

Sex-specific environmental sensitivity on the postnatal growth of a sexually size-dimorphic seabird

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The environment experienced during development is a key factor determining intraspecific variation in postnatal growth. In sexually size-dimorphic species, the larger sex typically grows at a higher absolute rate and consequently is more sensitive or vulnerable to restrictive environments. In addition, this sensitivity can be intrinsic when it is caused by physiological disadvantages of the larger sex, or extrinsic when it results from environments generated by social interactions among siblings. Here, we evaluated intrinsic and extrinsic drivers of sex-specific sensitivity in the postnatal growth of the Imperial Shag *Leucocarbo atriceps*, a sexually dimorphic seabird that typically produces one- or two-fledgling broods. Our objectives were to evaluate sex-specific effects of: (1) good and poor years on chicks fledging as singletons, (2) different rearing environments produced by the combinations of brood size and hatching order, and (3) sibling sex and brood sex composition in two-fledgling broods. Singletons exhibited suboptimal growth in poor years, with males and females equally affected. At an extrinsic level, males were more sensitive than females, as the reduction in fledging mass between best and worst social environments was twice as high in males as in females. In addition, the presence of a younger sibling in the nest had sex-specific consequences for the older chick. Fledging mass of older female chicks was unaffected by the presence of a younger sibling, whereas males reached the highest fledging mass when raised as singletons. The sex of the sibling and the brood sex composition did not affect chick growth in two-chick broods. Overall, our results suggest that females grow at their maximum rate even in moderately favourable social environments (as senior chicks in two-chick broods), whereas males require the most favourable environment (raised as singletons) to reach the highest growth.

Keywords: fledging mass, Imperial Shag, *Leucocarbo atriceps*, non-linear mixed models, offspring vulnerability.

Postnatal growth is a life-history trait that exhibits considerable intraspecific variation according to the environment experienced during development (Lack 1968, Gebhardt-Henrich & Richner 1998). Remarkably, the same environment often has differential effects on fitness-related traits of male and

female offspring (Kalmbach & Benito 2007). Such sex-specific environmental sensitivity (hereafter, SSES) can affect the relative reproductive value of the sexes and is therefore expected to influence parental investment strategies (Trivers & Willard 1973, Charnov 1982, Clutton-Brock *et al.* 1985, Clutton-Brock 1991, Hardy 2002, Uller 2006).

In sexually size-dimorphic species, the larger sex typically grows at a higher absolute rate

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(Richner 1991), requires more energy and investment (Weathers 1992, Anderson *et al.* 1993, Krijgsveld *et al.* 1998), and consequently is more vulnerable to restrictive environments or poor food conditions (Kalmbach & Benito 2007). In dimorphic birds, an increased sensitivity of the larger sex has been documented for traits as diverse as chick survival (Teather & Weatherhead 1989, Torres & Drummond 1997, Nager *et al.* 2000), fledging or peak mass (Brommer *et al.* 2003, Goymann *et al.* 2005, Kalmbach *et al.* 2005, Vedder *et al.* 2005b), growth rate (Daunt *et al.* 2001), age at maximum growth (Kalmbach *et al.* 2009), daily metabolizable energy intake (Vedder *et al.* 2005a) and immune function (Dubiec *et al.* 2006).

The quality of the environment experienced by the offspring at the brood level varies widely across years due to fluctuations in factors such as food availability and weather conditions (Martin 1987, Sydeman *et al.* 1991). Clutch size, breeding success, chick growth rate or fledging mass may reflect conditions during reproduction (Cairns 1987, Martin 1987, Teather & Weatherhead 1989, Sydeman *et al.* 1991). In poor years, the negative effects of restrictive conditions can be sex-specific with an exaggerated impact on offspring of the larger sex (Teather & Weatherhead 1989, Wiebe & Bortolotti 1992, Brommer *et al.* 2003). Also, the effective environment faced by the individual offspring can differ markedly within broods as a consequence of differences in sibling phenotype (Forbes 2011). In most altricial birds, asynchronous hatching generates a hierarchy both in age and in size among siblings that affect competitive abilities and, hence, access to food (Clark & Wilson 1981, Magrath 1990, Uller 2006). In dimorphic species with small brood size and marked differences in sibling size due to hatching asynchrony, the larger sex is usually more sensitive to the restrictive conditions imposed by later hatching (Drummond *et al.* 1991, Daunt *et al.* 2001, Råberg *et al.* 2005, Jones *et al.* 2009). Moreover, an additional level of complexity arises when sexes differ in their sensitivity depending on the sex of siblings and the sex composition of the brood (Bortolotti 1986, Velando *et al.* 2002). Although sex-specific effects of the hierarchy order have been documented for chick growth (Daunt *et al.* 2001, Goymann *et al.* 2005), evaluation of the effects of sibling's sex and brood sex composition has received less attention (Bortolotti 1986, Drummond *et al.* 1991).

Intrinsic vulnerability (or sensitivity) is the physiological disadvantage of the larger sex among siblings, while extrinsic vulnerability is the disadvantage due to interactions among siblings (Kalmbach & Benito 2007). Most studies of SSES have been carried out in broods that involve sibling interactions and competition (Kalmbach & Benito 2007). To assess the intrinsic sensitivity of sexes, studies conducted at single-chick broods or under individual experimental conditions are needed (Kalmbach *et al.* 2005, 2009).

