

EGG-SIZE VARIATION IN THE IMPERIAL CORMORANT: ON THE IMPORTANCE OF INDIVIDUAL EFFECTS

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Abstract. Although some of the components of egg-size variation in birds have been studied, there is a lack of approaches in which phenotypic variation is both partitioned and its causes are analyzed. We partitioned and analyzed the phenotypic variation in egg size in 1588 eggs from 572 clutches of the Imperial Cormorant (*Phalacrocorax atriceps*) over three breeding seasons (2004–2006) at Punta León, Argentina. We estimated repeatability and phenotypic plasticity of egg size, investigating the effects of year, date of laying, body size, and body condition on egg-size variation within and between clutches. Egg size varied widely, the largest egg being >2× as heavy as the smallest. The repeatabilities of both egg size and mean egg size (0.761 and 0.894, respectively) are among the highest reported for any bird. Most variation among clutches was due to differences among individuals, being weakly related to date of laying and unrelated to year, body size, or body condition. Egg size decreased with the egg's order. This general pattern was not related to year, date of laying, body size, or condition. Proximate constraints did not explain variation either within or among clutches. There is no obvious adaptive benefit of intra-clutch variation because the effect in brood reduction of intra-clutch variation in egg size was negligible. However, egg size was positively related with the survival time of the last (third) chick. Therefore, investing in a large third egg should benefit females of the Imperial Cormorant, a brood reducer, by keeping the last chick alive longer.

Key words: inter- and intra-clutch egg size variation, maternal effects, *Phalacrocorax atriceps*, phenotypic plasticity, repeatability, seabirds.

Variación en el Tamaño de los Huevos de *Phalacrocorax atriceps*: Sobre la Importancia de los Efectos Individuales

Resumen. A pesar de que varios estudios en aves han analizado algunos de los componentes de la variación en el tamaño de los huevos, son escasos los enfoques que simultáneamente consideraron la totalidad de la variación fenotípica y analizaron sus consecuencias. Dividimos y analizamos la variación fenotípica en el tamaño del huevo en 1588 huevos de 572 puestas de *Phalacrocorax atriceps* monitoreadas durante tres temporadas reproductivas (2004–2006) en Punta León, Argentina. Estimamos la repetibilidad y la plasticidad fenotípica en el tamaño del huevo, investigando también los efectos del año, la fecha de puesta, el tamaño corporal y la condición física materna en la variación en el tamaño del huevo entre y dentro de las puestas. El tamaño del huevo exhibió una gran variación, donde el huevo más grande representó más de dos veces el peso del más pequeño. Tanto la repetibilidad del tamaño del huevo como la repetibilidad del tamaño del huevo promedio registradas aquí (0.761 y 0.894, respectivamente) se encuentran entre los valores más altos reportados en aves. La mayor parte de la variación entre puestas fue causada por diferencias entre individuos, estando débilmente relacionada con la fecha de puesta, y no relacionada con el año, el tamaño corporal o la condición física de la hembra. El tamaño del huevo decreció con el orden de puesta. Este patrón general no estuvo relacionado con el año, la fecha de puesta, el tamaño o la condición física de la hembra. Restricciones próximas no explicaron ni la variación entre ni la variación dentro de las puestas. No encontramos un beneficio adaptativo obvio para la variación en el tamaño del huevo dentro de las puestas debido a que el efecto de esta variación en la reducción de nidada fue despreciable. Sin embargo, el tamaño del huevo estuvo positivamente relacionado con el tiempo de supervivencia del último (tercer) pichón. De ésta forma, el invertir en un tercer huevo grande beneficiaría a las hembras de *Phalacrocorax atriceps*, un ave marina con reducción de nidada, ya que esto mantendría vivo por un mayor periodo de tiempo al último pichón de la nidada.

