated food abundance. Our study  
40 provided no support for the hypothesis in a strict sense because in the “bad” year: a) asynchronous broods did  
41 not have higher nestling survival than synchronous broods, and b) the second-hatchling in asynchronous  
42 broods did not die more often than those in synchronous broods. Nonetheless, we found evidence supporting  
43 the hypothesis in a broad sense: in the “bad” year, younger siblings of 4-day asynchronous broods starved  
44 earlier than those of synchronous broods, and 2-day asynchronous broods fledged heavier young than  
45 synchronous broods.

46 **Keywords**

47 Brood Reduction Hypothesis, Hatching asynchrony, Magellanic Penguin, Nestling survival

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57 **Introduction**

58 Hatching asynchrony is the time elapsed between hatching of the first and the last egg of a clutch (Clark and  
59 Wilson 1981; Stoleson and Beissinger 1995). The early onset of incubation during the laying period is  
60 believed to be the mechanism responsible for hatching asynchrony (Wang and Beissinger 2009; Rebstock and  
61 Boersma 2011; Johnson et al. 2013). Hatching asynchrony results in a size hierarchy between the first and the  
62 last nestlings of a clutch, that sometimes entails an asymmetric growth and occasionally brood reduction  
63 (O'Connor 1978; Mock and Schwagmeyer 1990).

64 Some authors propose that hatching asynchrony is not adaptive and is the result of physiological or  
65 environmental constraints (i.e., constrains during the incubation period or during egg laying; reviewed all in  
66 Magrath (1990)). However, contrary to these non-adaptive explanations, other hypotheses view hatching  
67 asynchrony as a side-effect of selection for an early start of incubation (Nest failure hypothesis, Hurry-up  
68 hypothesis; reviewed all in Magrath (1990)); while others propose that the asynchrony happens because it  
69 increases the energy efficiency of parents for raising their nestlings (Peak load hypothesis, Sibling rivalry  
70 hypothesis, Dietary diversity hypothesis; reviewed all in Magrath (1990)).

71 Among the adaptive explanations, several hypotheses have been proposed to explain that hatching  
72 asynchrony may have evolved as a mechanism that facilitates adaptive brood reduction (Magrath 1990;  
73 Stoleson and Beissinger 1995), including the “Brood Reduction Hypothesis” (Lack 1947). This hypothesis  
74 links the parental benefit of hatching asynchrony to environmental unpredictability. When food abundance is  
75 low, hatching asynchrony would leave the youngest and smallest hatchling out of the competition for food.  
76 This should occur rapidly in the nestlings’ raising period to reduce parental effort (Mock and Forbes 1994), so  
77 that parents would not invest so much time and energy in a nestling that has a great chance of dying of  
78 starvation. With the reduction of the brood in a situation of low food availability, parents might be able to  
79 bring enough food to the remaining nestlings, maximizing their chances of survival in an otherwise bad  
80 situation. When food abundance is high, despite the hatching asynchrony and the size difference of the  
81 nestlings, the adults should be able to feed all nestlings of the clutch (Ricklefs 1965; Lack 1968; Clark and  
82 Wilson 1981).

83 A modification of the “Brood Reduction Hypothesis” considers the main effects of asynchrony in  
84 terms of quality, and not quantity, of fledglings (the “Offspring Quality Assurance Hypothesis”, Amundsen

85 and Slagsvold 1991a). A better quality of fledglings could alone explain the occurrence of asynchrony,  
86 although no brood reduction may occur (Slagsvold et al. 1995). In this sense, Amundsen and Slagsvold  
87 (1991b) found that synchronous broods produced more nestlings, but asynchronous broods produced better-  
88 quality fledglings.

89 The “Brood Reduction Hypothesis” has been studied in several penguin species (Jackass Penguin  
90 *Spheniscus demersus*: Seddon and Van Heezik 1991; Gentoo Penguins *Pygoscelis papua*: Williams and  
91 Croxall 1991; Chinstrap Penguin *Pygoscelis antarctica*: Moreno et al. 1994). In all these species hatching  
92 asynchrony does not seem to result in brood reduction. More so, in Chinstrap and Gentoo Penguins, brood  
93 reduction is not only inefficient but also apparently unrelated to hatching asynchrony (Williams and Croxall  
94 1991; Moreno et al. 1994). Similarly, the effects of hatching asynchrony on nestling survival have been  
95 studied in a non-manipulative work in Magellanic Penguins (*Spheniscus magellanicus*). This correlational  
96 study found little evidence in favor of the “Brood Reduction Hypothesis” (Boersma and Stokes 1995). It  
97 concluded that asynchrony is not directly related to brood reduction and that is the size asymmetry between  
98 the nestlings of the same clutch—which is not strongly related to asynchrony in this species—that is  
99 associated with the reduction (Boersma and Stokes 1995).

100 By trying to understand the ultimate cause of hatching asynchrony. Here, we will evaluate for the  
101 first time through a manipulative study both hypotheses: "Brood Reduction Hypothesis" and  
102 "Offspring Quality Assurance Hypothesis" in a penguin species. In addition, we will study the age of brood  
103 reduction as an indication of the potential benefit of asynchrony for the cost that foster parents faced, we  
104 present the results of an experiment designed to test the "Brood Reduction Hypothesis" in We will use as a  
105 model the Magellanic Penguin breeding at Isla Quiroga, Santa Cruz, Argentina. This species exhibits several  
106 characteristics in its breeding biology which makes it interesting to experimentally test the hypothesis despite  
107 the negative correlational results, mentioned above, found in a more northern colony (Boersma 1991;  
108 Boersma and Stokes 1995). Magellanic Penguins show an average 2-day hatching asynchrony between both  
109 eggs of the clutch, with a natural variation ranging from -1 to 4 days (Boersma et al. 1990). Previous studies  
110 have proposed that the species has facultative brood reduction (Lamey 1990), with a generally low breeding  
111 success (Boersma et al. 1990; Frere 1993). Food abundance is very variable between years (Boersma 2008),

Con formato: Inglés (Estados Unidos)

112 and has been shown to be determinant for nestling growth (Barrionuevo 2015). As a result, breeding success  
113 is also highly variable within the same colony between years (Boersma et al. 1990; Frere 1993).