The quantitative study of avian growth has benefited enormously from the influential papers published by Ricklefs (1968, 1973) five decades ago (Starck & Ricklefs 1998). More recently, the application of non-linear mixed models (Kalmbach *et al.* 2009, Sofaer *et al.* 2013, Aldredge 2016, Arnold *et al.* 2016, Hildebrandt & Schaub 2018) and the development of Richards equation (Tjørve & Tjørve 2010, 2017a,b, Svagelj *et al.* 2019) have improved our analytic capabilities, allowing an unbiased evaluation of growth parameters in data with multiple measurements on the same individual or on groups of related individuals (Giudici *et al.* 2017, Svagelj & Quintana 2017, Tuero *et al.* 2018, Svagelj *et al.* 2019). Here, we used this approach to analyse diverse drivers of sex-specific effects in the Imperial Shag *Leucocarbo atriceps*, a sexually dimorphic seabird with males being ~ 18 % heavier than females (Svagelj & Quintana 2007).

In Imperial Shags, the chick-rearing period lasts more than 2 months and the sexes begin to diverge in size at 15 days of age (Svagelj & Quintana 2011a,b, 2017, Svagelj *et al.* 2012). This monogamous seabird usually lays three-egg clutches but generates one or two fledglings per successful brood due to obligate brood reduction operating soon after hatching of the third chick (Svagelj & Quintana 2011a,b, 2017, Calderón *et al.* 2012, Svagelj *et al.* 2012, Giudici *et al.* 2017, Svagelj 2019). Thus, the Imperial Shag is a very interesting system to study intrinsic and extrinsic drivers of SSES under natural conditions.

In this paper, we evaluated SSES in the growth of Imperial Shag chicks during three breeding seasons. Our particular objectives were: (1) to evaluate sex-specific effects of good and poor years on chicks fledging as singletons (intrinsic SSES), (2) to evaluate the effect of different rearing environments generated by the combinations of brood size and hatching order (extrinsic SSES), and (3) to

assess the effects of sibling sex and brood sex composition (extrinsic SSES) in two-fledgling broods.

METHODS

Data were collected from October to December 2004, 2005 and 2017 at Punta León (43°05'S, 64°30'W), Chubut, Argentina. The years 2004 and 2005 were good seasons (see below) and their data were used to evaluate the extrinsic sex-specific effects of hierarchy order and brood size. The year 2017 was an unusually poor breeding season (see below) and its data were used to evaluate the intrinsic sensitivity of chicks by comparing growth in contrasting conditions (i.e. good vs. bad seasons). During egg hatching, we checked nests every 1–3 days to establish hatching date. Clutches of the Imperial Shag typically hatch over 4–5 days and intra-clutch egg size variation is minor in relation to variation among clutches (Svagej & Quintana 2011b, Svagej 2019). The interval between nest checks considered in our study is adequate to assign hatching date and hierarchy order based on nestling size and appearance. Nestlings were marked on the tarsus with tape bands labelled with their hatching order. At an age of ~ 20 days, chicks were ringed with numbered aluminium rings. During chick-rearing, we checked nests every 3–5 days to measure chicks until we were no longer able to capture them (35–40 days of age). We weighed birds using 100-, 300-, 600-, 1000- and 2500-g spring scales. When possible, we calculated mass at hatching from the estimated egg mass (Svagej & Quintana 2011b). Overall, the growth data analysed here correspond to 2303 measurements from 283 chicks (mean = 8.1, sd ± 1.5 measurements per chick) from 201 nests. In addition, for each chick, we obtained 3–4 drops of blood from the leg during the first week of life. We used these blood samples to determine the sex of chicks (134 males and 149 females) by established DNA-based techniques (Ellegren 1996, Fridolfsson & Ellegren 1999). In brief, the different size of introns within the highly conserved chromo-helicase-DNA binding protein (CHD1) gene was used to screen birds for sex differentiation using primers to amplify the CHD1-W and CHD1-Z genes located on the avian sex chromosomes. PCR products were separated by electrophoresis in an agarose gel to reveal the presence of one or two bands representing a male (ZZ) or a female (ZW) pattern, respectively. All details and

validation of DNA-based sexing used in this study are detailed in Quintana *et al.* (2008).

We analysed growth of fledglings using non-linear mixed models (Pinheiro & Bates 2000). These models allow the evaluation of the effect of predictor variables on growth parameters, as well as the inclusion of random effects allowing for random individual variation around the average values. Growth data were fitted to the Richards equation (Richards 1959) using the following parameterization: $W_{(t)} = A (1 + (d-1) \exp(-k(t-T_i)/d^{d/(1-d)}))^{1/(1-d)}$ (Sugden *et al.* 1981, Tjørve & Tjørve 2010), where $W_{(t)}$ is mass at age t , and A , k , T_i and d are the upper asymptote (i.e. predicted adult mass), maximum relative growth rate, age at maximum growth and shape parameter, respectively. We used the Richards equation because it provides a better fit than classic growth models (Svagej *et al.* 2019).

