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The Role of Hatching Asynchrony in a Seabird Species Exhibiting Obligate Brood Reduction

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Abstract.—Brood reduction is a within-brood partial mortality due to sibling rivalry, and, in some species, the death of at least one sibling in the brood is almost guaranteed (obligate brood-reducers). Imperial Cormorants (*Phalacrocorax atriceps*) usually lay three-egg clutches that hatch asynchronously over 4-5 days. This species exhibits obligate brood reduction, and last-laid (marginal) eggs serve as insurance against early failure of elder (core) members. Within-brood sibling asymmetries were manipulated to analyze their effects on breeding success, brood reduction, parental body condition and chick growth. Two types of symmetrical broods containing three similar-sized chicks at the beginning of chick-rearing (3-days old) and close to the peak in brood reduction (8-days old) were generated to contrast the natural asymmetrical brood. Breeding success and parental condition were unrelated to sibling asymmetry levels. Asymptotic mass of fledglings from 8-day old broods was lower than those for natural and 3-day old broods. Our results suggest that hatching asynchrony favors early brood reduction and improves fledging condition. Regardless of asymmetry levels, Imperial Cormorants were obligate reducers, and the insurance value provided by the marginal chick was negligible. Therefore, the insurance value of the marginal offspring appears to serve mainly at the egg stage. *Received 3 February 2017, accepted 14 April 2017.*

Key words.—fledging condition, Imperial Cormorant, insurance, marginal offspring, *Phalacrocorax atriceps*, sibling asymmetry.

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Asynchronous hatching is a widely observed pattern among birds occurring as result of the onset of incubation before clutch completion (Magrath 1990; Stoleson and Beissinger 1995). It leads to the establishment of a within-brood hierarchy in age, size and competitive abilities that affect sibling dynamics and, hence, fitness returns (Forbes and Mock 1994; Mock and Parker 1997). Furthermore, brood reduction is a within-brood partial mortality due to sibling rivalry (Mock 1994; Mock and Parker 1997), and asynchronous hatching is the main mechanism facilitating this process.

In brood-reducing species, asynchronous hatching structures offspring roles in two statuses: advantaged *core* offspring (i.e., subset of eggs or chicks that parents can normally raise) and disadvantaged *marginal* offspring (i.e., eggs or chicks that hatch later in the hatching sequence and suffer higher mortality rates due to parental imposed handicap; Mock and Forbes 1995; Mock and Parker 1997). According to the frequency of death events across nests, brood reduction can be

classified as facultative or obligate (Simmons 1988; Mock and Parker 1997). In facultative species, marginal offspring have a reasonable chance of surviving alongside core siblings, while in obligate brood-reducer species the death of at least one sibling is almost guaranteed (> 90% of nests; Simmons 1988; Mock and Parker 1997). Also, brood reduction can be classified according to the mechanism causing the offspring death (Mock and Parker 1997; Zieliński 2002). In both facultative and obligate systems, offspring death can be caused by fatal starvation, siblicide, or parental infanticide (Mock 1984; Mock and Parker 1997; Zieliński 2002). In the last 50 years, a large number of bird species from diverse taxa have been recognized as brood reducers, with most of the detailed studies focusing on siblicidal species (Edwards and Collopy 1983; Simmons 1988; Anderson 1990; Mock and Parker 1997). Remarkably, obligate brood reduction by fatal starvation is a rare form of brood reduction that has only been reported in some species of crested penguins (*Eudyptes* spp.; Lamey 1990, 1993).

The adaptive significance of hatching asynchrony is usually considered within the context of the brood reduction hypothesis developed by Lack (1947, 1954). According to this hypothesis, hatching asynchrony is an adaptation facilitating the competitive demise of marginal offspring in years when food resources are insufficient, with the entire brood being potentially reared in years when resources are more plentiful (Mock 1984; Magrath 1990). In obligate brood-reducer species, however, the death of the marginal offspring is typically independent of variations in food supplies, and this chick mostly serves as an insurance or replacement for core siblings that fail to hatch or die at an early age (insurance hypothesis; Dorward 1962; Forbes 1990; Mock and Forbes 1995). Thus, the adaptive significance of hatching asynchrony in obligate brood-reducer species mainly refers to the existence of an efficient brood reduction mechanism to remove the marginal offspring when it eventually becomes redundant because core offspring achieve a high probability of survival. Because asynchronous hatching facilitates the elimination of marginal chicks through an increased sibling asymmetry within the brood, the insurance reproductive value of marginal chicks decreases as hatching asynchrony increases. On the other hand, a smaller hatching span would reduce sibling asymmetry and thus increase the survival and insurance value of marginal chicks, although it could negatively affect breeding success, parental body condition, and survival, growth rates and fledging condition of core chicks (Forbes 1990; Stoleson and Beissinger 1997). While several studies showed that survival time of marginal chicks decreases as the hatching span increases (Shaw 1985; Anderson 1989; Evans 1996), the evidence for negative effects associated with more synchronous or symmetrical broods remains controversial (see Stoleson and Beissinger 1995).