114 In this study, we manipulated the onset of incubation during three years generating synchronous (0  
115 days), or asynchronous (2 or 4 days) broods. The years were categorized as “good” or “bad” according to  
116 estimated food abundance [based on chlorophyll \*a\* concentrations](#). We predict that in “bad years” but not in  
117 “good years”: *a*) the mortality of the last hatchling would be greater than the mortality of first born nestling in  
118 asynchronous broods, while we would find no difference within synchronous broods; *b*) last born nestlings of  
119 asynchronous broods would die more often than the last born nestlings of synchronous broods; *c*) mortality  
120 rates of both nestlings in asynchronous broods would be lower than in synchronous broods; and *d*) last  
121 hatchlings of asynchronous broods would die earlier in the nestling period—within the first half of the  
122 nestling period—than those of synchronous broods. Additionally, if what matters adaptively is the quality of  
123 offspring surviving (following the predictions of “The Offspring Quality Assurance Hypothesis”), *e*) we  
124 predict that fledglings from asynchronous broods would weigh more on average than those from synchronous  
125 ones.

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## 127 **Methods**

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### 129 Study site

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131 We carried out this study at Isla Quiroga (47°45'S, 65°53'W), located 80 m off the coast (Puerto Deseado,  
132 Santa Cruz Province, Argentina), during three breeding seasons: October-January 2010, 2011 and 2012.

133 About 1500 pairs of Magellanic Penguins breed in this area, nesting mostly under bushes. There are no  
134 terrestrial predators in the island (Frere, unpublished data), with Kelp Gulls (*Larus dominicanus*) being the  
135 main predators of eggs and nestlings. The climate is temperate-cold with annual temperatures not exceeding  
136 16° C on average. During the laying and incubation period of our study the ambient temperature was on  
137 average 11.8° C (minimum = 4.8° C, maximum = 22.7° C) (data provided by the National Weather Center,  
138 Puerto Deseado Station, 2.5 km apart from the study site).

139

140 Year quality categorization

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142 Magellanic Penguins vary their diet according to their latitudinal range of distribution (Frere et al. 1996). In  
143 northern colonies they eat mostly anchovy (*Engraulis anchoita*) (Gandini et al. 1999), but in our study site  
144 their diet is based on Sprat (*Sprattus fuegensis*), Squid (*Loligo gahi*), Silverside (*Odontesthes smitti*) and Hake  
145 (*Merluccius hubbsi*) (Frere et al. 1996). Their foraging distances reaches as far as 500 km away from their  
146 colony (Boersma and Rebstock 2009).

147 Direct estimation of food abundance for wild penguins is very difficult. Also, manipulating their  
148 food abundance, i.e.: by trying to feed wild animals of this species, is also complicated. Therefore, we ran our  
149 experiment during several years in order to cover a wide range of environmental scenarios. The year is  
150 usually used as an indicator of the environmental conditions experienced by penguins during a breeding  
151 season (Boersma and Stokes 1995; Boersma 2008): poor quality years—“bad years”—or high quality years—  
152 “good years”. Other studies in penguins categorized the years using the rates of nestling starvation (Boersma  
153 and Stokes 1995), mean mass of stomach contents of adults, average breeding success for a colony (Williams  
154 and Croxall 2001), or nestling growth and final brood size (Moreno et al. 1994). We categorized years  
155 according to inferred food availability through: a) the breeding success of control nests at Isla Quiroga; b) the  
156 breeding success of other colonies localized near Isla Quiroga; and c) the concentration of chlorophyll *a* in  
157 known foraging areas. Chlorophyll *a* can be a good estimator of ocean production in a given area (Boersma et  
158 al. 2009), therefore allowing us indirect calculations of ocean productivity and food availability in a given  
159 year.

160 To accomplish point a) we studied breeding success of control nests at Isla Quiroga and we used as a  
161 threshold value, by which we categorized the year as a “good” or a “bad” year, the average breeding success  
162 of our study site calculated for the 11 years prior to this study (0.9 nestlings/nest, range: 0.6–1.22, in an 11  
163 year study; Frere not published).

164 To carry forward point b) we used unpublished data on Isla de los Pájaros (47°75'S, 65°06'W) and  
165 Isla Chaffers (47°76'S, 65°88'W) for years 2011 and 2012. Both islands are located in the estuary “Ría  
166 Deseado” between 2 and 5 km away from Isla Quiroga, respectively. The breeding success for Isla de los

167 Pájaros in 2011 was: 0.69 and 2012 was: 0.56, and for Isla Chaffers in 2011 was: 0.76 and 2012 was: 0.64  
168 (Frere et al. not published)

169 ~~To conduct point c) we used chlorophyll *a* concentrations as an estimate for ocean production.~~ We  
170 used data from the Ocean Productivity web site that base their estimation of chlorophyll concentration on the  
171 Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski 1997) as the standard  
172 algorithm. The VGPM is a "chlorophyll-based" model that estimates net primary production from chlorophyll  
173 using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency. For the VGPM,  
174 net primary production is a function of chlorophyll, available light, and the photosynthetic efficiency. Preys of  
175 Magellanic Penguins aggregate in tidal mixing fonts (Sánchez and de Ciechomsky 1995; Hansen et al. 2001)  
176 that are visible in satellite images as areas of high chlorophyll *a* (Acha et al. 2004; Rivas et al. 2006). In fact,  
177 Boersma et al. (2009) have shown that in Puerto Deseado foraging sites correspond to areas of high  
178 chlorophyll *a*. We used monthly net primary production for the months ~~preceeding~~proceeding the breeding  
179 period, August and September—during these months penguins are arriving to the breeding sites (Frere pers.  
180 obs.)—and for the whole breeding period: October, November, December and January and then we summed  
181 the whole concentrations. We also determined the sites were penguins most often forage in the area using  
182 published works. Boersma et al. (2009) and Sala et al. (2012) agree that penguins forage north from Puerto  
183 Deseado, in the southern end of the Golfo San Jorge and east of the mouth of “Ría Deseado”, both studies  
184 were carried out during the nestlings’ stage. Using their maps we determined the coordinates of both locations  
185 which were defined as site A and site B, respectively. For the final result of chlorophyll *a* concentrations we  
186 summed also the sites.