We evaluated three hypotheses regarding different types of sex-specific effects. First, in chicks fledging as singletons, we assessed intrinsic sex-specific effects due to differences in environmental conditions across years. In this analysis, we considered chicks that fledged as singletons irrespective of the size of brood at hatching and that will have experienced some partial brood loss. Unpublished data suggest that mortality is unrelated to chick sex or brood sex composition (W. S. Svagej & F. Quintana unpubl. data). Considering mean breeding success as an indicator of the quality of the breeding season, the years 2004 and 2005 were good seasons (1.15 and 1.22 fledglings per nest, respectively), whereas 2017 was a poor season (0.50 fledglings per nest; W. S. Svagej & F. Quintana unpubl. data). Therefore, we predict that during 2017 (the restrictive year) male singleton growth will be more affected than female singleton growth (interaction between sex and year). To test this hypothesis, the sex of the chick (male or female), year (2004, 2005 and 2017), and the interaction between sex and year were included as categorical predictor variables. In addition, to account for any potential differences in growth as seasons progressed, we included hatching date as a continuous covariate. For each brood analysed in this study, with one or two fledglings, we defined hatching date as the date of hatching of the oldest fledgling in the brood. We standardized hatching date across years before including it, entering it as a deviation from the median hatching date of the relevant year (subtracting the median date of

hatching in the particular year from the actual date) and dividing the result by the standard deviation for that year (Svagelj & Quintana 2011b). Because chicks that fledged as singletons may have been affected by sibling competition before fledging, we included age at which the fledgling effectively becomes the only chick at the nest (median = 14 days, $sd \pm 10$ days; range = 0–39 days) as a confounding covariate. This variable was included as a continuous covariate, entering as the deviation from the median and dividing by the standard deviation. In this analysis, we considered 941 measurements from 119 chicks that fledged as singletons; sample size of combinations between sex and year: male 2004 = 23, male 2005 = 17, male 2017 = 23, female 2004 = 18, female 2005 = 16, female 2017 = 22.

Secondly, we evaluated sex-specific effects due to rearing conditions generated by brood size and hatching order. Imperial Shags typically raise one- or two-fledgling broods (Svagelj & Quintana 2011a) with three dissimilar intra-brood rearing environments arising from the combination of brood size and hierarchy order (A1 = first chick in one-chick broods, A2 = first chick in two-chick broods, B2 = second chick in two-chick broods). Because the quality of the intra-brood environment decreases with brood size and hatching order (Giudici *et al.* 2017), we predict that male fledglings will suffer more than females in A2 and B2 environments in comparison with fledglings raised as A1 singletons (interaction between sex and rearing conditions). Because two-fledgling broods were extremely rare in 2017 (< 5 % of breeding attempts; W. S. Svagelj & F. Quintana unpubl. data), we excluded this year from the analysis. In the starting model, we included sex, rearing conditions (A1, A2 and B2), year (2004 and 2005), their interactions and hatching date as predictor variables (1942 measurements from 238 chicks at 156 nests; sample size of combinations between sex and rearing conditions: male A1 = 40, male A2 = 35, male B2 = 36, female A1 = 34, female A2 = 47, female B2 = 46).

Thirdly, we assessed sex-specific effects caused by the brood sex composition and the sex of the sibling in two-fledgling broods. We included sex, rearing conditions (A2 and B2), sex of the sibling (male or female) and their interactions, also including year (2004 and 2005) and hatching date as predictor variables. Because the sexual size dimorphism arises early during chick-rearing

(Svagelj & Quintana 2017), we predict that some combinations of sex (e.g. male : male combination) will suffer more than others (interaction between sex and rearing conditions and sex of the sibling; sample size of combinations: male : male = 17, male : female = 18, female : female = 28, female : male = 19). For this analysis, we used 1362 measurements from 164 chicks at 82 nests with two fledglings (hatching asynchrony: mean = 2.0 days, $sd \pm 1.1$ days; range = 0–5 days).

Predictor variables were evaluated for each one of the growth parameters (A , k , T_i and d). Growth parameters from nest identity and chick identity nested in brood were included as random intercept effects. For the analysis of singletons, only growth parameters from chick identity were included as random effects. Prior to the assessment of predictors, we discarded random effects with negligible levels of variability in a two-step process. First, we discarded without further evaluation those random parameters with standard deviations two orders of magnitude smaller than mean estimated parameters; and secondly, the significance of remaining random effects was evaluated using likelihood ratio tests, with non-significant random effects being eliminated (Pinheiro & Bates 2000). The significance of predictor variables and *post hoc* comparisons were evaluated using an F statistic. P -values of *post hoc* tests were adjusted by the number of comparisons using Holm's method (Pinheiro *et al.* 2020). To accommodate heteroscedasticity and autocorrelation, all non-linear mixed models included a power variance function where variance increases with fitted values and a first-order autoregressive correlation structure (Pinheiro & Bates 2000). In the singleton analysis, we also included a term modelling heteroscedasticity among years. We verified model assumptions by plotting residuals vs. fitted values and covariates. Growth rate curves (obtained from the first derivative of growth curves) and growth acceleration curves (obtained from the second derivative of growth curves) were plotted using growth parameters estimated from the final models (Wang *et al.* 2014, Svagelj *et al.* 2019).

In all analyses, we employed a backward selection procedure removing non-significant terms from the model, one by one, in decreasing level of interactions and in decreasing order of P -values within the same level (Crawley 2013). Statistical analyses were carried out using the nlme (Pinheiro

et al. 2020) package from R software, ver. 3.6.3 (R Development Core Team 2020). All tests were two-tailed, and differences were considered significant at $P < 0.05$. Results are presented as mean \pm se except where noted otherwise.