Besides, experimental studies analyzing the effects of hatching asynchrony—or consequent sibling asymmetries—on brood reduction have been carried out mostly on obligate siblicidal species (Anderson 1989;

Evans 1996), facultative siblicidal species (Mock and Ploger 1987; Osorno and Drummond 1995), and facultative brood-reducing species where the elimination of marginal chicks occurs by starvation (Hahn 1981; Amundsen and Stokland 1988; Amundsen and Slagsvold 1991a; Seddon and van Heezik 1991). Williams (1981) generated synchronous egg hatching in two nests of the eastern Rockhopper Penguin (*Eudyptes chrysocome filholi*), a species exhibiting obligate brood reduction by starvation. To our knowledge, beyond that work, no experimental study has assessed the role that hatching asynchrony plays in species exhibiting obligate brood reduction without sibling or parental aggression.

The Imperial Cormorant (*Phalacrocorax atriceps*) is a colonial seabird inhabiting southern South America. This monogamous seabird usually lays three-egg clutches that hatch asynchronously over 4–5 days (Svigelj 2009; Svigelj and Quintana 2011a, 2011b; Calderón *et al.* 2012). This hatching pattern yields an important asymmetry of age and size between core and marginal chicks, where probability of fledging drastically decreases with hatching order (Svigelj 2009). At the Punta León colony (northern Patagonia, Argentina), Imperial Cormorants exhibit obligate brood reduction where the last-hatched chick from three-hatchling broods usually starves to death within the first week of life (Svigelj 2009; Svigelj and Quintana 2011a, 2011b). In this population, three-fledgling broods are extremely rare (< 1% of breeding attempts), and third eggs serve as insurance against early failure of core members (Svigelj 2009; Svigelj and Quintana 2011a). Although different aspects of breeding biology and brood reduction have been studied in Imperial Cormorants (Svigelj 2009; Svigelj and Quintana 2011a, 2011b; Svigelj *et al.* 2012), the role of sibling asymmetry is yet to be understood.

In this study, we manipulated sibling-size asymmetries in broods of the Imperial Cormorant, examining the consequences of sibling asymmetries on breeding success, brood reduction, parental body condition, chick survival and chick growth. By swap-

ping chicks between nests, we generated three-chick broods with different combinations of asymmetry in age and, hence, size. Considering that hatching asynchrony represents an efficient brood reduction mechanism to remove the marginal offspring, we predicted that increasing levels of symmetry as offspring grow would generate: 1) lower reproductive success; 2) higher loss in parental body mass during the chick-rearing period; 3) higher survival time for marginal offspring; and 4) lower asymptotic mass for fledglings. In addition, to clarify the proximate mechanism causing brood reduction, we analyzed data on parental food allocation and begging behavior on natural (non-manipulated) broods within the first week after hatching of the marginal chicks.

METHODS

Study Area

We conducted the study from October to December over three consecutive breeding seasons (2010-2012) at Punta León (43° 05' S, 64° 30' W), Chubut, Argentina. Punta León is a mixed-species seabird colony where Imperial Cormorants reproduce jointly with seven seabird species (Yorio *et al.* 1994). During the 2010 breeding season, the Imperial Cormorant colony comprised approximately 4,100-4,200 breeding pairs (W. S. Svagelj and F. Quintana, unpubl. data).

Experimental Design

In 2010, we monitored 154 Imperial Cormorant nests, 101 of which were randomly assigned to treatments involving translocations of chicks. All nests were checked every 1-3 days before and after egg hatching, and hatching date and body mass of chicks were determined. When age and mass of chicks were suitable for manipulative treatments, chicks were removed and translocated to a foster nest. Each manipulated brood contained three swapped chicks that were ranked as A-, B- and C-chicks in decreasing order of hierarchy. Nestlings were marked on the tarsus with tape bands labeled with their associated order.

We designed four treatments on sibling asymmetry, comprising three-chick broods with different combinations of asymmetry and age of chicks: 1) *Natural asymmetry* (Nat) corresponded to natural three-chick broods without any manipulation or chick swapping (asynchronies: A-B chicks = 1.5 ± 0.9 days, A-C chicks = 4.1 ± 1.6 days, $n = 53$); 2) *Symmetric at day 3* (S3) corresponded to broods with three symmetric chicks at the beginning of chick rearing (mean age: 2.7 ± 1.9 days; mean mass: 76 ± 32 g; maximum asynchrony within nest: 0.7 ± 0.7 days, $n = 31$); 3) *Symmetric at day*

8 (S8) corresponded to broods with three symmetric chicks at an age close to the peak in brood reduction (mean age: 8.3 ± 1.6 days; mean mass: 247 ± 78 g; maximum asynchrony within nest: 0.9 ± 0.7 days, $n = 40$); and 4) *Control* (Con) treatment consisting of broods composed of three swapped chicks simulating natural hatching asynchrony (asynchronies: A-B chicks = 1.6 ± 0.9 days, A-C chicks = 3.9 ± 1.2 days, $n = 30$). This last treatment allowed us to assess the effect of chick swapping. Date of hatching (i.e., date of hatching of the elder chick in the nest, standardized) did not differ between treatments ($F_{3,150} = 1.0$, $P = 0.38$). Hatching spans did not differ between Nat and Con treatments (Mann Whitney tests; A-B chicks, $W = 871$, $P = 0.44$; A-C chicks, $W = 730$, $P = 0.53$). For asymmetrical (Nat and Con) broods, intra-brood hierarchy was determined by the age of nestlings, while in the case of symmetrical (S3 and S8) broods, which mostly contained chicks of similar age, hierarchy was determined according to nestling body masses at translocation. Age at translocation ($\bar{x} \pm SD$) for A-, B- and C-chicks from S3 broods was 3.1 ± 2.0 , 2.7 ± 1.9 and 2.4 ± 1.9 days, respectively, while corresponding body masses were 83 ± 33 , 76 ± 32 and 70 ± 32 g, respectively. For A-, B- and C-chicks from S8 broods, age at translocation was 8.6 ± 1.7 , 8.3 ± 1.6 and 8.0 ± 1.5 days, respectively, while resultant body masses were 266 ± 83 , 246 ± 78 and 229 ± 71 g, respectively. Considering mean breeding success as an indicator of the quality of the breeding season, the 2010 season (mean breeding success = 1.04 fledglings per nest) represented an average season (range of variation for 2004-2015 period: 0.80-1.33 fledglings per nest; W. S. Svagelj and F. Quintana, unpubl. data).