187

188 General field methods

189

190 Starting in early October, we randomly chose active nests (those nest sites that were occupied and defended  
191 by a breeding pair), and we identified these nests with flagging tape (Tapebrothers, Longwood, FL) with a  
192 unique nest number (approximately 200 nests per year). Each year we chose different nests to avoid taking  
193 repeated measurements of the same pair of breeders, given that the same couple usually returns to the same  
194 nest site every breeding season (Boersma et al. 1990). Nonetheless, when captured for estimation of body

Código de campo cambiado

195 condition, all adults were individually identified with permanent metal tags with a unique number ( $2 \times 10$   
196 mm; National Band and Tag Company, Newport, KY) attached to the foot webbing.

197         During hatching we visited nests every day, eggs were marked with their laying order number with a  
198 waterproof marker. During incubation we returned to the nests every four days to check for egg predation, we  
199 discarded predated nests from our analyses. Thirty-five days after the first egg was laid, we checked the nests  
200 daily to record the hatching date. We weighed nestlings from hatching to the age of approximately 52 days  
201 old at a 3-day interval with a series of spring scales (0-100:  $\pm 1$  g, 101-300 g:  $\pm 2$  g, 301-500 g:  $\pm 5$  g, 501-  
202 1000 g:  $\pm 10$  g, >1001 g:  $\pm 25$  g; Pesola AG, Baar, Switzerland). Nestlings within a nest were individually  
203 identified: first hatched nestlings were marked with permanent markers in the inner part of the right flipper  
204 and the right foot, while second hatched nestlings were marked on the left flipper and foot. As nestlings tend  
205 to move from the nest once they grow, we marked nestlings of contiguous nests with different colors. We  
206 assumed that nestlings fledged if at 52 days old they were heavier than 1900 g and had started to molt (Reid  
207 and Boersma 1990; Boersma and Rebstock 2009). Breeding success was estimated as the total number of  
208 nestlings fledged divided by the total number of clutches with two eggs hatched.

209         On the laying day of the second egg and when males returned to take their incubation spell  
210 (approximately 15 days after the laying period finished), we captured females and males of each nest to  
211 estimate body condition. We measured bill length and depth with a caliper ( $\pm 0.1$  mm, Mitutoyo, Illinois,  
212 USA), and flipper and foot length with a ruler ( $\pm 1$  mm) as described in Barrionuevo and Frere (2015), and we  
213 also weighed them with a spring scale ( $\pm 25$  g). With all the measurements we ran a Principal Component  
214 Analysis (PCA), and then we regressed the adults' mass against the first component of the PCA (Yorio et al.  
215 2001).

216

217 Control nests

218

219 We randomly chose a set of nests each year ( $n_{2010} = 49$  nests,  $n_{2011} = 44$  nests and  $n_{2012} = 51$  nests) for which  
220 the only manipulation we did on them was the procedure described above in "General field methods". These  
221 nests did not suffer any additional manipulations and were considered our control group.

222



223 Manipulated nests

224

225 In experimental nests, apart from the observations and measurements described in “General field methods”,  
226 we performed a manipulation of the onset of incubation by momentarily removing freshly laid eggs from their  
227 nests. On the laying day of the first eggs, we assigned nests to one of three treatments: synchronous broods  
228 (HA=0), asynchronous broods (HA=2), and extreme asynchronous broods (HA=4). In all treatments, we  
229 removed freshly laid eggs from the nest and stored them in an airtight, plastic container, and left in the nests  
230 an artificial egg instead (see below for information on artificial eggs). On the laying day of the second egg: a)  
231 for those nests in HA=0, we returned the first eggs to their original nests and removed the artificial eggs,  
232 leaving in the nests the first-laid eggs and the freshly laid second eggs ( $n_{2010} = 20$  nests,  $n_{2011} = 39$  nests and  
233  $n_{2012} = 44$  nests); and b) for nests in treatments HA=2 and HA=4, we removed the fresh second-laid eggs and  
234 stored them in an airtight plastic container, and we returned the first-laid eggs to each nest, leaving the first  
235 egg and one artificial egg in each nest. We then returned second eggs to their nests and removed the artificial  
236 eggs two days after the second egg was laid in HA=2 ( $n_{2010} = 8$  nests,  $n_{2011} = 11$  nests and  $n_{2012} = 17$  nests) or  
237 four days after the second egg was laid in HA=4 ( $n_{2010} = 14$  nests,  $n_{2011} = 23$  nests and  $n_{2012} = 27$  nests).

238 We identified each egg with their order and nest number with a waterproof marker before removing  
239 them. Eggs were stored in an airtight plastic container within egg cartons in a vertical position at the island.  
240 The container was covered with a white cardboard, which prevented the eggs from being directly exposed to  
241 the sun, but did not alter their exposure to the ambient temperature. Once eggs were stored they were no  
242 longer moved until we returned them to their nests. Artificial eggs were made of gypsum and had the same  
243 size and shape as penguin eggs. All females accepted these eggs as their own and continued the incubation  
244 without any problems (Wagner et al. 2013). This experiment allowed us to conserve the laying order of the  
245 eggs and avoid variations related to the genetic background of the nestlings when performing cross-fostering  
246 experiments. By doing this we forced clutches to hatch synchronously or with two or four days of asynchrony  
247 covering the whole range of asynchronies of Magellanic Penguins.

248

249 Data analysis

250

251 In manipulated nests, HA=0 resulted in clutches with -1, 0 and 1 days of asynchrony, HA=2 only  
252 encompassed clutches with 2 days of asynchrony, and HA=4 resulted in clutches with 3, 4 and 5 days of  
253 asynchrony.