RESULTS

Sex-specific effects of good (2004–2005) and poor (2017) years on chicks fledged as singletons

For chicks fledging as singletons (rearing condition: A1), males attained higher asymptotic body mass and reached the maximum growth later than females (Table 1, Fig. 1). The maximum relative growth rate did not differ between the sexes ($F_{1,807} = 2.36$, $P = 0.125$; Table 1). In comparison with 2004–2005, the year 2017 was characterized by a suboptimal growth with reduced growth rate, delayed age at maximum growth and low growth acceleration throughout the rearing period (Table 1, Fig. 1). Despite that, the asymptotic

Table 1. Final Richards growth model in body mass for Imperial Shag fledglings raised as singletons (rearing conditions: A1). In the starting model, we included sex (male or female), year (2004, 2005 and 2017), their interaction, hatching date and age of singleton as the only chick in the nest as predictor variables, modelling A (asymptotic mass, in g), k (maximum relative growth rate, in 1/days), T_i (age at the inflection point, in days) and d (shape parameter) as growth parameters. Only significant predictor variables which remained in the final model are shown. Models were fitted as non-linear mixed models ($n = 119$ fledglings from 119 nests). See Methods for details.

Parameter	Predictor variable	Estimate \pm se	t	P
A	Intercept	1933 \pm 38	51.3	<0.001
	Sex (Male) ^a	266 \pm 38	7.0	<0.001
	Date	-66 \pm 23	-2.8	0.005
k	Intercept	0.0405 \pm 0.0011	37.3	<0.001
	Year (2004) ^b	-0.0001 \pm 0.0007	-0.1	0.917
	Year (2017) ^b	-0.0079 \pm 0.0009	-9.2	<0.001
	Date	0.0022 \pm 0.0007	3.1	0.002
T_i	Intercept	16.7 \pm 0.2	79.9	<0.001
	Sex (Male) ^a	0.5 \pm 0.2	3.5	<0.001
	Year (2004) ^b	-0.2 \pm 0.2	-0.7	0.490
	Year (2017) ^b	3.1 \pm 0.3	10.3	<0.001
d	Intercept	1.39 \pm 0.04	35.7	<0.001
	Date	0.09 \pm 0.03	2.8	0.005

^aRelative to value of sex (Female). ^bRelative to value of year (2005).

mass of fledglings did not differ between years ($F_{2,802} = 0.28$, $P = 0.757$; Table 1, Fig. 1). We did not detect a sex-specific effect of year on growth parameters (interaction sex : year; A : $F_{2,791} = 0.14$, $P = 0.866$; k : $F_{2,795} = 0.28$, $P = 0.753$; T_i : $F_{2,793} = 0.15$, $P = 0.860$; d : $F_{2,797} = 0.03$, $P = 0.968$; Table 1, Fig. 1). In addition, age at which fledglings were the only chick alive in the nest did not affect growth (A : $F_{1,800} = 0.06$, $P = 0.799$; k : $F_{1,801} = 0.01$, $P = 0.914$; T_i : $F_{1,805} = 0.13$, $P = 0.720$; d : $F_{1,804} = 0.15$, $P = 0.694$).

Sex-specific effects of rearing conditions due to brood size and hatching order (A1, A2 and B2)

The effect of rearing conditions (A1, A2 and B2) on the asymptotic mass of fledglings differed between males and females (sex : rearing conditions; $F_{2,1688} = 5.92$, $P < 0.005$; Table 2, Figures 2 and 3). The asymptotic mass of males decreased progressively as rearing conditions worsened (Table 2, Figure 3). Asymptotic mass of A1 males was higher than that of A2 males ($F_{1,1688} = 9.03$, $P < 0.005$) or B2 males ($F_{1,1688} = 64.24$, $P < 0.001$), whereas A2 males were heavier than B2 males ($F_{1,1688} = 35.98$, $P < 0.001$; Figure 3). The asymptotic mass of B2 females was lower than that of A1 females ($F_{1,1688} = 16.63$, $P < 0.001$) or A2 females ($F_{1,1688} = 26.43$, $P < 0.001$), but no differences were found between A1 and A2 females ($F_{1,1688} = 0.11$, $P = 0.738$; Figure 3). No other sex-specific effects of rearing conditions were significant (sex : rearing conditions; k : $F_{2,1666} = 0.14$, $P = 0.873$; T_i : $F_{2,1671} = 0.36$, $P = 0.699$; d : $F_{2,1669} = 0.71$, $P = 0.492$). The sex-specific effects of rearing conditions did not vary among years (sex : rearing conditions : year; A : $F_{2,1657} = 0.12$, $P = 0.884$; k : $F_{2,1653} = 0.09$, $P = 0.910$; T_i : $F_{2,1659} = 0.32$, $P = 0.726$; d : $F_{2,1655} = 0.08$, $P = 0.922$). Also, there were no sex-specific effects of year (sex : year; A : $F_{1,1668} = 0.38$, $P = 0.537$; k : $F_{1,1665} = 0.01$, $P = 0.929$; T_i : $F_{1,1674} = 1.10$, $P = 0.295$; d : $F_{1,1673} = 1.70$, $P = 0.193$).