INTRODUCTION

Egg size is an important life-history trait mediating maternal effects on the phenotype of offspring (Rossiter 1996, Mousseau and Fox 1998). Females can influence the quality of their off-

spring through both genetic contributions to their young and early maternal investments such as deposition of micro- and macronutrients into their eggs (Clutton-Brock 1991, Rossiter 1996, Mousseau and Fox 1998). Because large eggs contain more nutrients than do smaller eggs (Ankney 1980, Arnold and

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Green 2007), hatchlings from large eggs are usually structurally larger or hatch at a more advanced stage of development (Croxall et al. 1992, Finkler et al. 1998) and have absolute nutrient reserves larger (Parsons 1972, Ankney 1980) than those of hatchlings from smaller eggs. Several experimental studies have demonstrated that egg size per se is positively correlated with hatching success (Croxall et al. 1992), chick growth (Smith et al. 1995, Amundsen et al. 1996, but see Viñuela 1997) and, to a lesser extent, chick survival (Ankney 1980, Bolton 1991, but see Amundsen et al. 1996). However, resources allocated to eggs are usually expensive for laying females (Perrins 1996, Williams 2005 and references therein). As a consequence, if egg size is related to fitness, females should maximize their reproductive output by adjusting the amount of resources invested in particular eggs (Eising et al. 2001).

In birds, egg size varies greatly within a species, with the largest egg in a population generally being 50–100% bigger than the smallest (Williams 1994, Christians 2002). Such large variability in egg size can be partitioned into several components, allowing for an estimation of the relative importance of the various determinants of the phenotype (Falconer and Mackay 1996). For example, in species that lay one multi-egg clutch per year, egg size may vary from female to female (*inter-clutch variation*), within a single clutch of one female (*intra-clutch variation*), and from year to year among clutches of one female (*phenotypic plasticity*; see Falconer and Mackay 1996, Flint et al. 2001). Furthermore, if phenotypic variation within an individual and that between individuals are analyzed separately, the *repeatability* (i.e., the proportion of variation in a trait that is due to permanent differences among individuals; Boag and van Noordwijk 1987, Falconer and Mackay 1996) can be estimated. Estimates of repeatability are useful in the context of quantitative genetics because they may set upper limits to levels of heritable variation (Falconer and Mackay 1996).

For both inter- and intra-clutch variation in egg size, proximate and ultimate (adaptive) causes have been proposed. Because resources allocated to eggs are usually expensive for females (Williams 2005), this expense may constitute a proximate energetic or nutritional constraint on the laying female during oogenesis (Otto 1979, Nager and van Noordwijk 1992). In accordance with this hypothesis, some studies have found either mass or body condition of the female to be positively correlated with egg size (Potti 1993, Smith et al. 1993, Hargitai et al. 2005).

At least three potential causes of intra-clutch egg size variation have been identified. First, as has been proposed for inter-clutch variation, nutritional or energetic constraints operating on the laying female may explain intra-clutch egg-size variation (Rydén 1978, Slagsvold and Lifjeld 1989, Nilsson and Svensson 1993). Such constraints may be especially applicable in cases where, within a clutch, an egg's size declines with the order in which it was laid, because the relative size of

the last eggs is presumed to depend on the female's energy reserves (Rydén 1978, Pierotti and Bellrose 1986, Sydeman and Emslie 1992).

Second, variation in egg size within clutches may be an adaptive response mitigating or reinforcing sibling competition by imposing a hierarchy in hatchlings' sizes (Howe 1976, Slagsvold et al. 1984). In most altricial birds, eggs hatch asynchronously because incubation begins before the clutch is complete (Stoleson and Beissinger 1995, Stenning 1996), resulting in a hierarchy by age and size within the brood, with the youngest sibling being at a significant initial disadvantage (Howe 1976, Aparicio 1999, Viñuela 2000). Thus, if egg size affects hatchling size (Stokland and Amundsen 1988, Nilsson and Svensson 1993, Aparicio 1999, D'Alba and Torres 2007), variation in egg size relative with order of laying may have evolved to influence the degree of sibling competition. Howe (1976) suggested that an increase in egg size with sequence of laying is an adaptation to counteract the effect of asynchronous hatching ("brood-survival strategy" sensu Slagsvold et al. 1984), whereas a decline with sequence of laying should accentuate the effect of asynchronous hatching, facilitating brood reduction ("brood-reduction strategy," Slagsvold et al. 1984).