254 To determine prediction *a*—see Introduction for a detailed description of predictions—in “bad  
255 years” in asynchronous broods last hatchlings would die more often than first hatchlings) and *b* (in “bad  
256 years” last hatchlings of asynchronous broods would die more often than those of synchronous broods), we  
257 ran a Generalized Linear Mixed Model (GLMM) with a Binomial distribution and log link function. The  
258 response variable was whether the nestling fledged or not, the predictor variables were hatching asynchrony  
259 (as a three level factor: 0, 2 and 4 days), hatching order (as a two level factor: first or second-hatchling), year  
260 (as a three level factor: 2010, 2011 or 2012), the triple interaction and all the possible double interactions. We  
261 also added the nest as a random factor to account for the lack of independency of the nestlings of the same  
262 clutch.

263 To determine prediction *c* (in “bad” years, mortality rates in asynchronous broods would be lower  
264 than in synchronous broods), we ran a Generalized Linear Model (GLM) with Poisson distribution and log  
265 link function. Here, the response variable was the number of dead nestlings within a clutch (0, 1 or 2  
266 nestlings). The predictor variables were hatching asynchrony (as a three level factor: 0, 2 and 4 days), year (as  
267 a three level factor: 2010, 2011 or 2012), and the double interaction between both factors.

268 To study prediction *d* (last hatchling of asynchronous broods would die earlier than those of  
269 synchronous broods), we only used those nests in which brood reduction of the second hatchling occurred. To  
270 analyze when brood reduction occurred—nestling age—we used a Linear Model (LM) with mortality age as  
271 the response variable, and year (as a two-level factor: “good” years—2010 and 2011—and “bad” year—  
272 2012), hatching asynchrony (as a three-level factor: 0, 2 and 4), and the interaction between both variables, as  
273 predictor variables. We additionally analyzed the variables affecting the mass asymmetry on the previous  
274 measurement to the reduction of the brood. For this, we ran a LM with mass asymmetry on the previous  
275 measurement to the death of the nestling (live nestling minus dead nestling) as response variable, and year (as  
276 a three-level factor: 2010, 2011 and 2012), hatching asynchrony, and the interaction between both factors as  
277 response variable.

278 In all models we used a backwards selection procedure removing the terms one by one following a  
279 decreasing level of complexity (interactions first) and a decreasing  $p$  value, comparing the models with and  
280 without the eliminated variable with the function “anova” using the goodness-of-fit chi-square test ( $\chi^2$   
281 parameter) in the GLMM and GLM, and F-stat in LM (Crawley 2007). Sometimes, we also used Tukey’s  
282 HSD tests to compare the levels of the significant factors. We used the R software version 2.12.1 (R  
283 Development Core Team 2010), the package “multcomp” and “lme4” and the function “lmer” for the GLMM,  
284 the function “glm” for the GLM, and the function “lm” for the LM analysis. We also used the packages  
285 “multcomp” and the function “glht” for the Tukey comparisons. In the GLM we report results of the “anova”  
286 as the change in the deviance between models (Deviance).

287 To test all the mentioned predictions, we used only those nests in which nestlings starved and did not  
288 die by other causes. To decide if the nestlings died of starvation or not, we made a curve adjusted to a  
289 Gompertz equation (Barrionuevo 2015) with the nestling mass and age of successfully fledged nestlings from  
290 the control nests using the program Sigma Plot (Systat Software Inc. 2006). With the resulting parameters ( $a$ :  
291 asymptotic mass,  $b$ : inflexion point and  $c$ : increment rate) we constructed an equation with which we  
292 calculated for each age the corresponding mass with their standard error. If a nestling mass was above the  
293 values calculated with the curve the last time it was measured (before it died), we discarded that nest because  
294 it is likely that the nestling died of another cause other than starvation.

295 To analyze prediction  $e$  (fledglings from asynchronous broods would weigh more on average than  
296 those from synchronous ones), we studied nestling mass at fledging. We adjusted each nestling’s growth  
297 curve (age vs. mass) to a Gompertz curve and extracted the asymptotic mass (with R software v. 2.12.1). We  
298 did not follow nestlings until they fledged; therefore the asymptotic mass is an estimation of the nestlings’  
299 mass at fledging. Using the last mass measured would add much error because the mass is highly variable  
300 between measures depending on whether the nestlings had just received food. As our objective was to  
301 compare nestling quality between treatments we pooled together broods with one and two fledged nestlings.  
302 We ran a Factorial ANOVA with nestling asymptotic mass as the dependent variable and year and hatching  
303 asynchrony as the categorical factors, including effects between both factors. We ran this analysis with  
304 Statistica v.7 (Statsoft Inc. 2004).

305 All other statistical analyses were performed using Statistica v.7. We report values as mean  $\pm$  SE and  
306 considered differences to be significant at  $p < 0.05$ . Graphs were plotted using Statistica v. 7 or Sigma Plot.

307

## 308 **Results**

309

### 310 Hatching asynchrony and breeding success

311

312 Hatching asynchrony in control nests was  $1.61 \pm 0.10$  days ( $n = 94$  nests), ranging from -1 (first laid eggs  
313 hatched after than second laid eggs) to 4 days. Large asynchronies were unusual in control nests (3 % of the  
314 nests had -1 and 4 days asynchronies, each, 11 % had 0 and 18 % had 3 days asynchronies). In manipulated  
315 nests asynchronies ranged from -1 to 5 days and 31 % of the clutches had extreme asynchronies: 3, 4 and 5  
316 days: [mean asynchrony was  \$1.71 \pm 0.18\$  days.](#) In these nests the hatching asynchrony highly explained the  
317 initial mass asymmetry (first minus second nestling's mass on the hatching day of the second nestling)  
318 (Simple Regression,  $r^2 = 0.67$ ,  $p < 0.0001$ ,  $y = -12.9 + 33.1 x$ ).