Sex-specific effects of brood sex composition and sibling sex in two-fledgling broods

The asymptotic mass in two-fledgling broods was not affected by brood sex composition (sex :

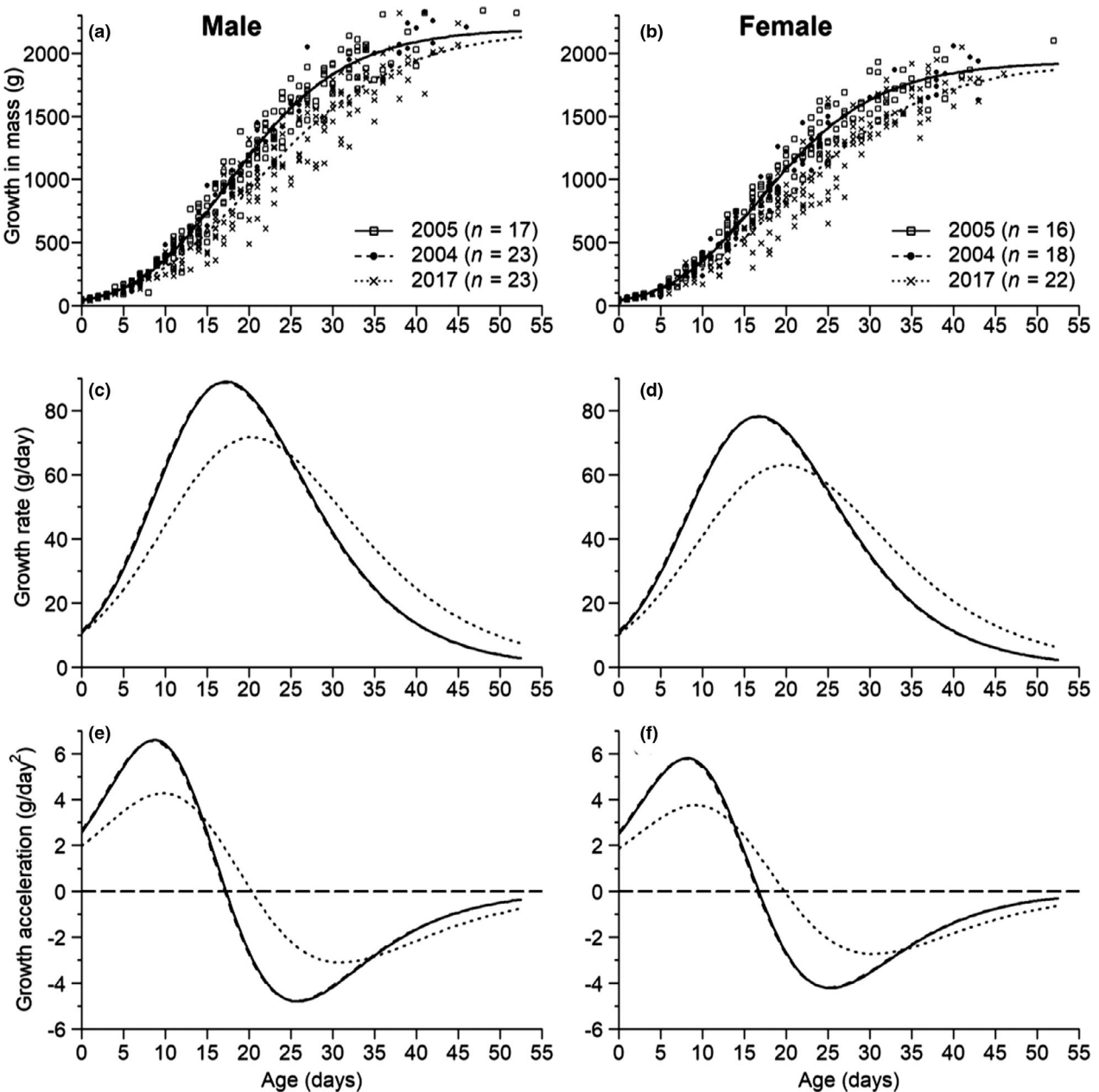


Figure 1. Growth in body mass for male (left) and female (right) fledglings of the Imperial Shag raised as singletons (rearing condition: A1) in good (2004 and 2005) and poor (2017) years. Body mass measurements are represented by empty squares (2005), circles (2004) and crosses (2017). (a,b) Adjusted growth models in body mass. (c,d) Instantaneous growth rate curves. (e,f) Acceleration curves. All curves were fitted using estimates from the final non-linear mixed model reported in Table 1. Sample size is shown within parentheses. See Methods for details.

rearing conditions : sibling sex: $F_{1,1160} = 1.55$, $P = 0.214$; Table 3). Furthermore, sex-specific effects of brood sex composition for the remaining growth parameters were absent (sex : rearing conditions : sibling sex; k : $F_{1,1161} = 1.44$, $P = 0.230$;

T_i : $F_{1,1162} = 1.16$, $P = 0.281$; d : $F_{1,1159} = 0.00$, $P = 0.987$). No two-way interactions involving sex, rearing conditions or sex of the sibling were significant (all $P > 0.20$). Finally, sex of the sibling in the brood was not relevant for any growth

Table 2. Final Richards growth model in body mass for Imperial Shag fledglings raised in good (2004 and 2005) years by rearing conditions. In the starting model, we included sex (male or female), rearing conditions (A1 = first chick in one-chick broods, A2 = first chick in two-chick broods, B2 = second chick in two-chick broods), year (2004 or 2005), their interactions and hatching date as predictor variables. Only significant predictor variables which remained in the final model are shown. Models were fitted as non-linear mixed models ($n = 238$ fledglings from 156 nests). See Methods for details