Nest Monitoring, Nestling Growth and Change in Adult Body Mass During Chick Rearing

During the chick-rearing period, nests were visited every 3-5 days to determine growth and survival of chicks. Body mass was recorded using 100-g, 300-g, 600-g, 1,000-g and 2,500-g spring scales. When possible, mass at hatching was calculated from egg mass using the equation $Hatchling\ mass = 0.80 \times Egg\ mass - 5.14$ (Svagelj and Quintana 2011b). Imperial Cormorants are sexually dimorphic in size with males being larger and heavier (~18%) than females, and with dimorphism arising during chick rearing (Svagelj and Quintana 2007, 2017). To determine the sex of chicks, we measured tarsus and head length of chicks with a digital caliper when they were 25-days old or older. By the application of discriminant functions according age of chicks, sex can be determined with up to 94% accuracy (Svagelj and Quintana 2017).

Finally, we used the change in adult body mass during the chick-rearing period as an indicator of parental effort. Adults were captured and weighed on two occasions: when A-chicks were approximately 8-days old (to standardize the onset between treatments) and approximately 20 days later. Breeding adults were identified with plastic and metal bands and sexed by their vocalizations, a method with 100% accuracy (Svagelj and Quintana 2007).

Begging and Parental Food Allocation

To elucidate the proximate mechanism causing brood reduction, we present data on parental food allocation for 30 feeding events (27 for females and 3 for males; one feeding event per brood) at natural broods from 2010 ($n = 6$), 2011 ($n = 18$) and 2012 ($n = 6$). Considering that brood reduction usually occurs within the first week after hatching of the marginal chick (Svagej 2009), feeding events were documented when marginal chicks were up to 7-days old ($\bar{x} = 2.6$, $SD = 1.7$ days). Nestlings were marked on the head and neck using non-toxic paint, and weighed before and after the feeding event. At each brood, the color of paint (white, pale orange and blue) was randomly assigned to nestlings. Begging behavior of nestlings was video recorded on 23 of these feeding events (4 in 2010, 13 in 2011 and 6 in 2012) by using Sony DCR-SR 88 video cameras. During early chick rearing, breeding adults usually perform a single foraging trip per day with females foraging throughout the morning and males foraging exclusively in the afternoon (Harris *et al.* 2013). Video cameras were installed 2-3 m from nests before the estimated arrival of adults with food. A feeding event ($\bar{x} = 12.4$, $SD = 4.8$ min) started when an adult with food arrived at the nest and at least one chick begged for food, and ended when no chicks were begging or after 5 min without parental response to begging calls.

Data Analyses

To test the effect of sibling asymmetry on breeding success (i.e., number of chicks fledged per nest), we employed generalized linear models with Conway-Maxwell-Poisson (COM-Poisson) distribution (Shmueli *et al.* 2005; Sellers and Shmueli 2010). It is a flexible distribution that can account for underdispersion usually encountered in count data (Shmueli *et al.* 2005). In our case, COM-Poisson models on breeding success fitted the data better ($\chi^2_1 = 58.6$, $P < 0.001$) than standard Poisson, which exhibited underdispersion ($\hat{c} = 0.33$). Chicks were considered to have fledged if they reached 30 days of age (Svagej and Quintana 2011a; Svagej *et al.* 2012). Hatching date was also included as predictor variable. In all analyses, we standardized date of hatching, entering it as a deviation from the median hatching date (subtracting the median date of hatching from the actual date) and dividing the result by the standard deviation. Also, we employed generalized linear models with a binomial family distribution (Crawley 2013) to evaluate the effects of sibling asymmetry and hatching date on the probability of total breeding failure (1 = failure, no chicks fledged; 0 = successful, at least one chick fledged).

To test the effect of sibling asymmetry on the change in adult body mass during the chick-rearing period, we used linear mixed models (Pinheiro and Bates 2000) with nest identity (a unique code for each nest) included as a random effect. Change in adult body mass was calculated as the difference between adult mass when A-chicks were approximately 8-days old and approximately 20 days later, with positive and negative val-

ues indicating an increase or decrease in body mass, respectively. Sex of the breeding adult and hatching date were also included as predictor variables. Also, we included the number of days elapsed between body mass measurements ($\bar{x} = 20.3$, $SD = 2.6$ days) as a covariate. Similarly to hatching date, the number of days elapsed between body measurements was also standardized subtracting the median of days from the actual number of days and dividing the result by the standard deviation. Adults that were not captured twice were excluded from statistical analyses.