319 In experimental nests, female and male body condition did not significantly differ between study  
320 years (One-Way ANOVA: females:  $F_{2,191} = 0.27$ ,  $p = 0.75$ ; males:  $F_{2,189} = 0.15$ ,  $p = 0.86$ ). Likewise, the body  
321 condition of adults did not differ between treatment groups (hatching asynchronies) (One-Way ANOVA:  
322 females:  $F_{2,191} = 1.63$ ,  $p = 0.19$ ; males:  $F_{2,191} = 0.51$ ,  $p = 0.60$ ). Therefore, we discarded the possibility that  
323 differences in body condition between years or treatments could have influenced our experiment.

324 In control nests, 0.37 % of the eggs failed to hatch (i.e., the eggs remained on their nests after the  
325 supposed hatching date and when broken there was no or little development of the embryos), while 0.53 % of  
326 the manipulated eggs failed to hatch.

327 Breeding success in control nests during the study year was: 1.45 fledglings per nest in 2010 ( $n = 49$   
328 nests), 1.61 fledglings per nest in 2011 ( $n = 44$  nests) and 0.71 fledglings per nest in 2012 ( $n = 51$  nests). In  
329 manipulated nests, breeding success during the study years was: 1.09 fledglings per nest in 2010 ( $n = 42$   
330 nests), 1.52 fledglings per nest in 2011 ( $n = 73$  nests) and 0.89 fledglings per nest in 2012 ( $n = 88$  nests). We  
331 did not find significant differences between control and manipulated nests within years (Mann-Whitney U

332 test: 2010:  $z = -1.84$ ,  $p = 0.06$ ; 2011:  $z = -0.93$ ,  $p = 0.35$ ; and 2012:  $z = 1.31$ ,  $p = 0.18$ ). This shows that the  
333 manipulation did not affect breeding success.

334

335 Year quality categorization

336

337 In control nests at Isla Quiroga the highest breeding success was in 2011, while 2010 had similar results, and  
338 both are above our threshold value of 0.9 fledglings/nest. So, by this method, both years could be categorized  
339 as “good” years. Year 2012 had a significant lower value, so could be categorized as a “bad” year. In other  
340 colonies of “Ria Deseado”, we also observed that 2011 was a better year than 2012 having higher breeding  
341 success (see Methods).

342 2011 had the major According to the concentrations of chlorophyll  $a$  of the three years, 6090 mgC/m<sup>2</sup>/day,  
343 2010 had 4764 mgC/m<sup>2</sup>/day and 2012 4243 mgC/m<sup>2</sup>/day. This result is achieved by adding both foraging sites  
344 and every month of study (August to January). So, 2011 was the year with the largest food abundance and  
345 2012 the worst year. 2010 could be categorized as an “intermediate”-quality year. during the months previous  
346 to the breeding period (August and September) years 2010 and 2012 had similar values and lower than 2011.  
347 During October, November, 2010 had similar values with 2011, while 2012 had lower values than both.  
348 Finally, during December and January concentrations were similar between years (Table 1). So, 2012 was the  
349 worst year during the first stages of breeding, while 2011 was the best year. 2010 was similar to the “bad”  
350 year before reproduction, but similar to the “good” year during breeding, so it could be categorized also as a  
351 “good” year.

352

353 Survival

354

355 In the model (GLMM) run to corroborate predictions  $a$  and  $b$ , we found that the triple interaction between  
356 hatching asynchrony, year and hatching order significantly affected nestling survival (GLMM:  $\chi^2 = 10.9$ ,  $p =$   
357 0.03). Supporting prediction  $a$ , we found that in the “bad” year and not in the “good” and “intermediate” years  
358 second hatchlings (2N) died more often than first hatchlings (1N) in the asynchronous broods (HA=4) (Tukey  
359 Contrasts: 1N-HA=4-2012 vs. 2N-HA=4-2012:  $z = 4.28$ ,  $p < 0.01$ ; 1N-HA=4-2011 vs. 2N-HA=4-2011:  $z =$

**Comentado [R1]:** Saqué lo del ‘xito rproductivo y dejé solo lo d la clorofila. Además sumé cada sitio y los meses.

**Con formato:** Sangría: Primera línea: 0 cm

**Con formato:** Superíndice

360 1.55,  $p = 0.98$ ; and 1N-HA=4-2010 vs. 2N-HA=4-2010:  $z = 1.45$ ,  $p = 0.99$ ). Also, this difference was not  
361 significant for synchronous broods (Tukey Contrasts: 1N-HA=0-2012 vs. 2N-HA=0-2012:  $z = 2.22$ ,  $p = 0.65$ )  
362 or for 2-day asynchronous broods (Tukey Contrasts: 1N-HA=2-2012 vs. 2N-HA=2-2012:  $z = 1.55$ ,  $p = 0.95$ )  
363 in the “bad” year. Rejecting prediction *b*, in the “bad” year, second hatchlings of 4-day asynchronous broods  
364 did not die more often than second hatchlings of synchronous broods (Tukey Contrasts: 2N-HA=4-2012 vs.  
365 2N-HA=0-2012:  $z = -1.66$ ,  $p = 0.95$ ). Neither did this happen between 2-day asynchronous and synchronous  
366 broods (Tukey Contrasts: 2N-HA=2-2012 vs. 2N-HA=0-2012:  $z = -0.15$ ,  $p = 0.99$ ). However, in 2012 second  
367 hatchlings of HA=4 died more than first hatchlings of HA=0 (Tukey Contrasts:  $z = 3.39$ ,  $p = 0.046$ ), and  
368 second hatchlings of HA=0 died more than first hatchlings of HA=4 (Tukey Contrasts:  $z = 3.39$ ,  $p = 0.046$ ).  
369 All the other combinations of the Tukey Contrasts were not significant.