Parameter	Predictor variable	Estimate \pm se	t	P
A	Intercept	1912 \pm 30	64.8	<0.001
	Sex (Male) ^a	300 \pm 36	8.4	<0.001
	Rearing conditions (A2) ^b	-11 \pm 33	-0.3	0.738
	Rearing conditions (B2) ^b	-136 \pm 33	-4.1	<0.001
	Sex (Male) ^a : Rearing conditions (A2) ^b	-95 \pm 43	-2.2	0.025
	Sex (Male) ^a : Rearing conditions (B2) ^b	-146 \pm 42	-3.4	<0.001
k	Intercept	0.0416 \pm 0.0006	71.0	<0.001
	Year (2004) ^c	-0.0012 \pm 0.0003	-3.5	<0.001
T_i	Intercept	16.4 \pm 0.2	88.7	<0.001
	Sex (Male) ^a	0.9 \pm 0.2	5.6	<0.001
	Rearing conditions (A2) ^b	-0.3 \pm 0.2	-1.4	0.176
	Rearing conditions (B2) ^b	0.4 \pm 0.2	1.9	0.059
	Year (2004) ^c	0.4 \pm 0.1	2.7	<0.01
d	Intercept	1.39 \pm 0.03	54.3	<0.001
	Sex (Male) ^a	0.05 \pm 0.02	2.8	<0.01
	Rearing conditions (A2) ^b	-0.01 \pm 0.02	-0.5	0.613
	Rearing conditions (B2) ^b	0.07 \pm 0.02	3.3	0.001

^aRelative to value of sex (Female). ^bRelative to value of rearing conditions (A1). ^cRelative to value of year (2005).

parameter (A : $F_{1,1181} = 1.21$, $P = 0.272$; k : $F_{1,1176} = 0.00$, $P = 0.956$; T_i : $F_{1,1184} = 1.82$, $P = 0.177$; d : $F_{1,1182} = 1.27$, $P = 0.261$).

DISCUSSION

In this study, we evaluated the environmental sensitivity of male and female fledglings of the Imperial Shag during growth. We did not find any intrinsic sex-specific effect of year on singleton growth in spite of the detrimental effects of poor years. However, male fledglings were more sensitive than females to restrictive conditions of the extrinsic environment set by brood size and hatching order.

Overall, there was concordance between yearly variation in mean breeding success and estimated growth parameters. The year 2005 was slightly better than 2004 (as suggested by higher growth rate and earlier peak growth in two-fledgling broods), and both good years were considerably better than 2017, a very restrictive year. In 2017, we found a strong negative effect on chick growth characterized by reduced growth rate, delayed age at maximum growth and reduced acceleration in growth. Despite these striking differences among good and poor years, the effects on singletons were

the same for males and females, without any sex-specific outcome. Interestingly, fledglings from 2017 exhibited catch-up growth (Hector & Nakagawa 2012, Aldredge 2016), attaining an asymptotic mass similar to that in good years. This strategy could be advantageous because fledglings reach the typical final mass without incurring the costs of compensatory growth (i.e. faster than typical growth rate) in terms of cellular damage and their negative fitness consequences (Metcalf & Monaghan 2001, 2003). In our study, the catch-up growth in 2017 could be a consequence of an increased foraging effort of parents during poor years. In this sense, foraging behaviour data of instrumented adults (i.e. GPS) from the same colony showed that the amount of time adult breeders spent searching for food was significantly higher during 2017 than during 2004 and 2005 (F. Quintana & A. Gómez-Laich unpubl. data). In addition, we cannot rule out that only skilled or high-quality breeders successfully reproduced in 2017. Because singleton broods could be a biased sub-set of the population and the biases are likely to differ across years, our results comparing singleton growth should be interpreted with caution. Also, as differences in parental quality could modulate the impact of sex-specific effects, future