Finally, and as an alternative to the hypothesis mentioned above, egg size variation within a clutch may be an adaptive response modulating sibling competition by increasing or decreasing asynchrony of hatching (Parsons 1972). If the incubation period for larger eggs is longer (Parsons 1972, Aparicio 1999, but see Viñuela 1997, D'Alba and Torres 2007), a smaller last egg may reduce the asynchrony of hatching and therefore differences in size of the offspring within the brood (Parsons 1972, Aparicio 1999).

Although several studies have analyzed some of the components of egg-size variation in birds (Flint et al. 2001, Kontiainen et al. 2008), studies both considering phenotypic variation within and between individuals and analyzing its causes are lacking. In this paper, we analyzed 3 years of data on egg-size variation in the Imperial Cormorant (*Phalacrocorax atriceps*) population of Punta León, Argentina. Our main objectives were (1) to analyze inter- and intra-clutch variation in egg size, determining repeatability and phenotypic plasticity, (2) to assess the relative effects of year, date of laying, body size of the female, and condition of the female on egg size, and (3) to interpret our results in relation to different hypotheses accounting for inter- and intra-clutch variation in egg size. In addition, we evaluated the effect of egg mass on hatchling mass, incubation length, and hatching success and the effect of intra-clutch variation in egg size on brood reduction.

METHODS

Our study extended over three consecutive breeding seasons (2004–2006) at the Punta León colony (43° 05' S, 64° 30' W), Chubut, Argentina. We recorded data from 572 Imperial

Cormorant nests (140, 187, and 245 during the 2004, 2005, and 2006 seasons, respectively). The Imperial Cormorant is sexually dimorphic (males: 2317 g, females: 1966 g; Svagelj and Quintana 2007) and preys on fish by foot-propelled diving (Johnsgard 1993). Its clutch usually consists of three eggs (Malacalza and Navas 1996, Svagelj and Quintana 2011) with the third egg being smaller than the first and second (Punta et al. 2003, but see Malacalza and Navas 1996). Both parents share the incubation of eggs for ~29 days (Malacalza 1988). In comparison with those of other birds, eggs of cormorants (family Phalacrocoracidae) are relatively inexpensive to produce because the ratio of the mass of the clutch to that of the female is low, the albumen is low in protein, and the yolks are small and low in fat (Lack 1968, Williams et al. 1982, Johnsgard 1993, Whittow 2002). The nest-site fidelity of Imperial Cormorants breeding at Punta León is high (Svagelj and Quintana, unpubl. data), so banded individuals and their clutches can be monitored over multiple years. Therefore, our study system appears particularly appropriate for studying variation in egg size in a wild population of birds that make a relatively low investment in egg production.

NEST-MONITORING PROTOCOL

We checked nests every 1–3 days during egg laying until the clutch was complete. Using a permanent marker, we numbered each egg, identifying its nest and the order in which it was laid. We measured the length and width of the eggs with digital calipers to the nearest 0.01 mm. We measured all eggs in 572 clutches, but knew the sequence of laying in only 523 of them. During hatching, we also checked nests every 1–3 days (most daily) to establish the each egg's hatching success with respect to the order in which it was laid. We marked hatchlings on the tarsus with fiber-tape bands labeled with its associated order. Chicks surviving until day 20 were banded with numbered aluminum bands. During chick rearing, we visited nests every 3–5 days to determine the fate of chicks until it proved impossible to capture them further, at an age of ~40 days.

As part of wider research on the behavioral ecology of the Imperial Cormorant, we captured and banded 480 breeding adults to identify individuals through multiple attempts at breeding. We handled 170 breeding females in one or more breeding seasons. To estimate their body size and condition, we measured their bill length, bill depth, head length, wing length, tarsus length, and body mass (see Svagelj and Quintana 2007 for more details). The Imperial Cormorant is susceptible to human disturbance, mainly during egg laying and early incubation (Yorio and Quintana 1996). To avoid nest desertion and to minimize disturbance, we captured all adult birds between middle incubation and early chick rearing. We sexed all adult birds applying discriminant functions to their body measurements and by their vocalizations during courtship and nest defense (Svagelj and Quintana 2007).