370 In the model (GLM) in which we try to corroborate the prediction *c*, we found that neither the  
371 interaction between hatching asynchrony and year (GLM: Deviance =  $-0.18$ ,  $p = 0.67$ ), nor hatching  
372 asynchrony (GLM: Deviance =  $-0.03$ ,  $p = 0.86$ ; breeding success (fledgling/nest): HA=0: 1.17, HA=2: 1.08,  
373 HA=4: 1.20) affected the number of nestlings that starved per nest. So, in the “bad” year nestlings of HA=4 or  
374 HA=2 did not die less than nestlings of synchronous clutches as expected by prediction *c* (Fig. 1). We did find  
375 that in 2011 more nestlings survived per nest than in 2010 (Tukey Contrasts:  $p=0.003$ ) and 2012 (Tukey  
376 Contrasts:  $p < 0.0001$ ) (Significance of year in GLM: Deviance =  $-4.29$ ,  $p = 0.04$ ).

377

378 Brood reduction: nestlings’ age and mass

379

380 In those nests in which brood reduction of the second nestling occurred, the average age for this event was  
381  $20.7 \pm 1.66$  days. The age of hatchlings at brood reduction varied across years (LM:  $F_{1,102} = 3.43$ ,  $p = 0.04$ ),  
382 with nestlings in 2011 dying earlier (12.6 days) than nestlings born in 2010 (23.6 days,  $t = 2.17$ ,  $p = 0.03$ ) and  
383 2012 (22.5 days,  $t = 2.37$ ,  $p = 0.02$ ). Hatching asynchrony was not significant in the model (LM:  $F_{2,102} = 2.54$ ,  
384  $p = 0.08$ ). Nonetheless, the interaction between hatching asynchrony and year was significant (LM:  $F_{8,102} =$   
385  $3.01$ ,  $p = 0.02$ ), but the results of the Tukey Contrast showed [no](#) significant differences between the  
386 possible combinations of the interactions ( $0.08 < p < 0.99$ ). Yet, it should be noticed that in “good” years  
387 nestlings’ age at death is very similar between treatments (HA=0: 19.3 days, HA=2: 17.1 days, HA=4: 17.6

388 days), while in the “bad” year nestlings’ age at death appears to be different (Fig. 2). Therefore, we performed  
389 an a posteriori Fisher LSD-test, and found significant differences in the “bad” year between treatments HA=0  
390 and HA=4 ( $p = 0.02$ ), with nestlings in HA=0 dying later than nestlings in HA=4 (26.5 days vs. 15.2 days,  
391 Fig. 2), as predicted by prediction *d*.

392 The year (LM:  $F_{2,108} = 0.56, p = 0.57$ ) and the interaction between year and hatching asynchrony  
393 (LM:  $F_{8,108} = 1.58, p = 0.19$ ) did not affect the mass asymmetry between siblings at brood reduction, but the  
394 mass depended positively on the hatching asynchrony (LM:  $F_{2,108} = 5.11, p = 0.01$ ). The mass asymmetry  
395 between nestlings of HA=4 was 279 g larger than of those of synchronous broods (Tukey Contrasts:  $t = 3.18,$   
396  $p = 0.006$ ). On the other hand, the initial mass asymmetry was related to the mass asymmetry at brood  
397 reduction (Simple Regression:  $r = 0.28, F_{1,105} = 8.74, p = 0.004$ , Fig. 3).

398

399 Fledglings’ mass

400

401 Asymptotic mass of fledglings differed with respect to the treatment (ANOVA:  $F_{2,167} = 4.90, p = 0.01$ ), year  
402 (ANOVA:  $F_{2,167} = 59.5, p < 0.0001$ ) and the interaction between those factors (ANOVA:  $F_{4,167} = 3.29, p =$   
403  $0.04$ ) (Fig.4). Within the “good” years 2010 and 2011 there was no difference between treatments (Fig. 4). In  
404 the “bad” year nestlings’ mass of HA=0 (mean: 2697 g) was lower than nestlings’ mass of HA=2 (mean: 3174  
405 g) (Tukey Contrasts,  $p = 0.01$ ), but we found no differences between HA=0 and HA=4 (Tukey Contrasts,  $p =$   
406  $0.71$ ). Synchronous clutches had heavier fledglings in the “good”/“intermediate” years than in the “bad” year  
407 (Tukey Contrasts, 2012 vs. 2010 and 2012 vs. 2011: all  $p < 0.0001$ ). In HA=2 there were no differences in  
408 fledglings’ mass between years, while in HA=4 there were only differences between the best and the worst  
409 years (Tukey Contrasts, 2012 vs. 2011  $p < 0.0001$ ).

410

411 **Discussion**

412

413 Through a manipulation of the onset of incubation of Magellanic Penguins we generated different hatching  
414 asynchronies, within the natural range found in wild colonies and increasing the sample size of extreme  
415 asynchronies, which allowed us to test the “Brood Reduction Hypothesis”. The manipulation did not affect

Comentado [R2]: Cambiale el enfoque hacia lo novedoso!

416 the breeding success because there were no differences within years and also the hatching asynchrony reached  
417 through the manipulation was representative of the real asynchrony found in control nests. In this sense, we  
418 were able to test the effect of the asynchronies on nestling survival and fledgling quality, in three different  
419 years, ~~two~~ one “good”-quality year (2011), one “intermediate”-quality year (2010), and one “bad”-quality year  
420 (2012), which conferred us different scenarios of food abundance and environmental conditions. We did not  
421 find ~~a clear~~ support to the “Brood Reduction Hypothesis” in its strict sense (Lack 1947), especially because  
422 we found that asynchronous broods (HA=2 and HA=4) did not have a higher survival rate than the survival  
423 rate in synchronous broods (HA=0) in “bad” years. Nonetheless, we found for the first time in the study  
424 species that the asynchrony could be adaptive in the sense that it could be beneficial for the quality of  
425 fledglings and for the reduced costs that face parents when raising nestlings. ~~did find that~~ Synchronous  
426 broods were negatively affected in the “bad” year because their fledglings were lighter and died later than  
427 nestlings of asynchronous broods. These results demonstrate that for this study-species the “Brood Reduction  
428 Hypothesis” may be supported in a broad sense (Amundsen and Slagsvold 1991a), ~~although, w~~ We think,  
429 further studies are needed to test if the apparent benefits of asynchronous over synchronous broods could  
430 benefit adults’ breeding success. In another study in Magellanic Penguins, with un-manipulated nests, but  
431 with many years of study (6), neither fledging success nor fledging mass were related to hatching asynchrony,  
432 but the initial size asymmetry within a brood explained the reduction in the brood (Boersma and Stokes  
433 1995). Nonetheless, in this study Boersma and Stokes (1995) did not find a strong relationship between  
434 hatching asynchrony and initial size asymmetry as we did.