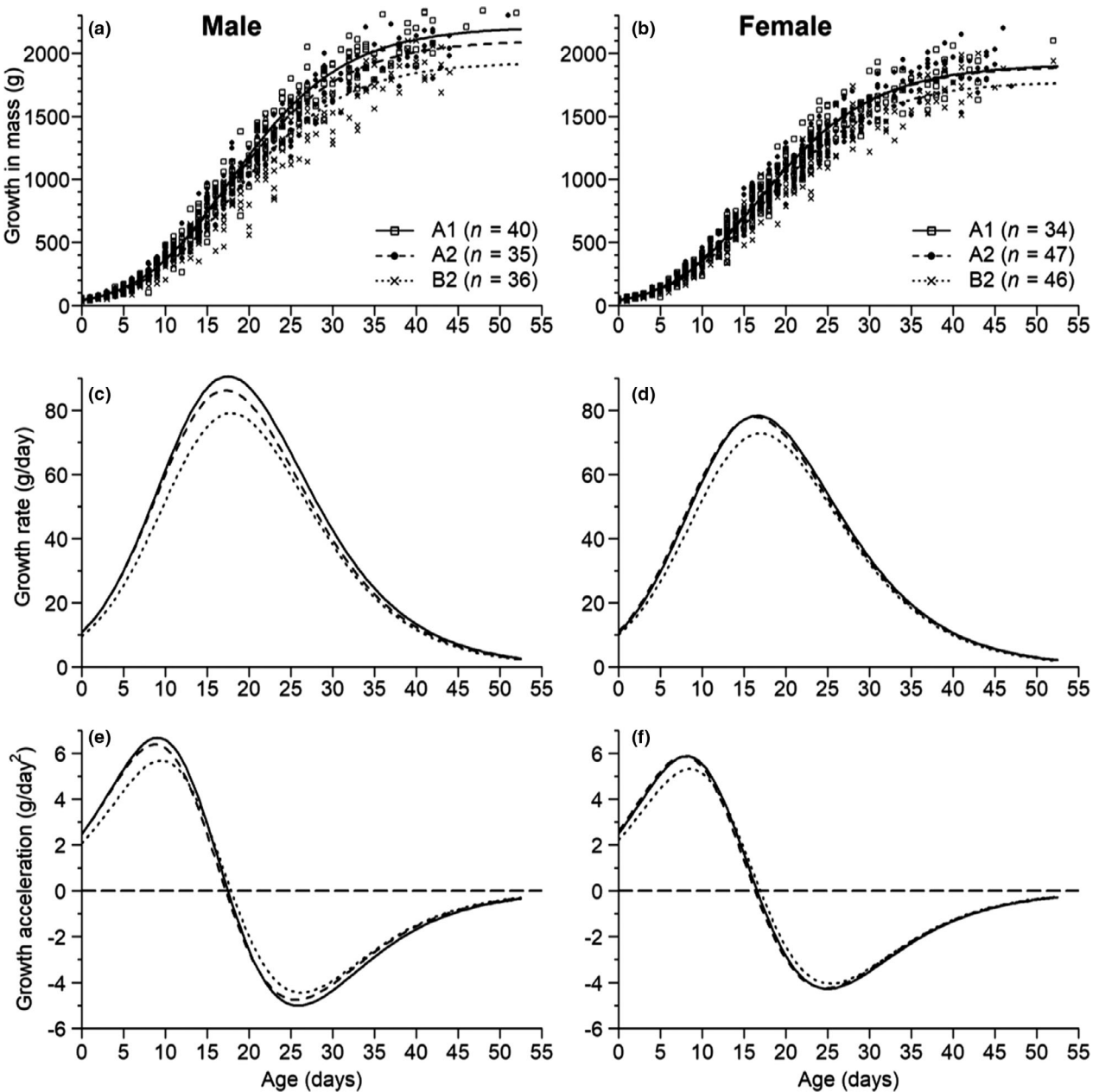


Figure 2. Growth in body mass for male (left) and female (right) fledglings of the Imperial Shag according to rearing conditions (A1 = first chick in one-chick broods, A2 = first chick in two-chick broods, B2 = second chick in two-chick broods). Body mass measurements are represented by empty squares (A1), circles (A2) and crosses (B2). (a,b) Adjusted growth models in body mass. (c,d) Instantaneous growth rate curves. (e,f) Acceleration curves. Curves were fitted using estimates from the final non-linear mixed model reported in Table 2. All curves are for an average good year (2004–2005). Sample size is shown within parentheses. See Methods for details.

studies considering the effects of parental experience and parental foraging effort on chick growth are needed to clarify that. Also, parental provisioning strategies by nestling sex should be explored in future studies.

As a typical pattern in the Imperial Shag, we corroborated that the quality of the intra-brood environment progressively decreases with brood size and hatching order (Svagej 2009, 2019, Svagej & Quintana 2011b, Giudici *et al.* 2017).

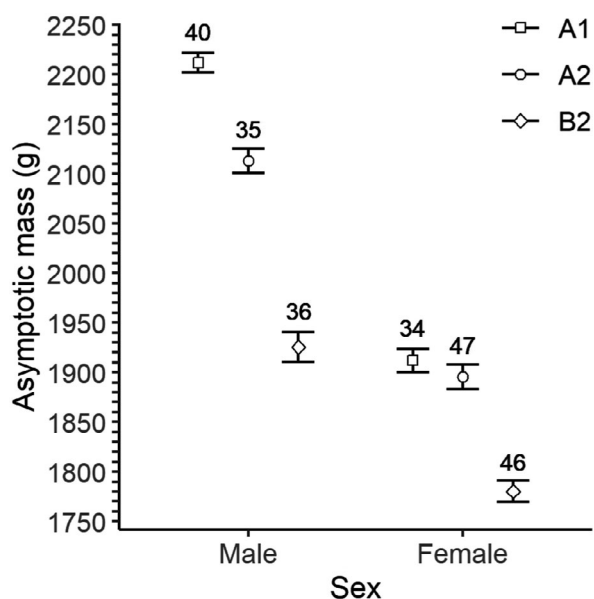


Figure 3. Mean \pm se estimated asymptotic mass (A , in g) of Imperial Shag fledglings by sex (male or female) and rearing conditions (A1, A2 and B2). Values were obtained from the final non-linear mixed model reported in Table 2. Sample size is shown above bars.

Younger chicks from two-fledgling broods experienced the worst social environment, showing the lowest fledging mass and delayed age at maximum growth.

Here, brood size and hierarchy order had sex-specific effects. Males were more sensitive than

females when compared between best (A1) and worst (B2) conditions. Interestingly, the presence of a younger sibling in the nest had sex-specific consequences for senior chicks. Fledging mass of senior females was unaffected by the presence of a junior sibling in the brood, whereas senior males reached a higher fledging mass when raised as singletons than when fledged in two-chick broods. This result suggests that females grow at their maximum even in moderated social environments (as senior chicks in two-chick broods), whereas males must be raised in the best conditions (as singletons) to reach their maximum fledging mass. If mass at fledging affects juvenile survival or recruitment probabilities (Gebhardt-Henrich & Richner 1998), sex-specific trade-offs between offspring quality and brood size at fledging (Stearns 1992, Hardy 2002) could be relevant in Imperial Shags. Future studies analysing sex allocation, sex-specific brood reduction and recruitment probabilities according to sex and rearing conditions are needed to elucidate this in Imperial Shags. In addition, we found that sex-specific effects of rearing conditions did not change across good years (2004–2005). Unfortunately, the lack of two-fledgling broods in 2017 prevented us from fully evaluating the inter-relationship between intrinsic and extrinsic drivers of sex-specific sensitivity.