We analyzed chick survival time by applying log-rank tests on Kaplan-Meier estimates of survival (Kalbfleisch and Prentice 2002). First, we evaluated the effect of sibling hierarchy (i.e., A-, B- and C-chicks) on chick survival time for each treatment on sibling asymmetry. Second, we compared chick survival time between asymmetry treatments for each order in the sibling hierarchy (i.e., three analyses, for A-, B- and C-chicks). To assess differences in early chick growth (i.e., first week from the onset of treatment) according the sibling hierarchy order, we fitted growth curves in body mass for each treatment on sibling asymmetry. For each treatment, we ran linear mixed models with hierarchy order, linear and quadratic terms of chick's age, and the interactions between hierarchy order and linear and quadratic terms of chick's age as predictor variables. Nest and chick identity nested on nest were included as random effects. Heteroscedasticity was modeled considering a variance function where variance increases linearly with the fitted values (Pinheiro and Bates 2000).

We analyzed growth in body mass of fledglings using non-linear mixed models (Pinheiro and Bates 2000). Growth data were fitted to Richards equation (Richards 1959) using the following parameterization: $y_t = A (1 + (d-1) \exp(-K(t-t_0)/d^{1/(1-d)}))^{1/(1-d)}$ (Tjørve and Tjørve 2010), where y_t is chick mass at age t , and A , K , t_0 and d are the upper asymptote, maximum relative growth rate, age at the inflection point and shape parameter, respectively. Non-linear mixed models allow the evaluation of the effect of predictor variables on growth parameters (Pinheiro and Bates 2000). Sibling asymmetry was included as a predictor variable. Because growth of Imperial Cormorants depends on fledging order and brood size at independence (W. S. Svagej and F. Quintana, unpubl. data), we also included rearing conditions (i.e., combination of the hierarchy order (O) and brood size (BS) at fledging: O1BS1 = first chick in one-chick broods, O1BS2 = first chick in two-chick broods, O2BS2 = second chick in two-chick broods) as a predictor. Also, chick sex and hatching date were included as predictor variables. Only growth parameters with biological meaning (A , K and t_0) were modeled by predictor variables. Growth parameters from nest and chick identity nested on nest were included as random effects. As for early growth models, heteroscedasticity was modeled considering a linear increase with the fitted values. Undernourished chicks seen alive at the last nest checking were also considered. Chicks that could not be captured and measured to be sexed were excluded from statistical analyses. Considering the main

goal of this study, only sibling asymmetry results are discussed.

Generalized linear mixed models with binomial distribution were used to evaluate if the probability of being effectively fed (1 = yes, 0 = no) differed with hatching order. We used linear mixed models to evaluate if the amount of food received by chicks (i.e., difference between body masses before and after the feeding event) differed according hatching order. We analyzed the videos using software OpenShot Video Editor (OpenShot Studios 2016). From the videos, we determined if chicks actively begged for food during the feeding event (1 = yes, 0 = no), and if agonistic interactions existed among chicks. We used generalized linear mixed models with binomial distribution to evaluate if the probability of begging differed with hatching order. Accounting for possible inter-annual variations, year was included as a random effect in all analyses. Feeding event nested on year was also included as random effect.

In all analyses, we employed a backward selection procedure removing non-significant terms from the model (Crawley 2013). Significance of random effects was evaluated using likelihood ratio tests, and non-relevant factors were discarded. For all response variables analyzed, there were no differences between Nat and Con treatments (all $P > 0.05$). Therefore, we did not detect any effect due to chick swapping, and Con treatment was excluded from further analyses. Statistical analyses were carried out using COMPOissonReg (Sellers and Lotze 2015), lme4 (Bates *et al.* 2016), nlme (Pinheiro *et al.* 2016), survival (Therneau 2016) and ggplot2 (Wickham *et al.* 2016) packages from statistical software R (R Development Core Team 2016). Values were reported as means \pm SE except where noted. All tests were two-tailed, and differences were considered significant at $P < 0.05$.

RESULTS

Only two broods (from S3 and S8 treatments) produced three-fledgling broods. Breeding success did not differ between sibling asymmetry treatments (Nat: 1.47 ± 0.09 , S3: 1.26 ± 0.13 , and S8: 1.35 ± 0.10 fledglings per nest; $\chi^2_2 = 2.4$, $P = 0.30$). Hatching date was unrelated to variation in breeding success ($\chi^2_1 = 1.0$, $P = 0.33$). Nine percent of nests ($n = 124$) failed and produced no fledglings. The probability of breeding failure did not differ with sibling asymmetry (percentage of failed nests; Nat: 8% ($n = 53$), S3: 13% ($n = 31$), S8: 8% ($n = 40$); $\chi^2_2 = 1.0$, $P = 0.60$). Also, the probability of breeding failure was not related to hatching date ($\chi^2_1 = 0.7$, $P = 0.41$).

The change in adult body mass during the chick-rearing period did not differ with sibling asymmetry (Nat: -69 ± 14 g, S3: -74

± 14 g, and S8: -92 ± 11 g; $F_{2,131} = 1.0$, $P = 0.36$). Sex of the breeding adult ($F_{1,130} = 0.2$, $P = 0.70$) and the number of days elapsed between mass measurements ($F_{1,133} = 3.2$, $P = 0.08$) were unrelated to changes in body mass. The mass loss during the chick-rearing period increased with hatching date ($\beta = -27.6 \pm 8.6$, $F_{1,134} = 10.2$, $P < 0.005$; Fig. 1).