435 Contrary to the “Brood Reduction Hypothesis” and to our predictions, we did not find that  
436 asynchronous broods conferred an advantage over synchronous broods in terms of nestling survival in the  
437 “bad” year. Similarly, we did not find support for our prediction that in the “bad” year second hatchlings of  
438 asynchronous broods would die more than those of synchronous ones; regardless of the hatching asynchrony,  
439 in the “bad” year second hatchlings tend to starve. The year, and not the asynchrony, was key to brood  
440 reduction. ~~in~~ In all the other penguin studies conducted to date there is also no effect of asynchrony in brood  
441 reduction (Seddon and Van Heezik 1991; Williams and Croxall 1991; Moreno et al. 1994; Boersma and  
442 Stokes 1995). We think that is worth to conduct our experiment over many more years in order to include a  
443 wider environmental variation, with, potentially, really bad years. As Slagsvold (1986) stated that conditions



444 have to be very poor before asynchronous broods fledge more nestlings than synchronous ones ~~and.~~ ~~In this~~  
445 ~~sense,~~ the breeding success of the “bad” year ~~(0.61 fledglings/nest)~~ was not so low when compared ~~the~~ ~~our~~  
446 threshold value ~~of this colony~~ (0.9 fledglings/nest-11 year study, Frere not published) and to what has been  
447 found in other penguin colonies (Boersma et al. 1990; Frere et al. 1998), ~~we think that is worth to conduct our~~  
448 ~~experiment over many more years in order to include a wider environmental variation, with, potentially, really~~  
449 ~~bad years.~~ ~~Nonetheless,~~ in all the other penguin studies conducted to date there is also no effect of  
450 asynchrony in brood reduction (Seddon and Van Heezik 1991; Williams and Croxall 1991; Moreno et al.  
451 1994; Boersma and Stokes 1995). ~~We think that is worth to conduct our experiment over many more years in~~  
452 ~~order to include a wider environmental variation, with, potentially, really bad years.~~

453 We found that Magellanic Penguins are indeed facultative brood reducers when food is scarce as  
454 proposed by Lamey (1990), and Boersma and Stokes (1995); at Isla Quiroga brood reduction of the last  
455 nestling occurred in the “bad” year. Furthermore, asynchrony facilitates this reduction, because second  
456 hatchlings died more than first ones in asynchronous broods and not in synchronous broods, which supports  
457 the “Brood Reduction Hypothesis” (Lack 1947). Also, as this difference is not noticed in the  
458 “good”/“intermediate”-quality years, this could be demonstrating that when food is abundant adults  
459 compensate the disadvantage of the last hatchlings, maybe by preferentially feeding them (but see Boersma  
460 and Stokes 1995), as has been shown in other species (Royle et al. 2002). In favor of the “Brood Reduction  
461 Hypothesis”, we found that brood reduction occurred early in the growing period (approximately at 20 days  
462 old), within the first third of the growing period, which agrees with the idea that younger nestlings are rapidly  
463 eliminated to reduce parental effort (Lack 1954). Furthermore, we found that in the “bad” year it occurred 10  
464 days earlier for 4-day asynchronous broods than for synchronous broods, conferring a possible advantage for  
465 asynchronous broods over synchronous ones. It is worth checking if feeding nestlings for 10 more days would  
466 cause a significant disadvantage for parents of this species, which feed their nestlings for many days—  
467 approximately 70 days (Boersma et al. 1990; Frere et al. 1998). Nonetheless, in *Pygoscelis* penguins, it has  
468 been found that brood reduction occurs later, during the crèche stage, when they have already invested  
469 heavily in nestlings, breaking down the “Brood Reduction Hypothesis” (Williams and Croxall 1991; Moreno  
470 et al. 1994). We also found that the more asynchronous the brood the larger the mass difference between  
471 siblings before the brood reduction occurred, another indication of the importance of hatching asynchrony.

472 Supporting the “Brood Reduction Hypothesis” in a broader sense (Amundsen and Slagsvold 1991a),  
473 in the “bad” year fledglings of 2-day asynchronous broods were heavier than those of synchronous broods.  
474 Remarkably, fledglings of 4-day asynchronous broods were not heavier than synchronous nestlings, but  
475 neither they were lighter than 2-day broods in the “bad” years. Maybe the 2-day interval is the optimal  
476 balance between avoiding a similar demand of both siblings and an extreme asymmetry between siblings. In  
477 the genus *Pygoscelis*, the quality advantage of asynchronous broods over synchronous broods disappears  
478 during the later crèche phase (Moreno et al. 1994) and hatching asynchrony was only related to the within-  
479 brood asymmetry at 15 days but not at 45 days of age (Belliure et al. 1999). In the Jackass Penguin, a  
480 congener of our study species, brood asymmetry remains until fledging (Seddon and Van Heezik 1991). Also,  
481 we still do not know if an advantage of 477 g in favor of asynchronous fledglings over synchronous ones  
482 could produce an adaptive advantage of asynchronous broods. On one hand, fledglings weigh 2-3 kg, so the  
483 increment would be in the order of a 25-26 % of total fledgling mass. On the other hand, there would still be a  
484 need to understand how fledgling mass could affect juvenile survival. The juvenile survival is very low in the  
485 study species (0.2) and has been shown to be affected by the breeding season (Pozzi 2015).