Our results provide additional support to previous studies on seabirds showing greater sensitivity of the larger sex. The Blue-footed Booby *Sula*

Table 3. Final Richards growth model in body mass of Imperial Shag fledglings from two-chick broods according to the brood sex composition. In the starting model, we included sex (male or female), rearing conditions (A2 and B2), sex of the sibling (male or female) and their interactions, also including year (2004 or 2005) and hatching date as predictor variables. Only significant predictor variables which remained in the final model are shown. Models were fitted as non-linear mixed models ($n = 164$ fledglings from 82 nests). See Methods for details.

Parameter	Predictor variable	Estimate \pm se	t	P
A	Intercept	1919 \pm 25	77.7	<0.001
	Sex (Male) ^a	179 \pm 23	7.7	<0.001
	Rearing conditions (B2) ^b	-145 \pm 20	-7.4	<0.001
k	Intercept	0.0416 \pm 0.0007	59.5	<0.001
	Year (2004) ^c	-0.0016 \pm 0.0004	-3.7	<0.001
	Date	0.0005 \pm 0.0002	2.0	0.045
T_i	Intercept	16.0 \pm 0.2	88.6	<0.001
	Sex (Male) ^a	0.9 \pm 0.2	4.7	<0.001
	Rearing conditions (B2) ^b	0.7 \pm 0.2	3.4	<0.001
	Year (2004) ^c	0.5 \pm 0.2	3.1	0.002
d	Date	-0.3 \pm 0.1	-3.1	0.002
	Intercept	1.37 \pm 0.03	48.7	<0.001
	Sex (Male) ^a	0.05 \pm 0.02	2.3	0.022
	Rearing conditions (B2) ^b	0.08 \pm 0.02	3.9	<0.001

^aRelative to value of sex (Female). ^bRelative to value of rearing conditions (A2). ^cRelative to value of year (2005).

nebouxii is a seabird exhibiting reversed size dimorphism, with females approximately 31–32% heavier than males (Torres & Drummond 1997, Velando 2002). In two-chick broods of this species, Drummond *et al.* (1991) found that senior and junior males attained a similar mass at 45 days of age, but senior females weighed more than junior females at that age. Thus, the larger sex was more vulnerable to the restrictive extrinsic environment imposed by the hatching order. Also, in two-chick broods of the Blue-footed Booby, Velando (2002) manipulated maternal investment and hence the chick-rearing environment by trimming the flight feathers of breeding females. Female fledglings raised after this experimental treatment had lower mass than control females, whereas the mass of male fledglings did not differ between experimental and control treatments (Velando 2002). Also, Daunt *et al.* (2001) assessed the effect of parental experience on the growth of European Shags *Phalacrocorax aristotelis*. In this species, males are approximately 20% heavier than females, and experienced parents exhibit higher foraging efficiency, deliver more food to the offspring and raise more fledglings compared with inexperienced parents (Daunt *et al.* 1999, 2001, 2007). A sex-specific effect of parental experience was found, as male fledglings raised by experienced parents had higher peak mass and growth rate than those from inexperienced breeders, but neither parameter differed with parental experience in female fledglings (Daunt *et al.* 2001). Our findings in Imperial Shags are particularly interesting because they show that sex-specific sensitivity can also vary with brood size for a given hierarchy order. Moreover, our study emphasizes the importance of analysing sex-specific sensitivity throughout the natural range of variation in brood size at fledging.

Some studies in dimorphic birds have reported a higher extrinsic sensitivity of the smaller sex (Oddie 2000, Hipkiss *et al.* 2002, Råberg *et al.* 2005). Even though that appears contradictory, a higher sensitivity of the smaller sex is usually found in species with large broods that hatch without a marked asynchrony, thus promoting a strong or scramble sibling competition (Råberg *et al.* 2005, Jones *et al.* 2009). Under these circumstances, parents would experience less control over food distribution, and the large size may be a competitive advantage for the larger sex that offsets the intrinsic disadvantage of increased food requirements (Råberg *et al.* 2005).

Finally, if sibling sex or brood sex composition affects offspring development, parents would allocate sex to maximize the quality of fledglings produced (Hardy 2002). In two-chick broods of European Shags, brood sex composition affects asymptotic mass of fledglings as the male–female combination produces the heaviest chicks, while female–male broods generate the lightest chicks (Velando *et al.* 2002). On the other hand, Daunt *et al.* (2001) in European Shags and Drummond *et al.* (1991) in Blue-footed Boobies reported that the effect of sibling sex on growth was irrelevant in two-chick broods of these species. Here, we did not detect any effects of sibling sex or the brood sex composition on chick growth. Thus, a particular parental allocation of sexes should not be advantageous in the Imperial Shag, at least in terms of chick growth for chicks fledging from two-chick broods.

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AUTHOR CONTRIBUTIONS

Walter S. Svagelj: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Writing-original draft (lead); Writing-review & editing (lead). **Agustina Gómez-Laich:** Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Writing-review & editing (supporting). **María Rita Pérez:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Resources (supporting); Writing-review & editing (supporting). **Gustavo M. Somoza:** Data curation (supporting); Formal analysis

(supporting); Methodology (supporting); Resources (supporting); Writing-review & editing (supporting). **Flavio Quintana**: Funding acquisition (lead); Project administration (lead); Resources (equal); Supervision (lead); Writing-review & editing (supporting).

Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Data.

Figure S1. Mean \pm se of estimated asymptotic mass (A , in g) of Imperial Shag fledglings according to their sex (male or female), rearing conditions (A2 and B2) and sex of the sibling (male or female).