Survival time of chicks decreased with hierarchy in all treatments on sibling asymmetry ($\chi^2_1 > 9.4$, $P < 0.005$, for all comparisons within asymmetry treatments; Fig. 2). When survival time was compared among asymmetry treatments for each order in the sibling hierarchy, sibling asymmetry did not affect survival time for either A- or B-chicks (A-chicks, $\chi^2_2 = 3.4$, $P = 0.19$; B-chicks, $\chi^2_2 = 2.2$, $P = 0.34$; Fig. 3A, 3B). Survival time of C-chicks differed between asymmetry treatments (median survival time: 6 days, 10 days, and 14.5 days for Nat, S3 and S8, respectively; $\chi^2_2 = 38.5$, $P < 0.001$; Fig. 3C). Survival time of C-chicks from Nat was lower than that for S3 ($\chi^2_1 = 8.4$, $P < 0.005$) and S8 ($\chi^2_1 = 39.7$, $P < 0.001$) treatments, while survival time from S3 was lower than that for S8 treatment ($\chi^2_1 = 4.7$, $P = 0.03$; Fig. 3C).

For both Nat and S3 broods, early growth in body mass showed no differences between A- and B-chicks, while both exhibited a high-

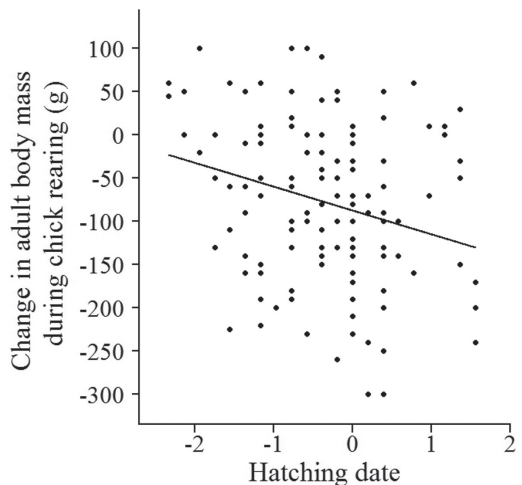


Figure 1. Relationship between change in adult body mass of Imperial Cormorants during chick-rearing period and standardized hatching date. The adjusted function was obtained from a general linear model.

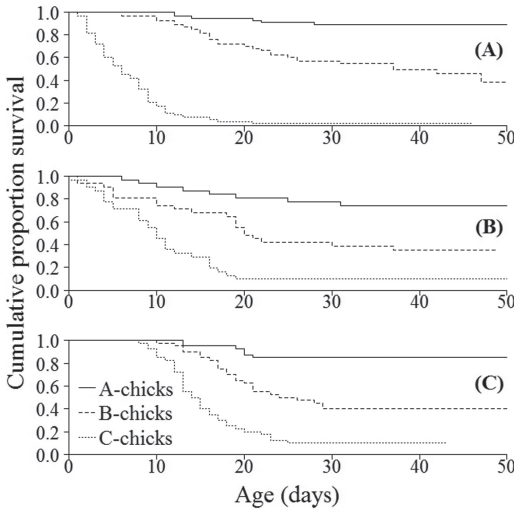


Figure 2. Kaplan-Meier survival estimates according to chick age (in days) and sibling hierarchy (solid, dashed and dotted lines, respectively, for A-, B- and C-chicks of the Imperial Cormorant) for (A) Nat = natural asymmetry, (B) S3 = symmetric at day 3, and (C) S8 = symmetric at day 8.

er growth than C-chicks (Table 1; Fig. 4A, 4B). For S8 broods, early growth progressively decreased with sibling hierarchy (Table 1; Fig. 4C).

Asymptotic body mass of fledglings was affected by sibling asymmetry ($F_{2,823} = 13.2, P$

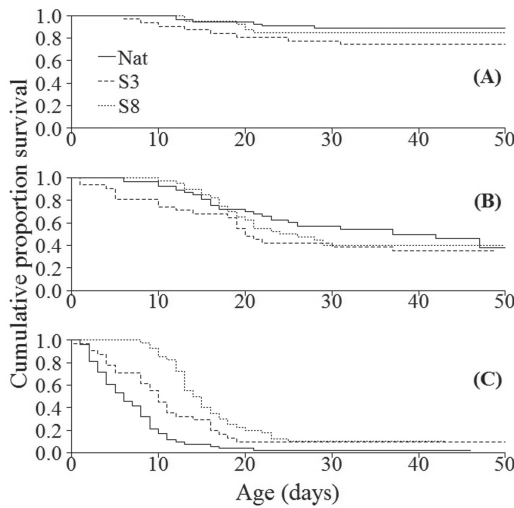


Figure 3. Kaplan-Meier survival estimates according to chick age (in days) and sibling asymmetry (solid lines: Nat = natural asymmetry, dashed lines: S3 = symmetric at day 3, dotted lines: S8 = symmetric at day 8) for (A) A-chicks, (B) B-chicks and (C) C-chicks of the Imperial Cormorant

Table 1. Final models describing early growth in mass (g) of Imperial Cormorant chicks according to sibling asymmetry treatments (natural asymmetry, symmetric at day 3 and symmetric at day 8). In each starting model, sibling hierarchy (A-, B- and C-chicks), linear and quadratic terms of chick age (in days) and the interaction terms were included as predictor variables. Only significant predictor variables that remained in the final model are shown.