486 Williams and Croxall (1991), and Moreno et al. (1994) suggested that asynchrony in penguins may  
487 be a secondary consequence of adults keeping their eggs warm immediately after laying. The species of those  
488 studies breed in extreme low ambient temperatures, which is not the case for Magellanic Penguins (Williams  
489 1995). Seddon and Van Heezik (1991) proposed that in a congener of Magellanic Penguins hatching  
490 asynchrony provides an advantage in nestling quality, as is suggested by the extended “Brood Reduction  
491 Hypothesis” (Amundsen and Slagsvold 1991a) and the “Sibling Rivalry Reduction Hypothesis” (Hahn 1981).  
492 The “Sibling Rivalry Reduction Hypothesis” proposes that asynchrony may reduce the rivalry of siblings  
493 during feeding (Hahn 1981), but also states that this advantage in terms of quality should be in “good” or  
494 “bad” years, which is not the case of Magellanic Penguins in the current study. Boersma (1991) suggested that  
495 asynchronies in Magellanic Penguins might function as a mechanism that increases the chances that both  
496 nestlings are fed soon after hatching. The key to understanding hatching asynchrony might be in how it is  
497 established. Rebstock and Boersma (2011) showed that parental behavior during incubation controls hatching  
498 asynchrony in Magellanic Penguins. Also, in other species, it has been shown that parents can control  
499 asynchrony by the amount of incubation that occurs during egg laying (Johnson et al. 2013). We have

**Comentado [R3]:** Este párrafo no se si lo dejaría? Queda medio colgado... Quizás pondría algo de por qué en otras especies o estudios de Magallanes no se encontró que mueran rápido ni tampoco una ventaja al peso al fledgling? Puede ser que en *Pygoscelis sea menor la ha? por lo q vi es 1???* Pero no tengo los libros de pingüinos!

500 previously shown that asynchrony is the result of a physiological constraint of the brood patch area on the  
501 laying day of the first eggs (Barrionuevo and Frere 2015). So, asynchrony might be a consequence of a  
502 balance between the need to begin the contact with the egg, so that the brood patch can properly develop (St.  
503 Clair 1992; Massaro et al. 2006), and the delayed development of the brood patch.

504 ~~Although~~ ~~w~~We think that asynchrony could bring a benefit for parents compared to synchronous  
505 broods in a “bad” year, ~~but there still needs to be studied~~ ~~we are not sure~~ to what extent those benefits could  
506 really affect Magellanic Penguin’s breeding strategies. In terms of survival, Boersma (1991) showed that the  
507 breeding success is highest in 2-day asynchronous broods, but we did not find a higher breeding success for  
508 that asynchrony. This asynchrony provides nestlings that survive a better condition that may be crucial for  
509 post fledging survival. This trait may have been important for a selection of this interval, because most control  
510 nests had this asynchrony. Although there are broods with extreme asynchronies, the percentage of these nests  
511 is very low. Even synchronous nests are at a disadvantage and 4-day asynchronous nests did not present a  
512 large advantage over 2-day broods.

513 To conclude, ~~we think that asynchrony could bring a benefit for parents compared to synchronous~~  
514 ~~broods in a “bad” year, but there still needs to be studied to what extent those benefits could really affect~~  
515 ~~Magellanic Penguin’s breeding strategies.~~ ~~w~~We could not find complete support for the “Brood Reduction  
516 Hypothesis” in Magellanic Penguins, mainly because during the “bad” years, in both synchronous and  
517 asynchronous nests, the second nestling died. However, we found support for the hypothesis in a broader  
518 sense because in “bad” years parents of asynchronous broods would invest less time feeding their nestlings—  
519 because they starve early—and, would produce higher quality fledglings than parents of synchronous broods.

520

#### 521 **Compliance with Ethical Standards**

522

523 Conflict of Interest: M. Barrionuevo declares that she has no conflict of interest. E. Frere declares that he has  
524 no conflict of interest.

525

526 Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of

**Comentado [R4]:** Creo que esto también lo sacaría

527 animals were followed.

528

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642 **Figure caption**

643 **Fig. 1** Number of nestlings that starved per nest for the different treatments of hatching asynchrony (0, 2 and  
644 4 days). Mean  $\pm$  coefficient intervals are show

645 **Fig. 2** Number of dead nestlings according to the hatching asynchrony-treatment (HA) discriminated by age  
646 in: a) “good” (2010 and 2011) and b) “bad” (2012) years. Different asynchronies are represented by different  
647 fill patterns in the bars and line fitting with different colors

648 **Fig. 3** Initial mass asymmetry calculated as the mass of the first minus the second-hatchling on the day the  
649 second nestling hatched vs. the final mass asymmetry on the previous measurement to the brood reduction  
650 calculated as the live nestling minus the dead nestling. Fitting equation is:  $y = 321 + 2.11 x$

651 **Fig. 4** Fledgling mass in relation to the study year and the hatching asynchrony (in days, denoted with  
652 different markers). Mean  $\pm$  0.95 confidence intervals are shown and letters denote significant differences

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664 **Table**

665 **Table 1** Concentrations of chlorophyll *a* in the three breeding seasons studying the Magellanic penguin  
666 colony. The concentrations are separated by months and sites. August and September are months were  
667 penguins are arriving at the colonies and are near the breeding area. October and November penguins lay eggs  
668 and incubate them and December and January is the nestling period. The foraging sites (A and B) are based  
669 on data of Boersma et al. (2009) and Sala et al. (2012). These sites are about 120 km north to Puerto Deseado  
670 (A) and east to the mouth of the Ría Deseado (B)

Breeding season	Month	Chlorophyll <i>a</i> in site A (mgC/m <sup>3</sup> /day)	Chlorophyll <i>a</i> in site B (mgC/m <sup>3</sup> /day)
2010-2011	August	479.91	517.56
	September	466.13	540.89
	October	665.75	616.02
	November	280.74	313.70
	December	192.81	227.90
	January	263.47	199.51
2011-2012	August	928.66	963.23
	September	947.80	748.91
	October	626.69	478.36
	November	316.38	239.85
	December	238.79	168.54
	January	225.15	208.34
2012-2013	August	532.73	534.53
	September	501.49	580.76
	October	317.86	413.13

November	<del>201.84</del>	<del>212.31</del>
December	<del>244.11</del>	<del>204.17</del>
January	<del>278.21</del>	<del>222.81</del>

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