DATA ANALYSIS

We calculated the eggs' mass from measurements of their length and width by the formula $\text{mass} = K_w \times \text{length} \times \text{width}^2$ (Hoyt 1979), where K_w is a species-specific mass coefficient determined for the studied population from 108 eggs measured and weighed within day they were laid ($K_w = 5.42 \times 10^{-4} \text{ g mm}^{-3}$). Calculated egg mass explained 97.7% of a fresh egg's mass ($r = 0.99$, $F_{1,106} = 4438$, $P < 0.001$), so we used calculated egg mass as a reliable estimator of egg size.

To test the effects of explanatory variables and their interactions on response variables we employed generalized linear mixed models (GLMM; Pinheiro and Bates 2000, Crawley 2007, Zuur et al. 2009), considering the non-independence of eggs within a clutch and of an individual female's attempts at breeding. Except where noted, we included "female" (band number, unique for each female) and "clutch, nested in female" (a unique code for each nesting attempt) as random effects. We evaluated the effect of the order in which an egg was laid by entering the order in the models as a three-level ordered factor. Year was included as three-level fixed factor. We standardized date of laying across years before including it, entering it as a deviation from the median laying date of the relevant year (subtracting the median date of laying in the particular year from the actual date) and dividing the result by the standard deviation for that year. We used a body-size index defined by the component scores from the first axis of a principal component analysis (PCA) based on bill height and bill, head, tarsus and wing length. To standardize the body size of females across years, we ran a separate PCA for each year (i.e., three analyses). We defined the index of a female's body condition as the residual of the regression of body mass on body size. Given that birds were captured and weighed on different days of the breeding cycle and that their body mass may vary through the season (Giudici, Svagelj, and Quintana, unpubl. data), we included the number of days elapsed between the start of egg laying and the date of the capture as a covariate in the regression.

Applying GLMM with a Gaussian family distribution and identity-link function, we analyzed egg-size variation at two levels. First, we partitioned total phenotypic variance in egg size in terms of the origin of the different components of variance (Falconer and Mackay 1996, Flint et al. 2001). Thus total phenotypic variance was partitioned into three components: among females (repeatability), within a female among years (phenotypic plasticity), and within a female within a year (residual variation). The order in which an egg was laid, year, and date of laying were included as covariates. For this analysis, we restricted our data set to include only clutches from those females banded in 2004 whose clutches were measured in all three breeding seasons ($n = 99$ clutches from 33 females). For the purposes of comparison with the literature, we also calculated the repeatability of mean egg size (Lessells and Boag 1987).

Second, we tested the effects of an egg's order, year, date of laying, the female's body size, and female's condition and their interactions on inter- and intra-clutch variation in

egg size on all three-egg clutches from all females ($n = 389$ clutches from 296 females). We restricted this analysis to three-egg clutches according to the species' modal clutch size in the study area (Svagej and Quintana 2011) and to properly evaluate the interaction terms between predictor variables and an egg's order. Of the 389 three-egg clutches, only 211 were laid by females that we had weighed and measured.

We evaluated the relationship between egg size and hatching mass with linear regression. We measured the mass of 124 chicks within 12 hr of hatching. Also with linear regression, we evaluated the relationship between egg size and incubation period for 42 third eggs monitored daily during laying and hatching. Incubation of Imperial Cormorant clutches usually begins before or when the second egg has been laid (Svagej and Quintana, unpubl. data). Therefore, the time elapsed between the laying and hatching of third eggs may be considered as good indicator of the species' incubation period.