Predictor Variable	Natural Asymmetry			Symmetric at Day 3			Symmetric at Day 8		
	Estimate ± SE	t_{191}	P	Estimate ± SE	t_{194}	P	Estimate ± SE	t_{296}	P
Intercept	40.7 ± 1.7	24.3	< 0.001	42.7 ± 3.4	12.7	< 0.001	37.8 ± 5.70	6.7	< 0.001
Age (linear)	5.01 ± 1.29	3.9	< 0.001	8.19 ± 1.27	6.5	< 0.001	10.56 ± 2.40	4.4	< 0.001
Age (quadratic)	2.42 ± 0.24	10.1	< 0.001	1.34 ± 0.17	8.0	< 0.001	1.84 ± 0.22	8.5	< 0.001
Sibling hierarchy (B) ¹	-1.31 ± 2.16	-0.6	0.544	-5.00 ± 3.47	-1.4	0.151	1.78 ± 11.86	0.1	0.881
Sibling hierarchy (C) ¹	-1.86 ± 2.19	-0.8	0.397	-3.88 ± 3.49	-1.1	0.268	14.66 ± 13.29	1.1	0.271
Age (quadratic) : Sibling hierarchy (B) ¹	0.07 ± 0.17	0.4	0.697	-0.10 ± 0.12	-0.8	0.417	-0.45 ± 0.14	-3.2	0.001
Age (quadratic) : Sibling hierarchy (C) ¹	-1.22 ± 0.18	-6.9	< 0.001	-0.53 ± 0.13	-4.2	< 0.001	-0.91 ± 0.15	-6.1	< 0.001

¹Relative variable to value of sibling hierarchy (A-chick).

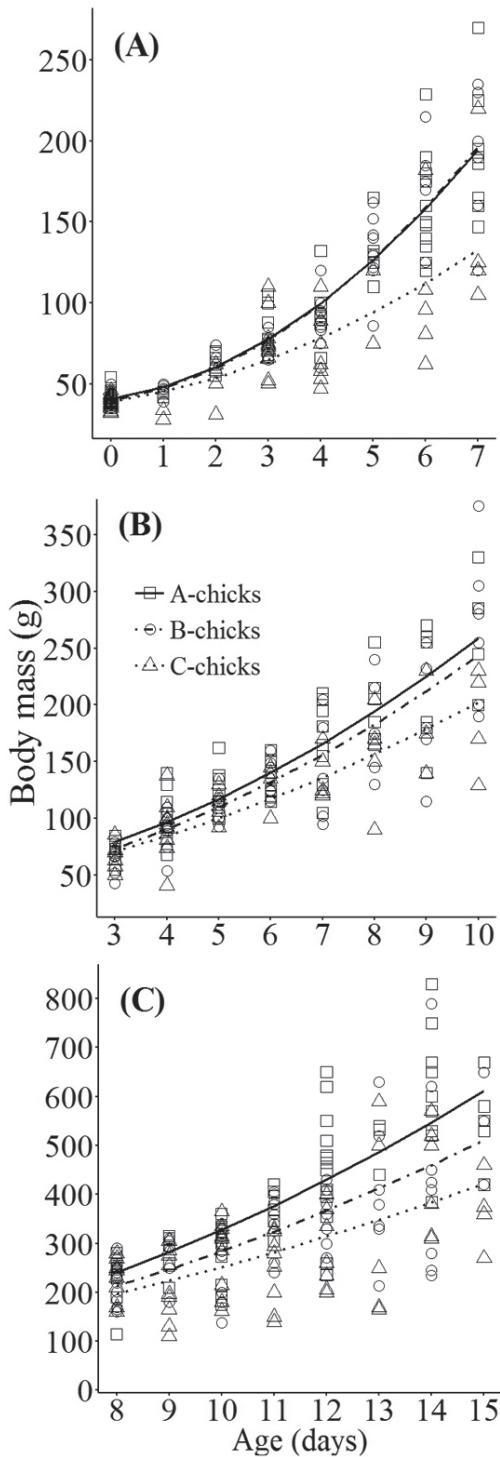


Figure 4. Early growth in body mass for Imperial Cormorant chicks according to sibling hierarchy (solid, dashed and dotted lines for A-, B- and C-chicks) for (A) Nat = natural asymmetry, (B) S3 = symmetric at day 3, and (C) S8 = symmetric at day 8). Adjusted curves were obtained from linear mixed models (see Table 1).

< 0.001; Table 2). Asymptotic mass of chicks from S8 treatment was 179 g lower than that for Nat ($t_{823} = -5.1, P < 0.001$) and 109 g lower than that for S3 ($t_{823} = -2.7, P < 0.01$) treatments, while no differences were found between chicks from Nat and S3 ($t_{823} = -1.7, P = 0.086$; Table 2). Chicks from S8 treatment reached the inflection point at an earlier age (17.2 days) than those from Nat (18.0 days; $t_{823} = -2.9, P < 0.01$) or S3 (18.0 days; $t_{823} = -2.6, P < 0.01$), while no differences were found between chicks from Nat and S3 treatments ($t_{823} = -0.1, P = 0.93$; Table 2).

Begging and Parental Food Allocation

Imperial Cormorants hatch naked with minor locomotive abilities, and eyes remain closed for several days. During the first week after hatching, begging behavior was mostly circumscribed to nestlings lifting their heads slightly over the nest rim with wobbly-head movements and the gular pouch distended, but without displacements within the nest. Chicks were fed by regurgitation in the usual way for cormorant species (i.e., the chick introduces its head inside of the adult beak). At that early age, parents down their head toward a particular chick and regurgitate food. Therefore, parents choose which chick to feed. There were no agonistic behaviors among chicks during feeding events, and only chicks that begged obtained food. The probability of begging activity during a feeding event did not differ with hatching order (A-chicks: 0.87, B-chicks: 0.87, and C-chicks: 0.83; $\chi^2_2 = 0.2, P = 0.89$). However, the probability of being fed differed with hatching order (A-chicks: 0.80, B-chicks: 0.57, and C-chicks: 0.20; $\chi^2_2 = 23.5, P < 0.001$). Probability of being fed for C-chicks was lower than that for A-chicks ($z = -4.3, P < 0.001$) and B-chicks ($z = -2.8, P = 0.013$), while no differences were found between A- and B-chicks ($z = -1.9, P = 0.14$). The amount of food received by chicks during the feeding event progressively decreased with hatching order (A-chicks: 25.4 ± 5.4 g, B-chicks: 12.6 ± 4.7 g, and C-chicks: 4.8 ± 4.2 g; $F_{2,85} = 17.9, P < 0.001$). A-chicks received more food than B-chicks ($z = -2.8, P = 0.014$) and C-chicks ($z = -4.9, P < 0.001$), while B-chicks received more food than C-chicks ($z = -3.7, P < 0.01$).

Table 2. Final Richards's growth model in mass (g) for Imperial Cormorant fledglings. In the starting model, sibling asymmetry (Nat = natural asymmetry, S3 = symmetric at day 3, S8 = symmetric at day 8), rearing conditions (O1BS1 = first chick in one-chick broods, O1BS2 = first chick in two-chick broods, O2BS2 = second chick in two-chick broods), sex and hatching date as predictor variables, modeling A (asymptotic mass), K (maximum relative growth rate) and t_i (age at the inflection point) growth parameters were included. d is a shape parameter. Only significant predictor variables that remained in the final model are shown. Models were fitted as non-linear mixed models.

Parameter	Predictor Variable	Estimate \pm SE	t_{823}	P
A	Intercept	1,970 \pm 44	45.1	< 0.001
	Sibling asymmetry (S3) ¹	-70 \pm 41	-1.7	0.086
	Sibling asymmetry (S8) ¹	-179 \pm 35	-5.1	< 0.001
	Rearing conditions (O1BS2) ²	-93 \pm 35	-2.6	0.008
	Rearing conditions (O2BS2) ²	-281 \pm 40	-7.0	< 0.001
	Sex (Males) ³	203 \pm 31	6.5	< 0.001
K	Intercept	0.040 \pm 0.001	45.1	< 0.001
t_i	Intercept	18.0 \pm 0.3	64.4	< 0.001
	Sibling asymmetry (S3) ¹	0.0 \pm 0.3	0.1	0.929
	Sibling asymmetry (S8) ¹	-0.8 \pm 0.3	-2.9	0.003
	Rearing conditions (O1BS2) ²	-0.3 \pm 0.2	-1.1	0.267
	Rearing conditions (O2BS2) ²	-0.7 \pm 0.3	-2.6	0.008
	Sex (Males) ³	0.5 \pm 0.2	2.5	0.014
	Hatching date	-0.5 \pm 0.1	-4.4	< 0.001
d	Intercept	1.49 \pm 0.05	31.4	< 0.001

¹Relative variable to value of sibling asymmetry (Nat).

²Relative variable to value of rearing conditions (O1BS1).

³Relative variable to value of sex (Females).

DISCUSSION

Avian species present a wide variety of hatching patterns modeled by intrinsic and extrinsic selective forces that differ among taxa and life history strategies (Magrath 1990; Stoleson and Beissinger 1995). In species exhibiting obligate brood reduction, last-laid eggs can only survive until fledging when they replace earlier eggs or chicks that fail due to accidents, predation or congenital/developmental defects (Dorward 1962; Cash and Evans 1986; Humphries *et al.* 2006). In these species, asynchronous hatching would facilitate the reduction in brood size if all eggs hatch (Forbes 1990; Magrath 1990; Forbes *et al.* 1997; Mock and Parker 1997). Also, it has been proposed that hatching asynchrony ensures that at least some of the offspring fledge in good quality (the offspring quality assurance hypothesis; Amundsen and Slagsvold 1991b). In this sense, several experimental studies have demonstrated that fledglings from asynchronous broods were heavier than those from synchronous ones (reviewed in Amundsen and Slagsvold 1991b).

Our results suggest that hatching asynchrony and consequent sibling asymmetry within broods of Imperial Cormorants favor early brood reduction and improve body condition of fledglings. While breeding success, probability of breeding failure and change in parental body condition during chick-rearing were unrelated to levels of sibling asymmetry, the age at death of marginal chicks progressively decreased as sibling asymmetry increased. In addition, asymptotic body mass of fledglings decreased as symmetry increased, probably due to the presence of older marginal chicks in these broods. It must be noted, however, that differences were only detectable for S8 treatment, which exhibited the lowest fledgling mass. Lack of statistical differences between Nat and S3 treatments could be a consequence of low statistical power due to sample size. Also, fledglings from S8 reached their maximum relative growth sooner than those from Nat or S3. Although this may seem contradictory, this result is probably due to a lower gain in mass at the final stage of chick rearing. Our findings agree with the trade-off between the

insurance contribution of marginal chicks and quality of offspring produced (Forbes 1990; Amundsen and Slagsvold 1991b; Mock and Parker 1997). Even though prolonged survival time of marginal chicks would seem beneficial because it extends their insurance function as a replacement, lowering asymmetries among nestlings is detrimental to the quality of fledglings.

Obligate brood reduction in Imperial Cormorants occurred irrespective of the level of sibling asymmetry. Only two of 124 broods fledged three chicks, both from symmetrical broods. Besides those two marginal fledglings surviving alongside core siblings, only six marginal chicks fledged from broods where the death of a core chick occurred ($n = 77$), and just one of them corresponded to a natural asynchronous brood. Three important considerations arise from these results. First, hatching asynchrony or within-brood asymmetries at the beginning of the chick-rearing period are not essential for obligate brood reduction to occur in Imperial Cormorant broods. Various studies showed that asynchronous hatching is not indispensable for brood reduction to occur (Amundsen and Slagsvold 1991a; Seddon and van Heezik 1991). Moreover, our results agree with some studies in siblicidal species where obligate brood reduction occurred even in experimentally synchronized broods (Dorward 1962; Gargett 1982; Evans 1996). Second, even for symmetrical broods where asymmetries in age and size among nestlings were minor, within-brood asymmetries increased as offspring grew and determined the fate of marginal chicks. Several studies have demonstrated that conspicuous size hierarchies may develop even within synchronous or symmetrical broods (Amundsen and Slagsvold 1991a; Evans 1996). Third, the insurance value provided by the marginal offspring appears to serve mainly against early failures of core offspring in the egg stage. Svagelj (2009) showed that 16% of marginal eggs from three-egg clutches survive until fledging, serving as replacement for early failures of core members due to egg accidents, egg predation, infertility or hatching failures. In our study, 2% ($n = 53$)

of marginal chicks from natural three-chick broods survived until fledging, showing that the insurance benefit drops considerably if all eggs hatch.

The Imperial Cormorant belongs to the "blue-eyed shag" complex, a group of closely related species widely distributed in the Southern Hemisphere. Like the Imperial Cormorant, other blue-eyed shag species also exhibit considerable asynchronous hatching (averaging 4-5 days), a decrease in survival probabilities according hatching order, and strong brood reduction (South Georgia Shag, *P. georgianus*: Shaw (1985); Crozet Shag, *P. melanogenis*: Derenne *et al.* (1976), Williams and Burger (1979)). Shaw (1985) experimentally reduced within-brood sibling asymmetries in South Georgia Shags by translocating chicks that were 1-2 days of age. He found no differences in percentages of chick survival between symmetrical and normal broods, but symmetrical broods presented higher nest failure in one year and lighter asymptotic weight of fledglings, similar to B-chicks from natural three-hatchling broods (Shaw 1985). Thus, our results of no effects of sibling asymmetry on breeding success and lower fledging mass at symmetrical broods were similar to those obtained by Shaw (1985) in South Georgia Shags. Unfortunately, Shaw (1985) did not determine the intra-brood hierarchy in symmetrical broods; consequently, his results can be compared only at the brood level.

Chick rearing duties affected body condition of breeding adults, with Imperial Cormorants losing approximately 80 g (3-4% of body mass; Svagelj and Quintana 2007), on average, during the initial phase of the chick-rearing period. The loss in body mass was unrelated to the level of asymmetry in the brood, probably due to the prompt elimination of marginal chicks in all treatments. Mass loss increased with hatching date, likely due to younger and inexperienced birds breeding later in the season (Moreno 1998; Svagelj and Quintana 2011a).

Finally, our data on food allocation and begging at the age at which most C-chick deaths occurred show that the death of marginal chicks is caused by selective star-

vation by their parents, which mostly ignore the begging behavior of marginal chicks. The amount of food delivered to three-chick broods during feeding events the first week after hatching (45 ± 47 g) is several times less than for two-chick broods close to fledging (289 ± 129 g; P. I. Giudici, F. Quintana and W. S. Svagelj, unpubl. data), and Imperial Cormorants from Punta León frequently raise two chicks until independence (Svagelj and Quintana 2011a). Moreover, the amount of food delivered daily during the first week after hatching represents only a minor portion of the estimated daily food consumption of Imperial Cormorants in this colony (Gómez-Laich *et al.* 2013). In addition, between the 2004 and 2015 seasons, less than 1% ($n = 1,693$) of breeding attempts of Imperial Cormorants from Punta León generated three-fledgling broods (W. S. Svagelj and F. Quintana, unpubl. data). Irrespective of possible natural variations in sea conditions and food availability across years, three-hatchling broods of the Imperial Cormorant consistently exhibit an obligate brood reduction by starvation (W. S. Svagelj and F. Quintana, unpubl. data), suggesting that feeding of marginal chicks is mainly limited by parents rather than the environment.

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