We modeled the effect of egg size on hatching success by means of GLMM with a binomial error structure, a logit-link function, and the Laplace approximation method (Crawley 2007, Bolker et al. 2009, Zuur et al. 2009). Although Perrins (1996), Valkama et al. (2002), and Serrano et al. (2005) have shown that hatching success increases with egg size, Nordskog and Hassan (1971) and Kontiainen et al. (2008) also found that extremely large eggs hatch less frequently than intermediate-sized ones. Detecting this decrease in hatchability for extremely large eggs requires the inclusion of a quadratic term for egg size because this term allows a change in the hatchability trend for large values of the predictor variable (i.e., large eggs). Therefore, to evaluate for a possible decrease in hatching success for extremely large eggs of the Imperial Cormorant, we also included a quadratic term for egg size. The order in which the egg was laid, year, and date of laying were included as covariates. We determined the hatching success (i.e., hatched or not) confidently for 918 eggs that completed the incubation period and were also measured. Because random effects were not significant [female: $\chi^2_1 = 0.3$, $P = 0.59$; female (clutch): $\chi^2_1 = 1.6$, $P = 0.20$], we finally analyzed hatching success by using generalized linear models with fixed effects.

In the Imperial Cormorant, brood reduction operates on the third chick in three-hatchling broods, with the last chick usually starving to death during its first days of life (Svagej 2009, Svagej

and Quintana, unpubl. data). Here, we evaluated the effect of intra-clutch variation in egg size on brood reduction by applying a Cox proportional-hazards regression (Therneau and Grambsch 2000) to the survival time of the third chick from three-hatchling broods ($n = 163$). For this analysis, we evaluated the effect of intra-clutch variation in egg size as the deviation in egg size between the third and the other eggs in the clutch, calculating it as $C - (A + B)/2$, with A , B , and C being the masses of the first, second, and third eggs, respectively. We included egg size, year, date of laying, asynchrony of hatching (i.e., number of days between hatching of first and third eggs), and previous death of an elder sibling (i.e., a categorical variable with two values, 0 = no elder sibling died in the brood and 1 = at least one elder sibling died) as covariates to control for confounding effects. In a Cox regression analysis, covariates with positive ($\beta > 0$) and negative ($\beta < 0$) regression coefficients are associated with decreased and increased survival times, respectively (Therneau and Grambsch 2000).

In all analyses we employed a backward selection procedure, removing nonsignificant terms from the model, one by one, in decreasing level of interactions and in decreasing order of P within the same level (Crawley 2007). We evaluated the significance of random effects with a likelihood-ratio test (Pinheiro and Bates 2000, Crawley 2007, Bolker et al. 2009). For statistical analyses, we used the NLME, LME4, and SURVIVAL packages from R software, version 2.12.1 (R Development Core Team 2010). We report values as means \pm SE except where noted. All tests were two-tailed, and we considered differences significant at $P < 0.05$.

RESULTS

Overall mean egg mass was 54.2 g, standard deviation 4.7 g ($CV = 8.7\%$, $n = 1588$ eggs in 572 clutches). Egg mass ranged from 39.1 to 81.1 g, the largest egg being 107% heavier than the smallest (runt eggs excluded). Egg size averaged 62.40 ± 0.07 mm \times 40.00 ± 0.03 mm (range 53.97–72.49 mm \times 34.83–45.74 mm, $n = 1588$). Mean egg mass in clutches of different sizes did not differ ($F_{3,125} = 0.4$, $P = 0.76$; Table 1).

REPEATABILITY AND PLASTICITY IN EGG SIZE

After correction for fixed effects included in the model (Table 2), the GLMM attributed 76.1% of the variance in egg

TABLE 1. Mean mass \pm SE of Imperial Cormorant eggs in relation to clutch size and position in the sequence of laying ($n = 523$ clutches).

Clutch size	n	Position in sequence				Mean \pm SE
		First	Second	Third	Fourth	
1	7	54.64 \pm 1.77				54.64 \pm 1.77
2	117	54.24 \pm 0.44	53.78 \pm 0.43			54.01 \pm 0.31
3	389	55.21 \pm 0.22	54.80 \pm 0.23	52.55 \pm 0.23		54.18 \pm 0.13
4	10	55.47 \pm 2.29	54.49 \pm 2.16	54.50 \pm 1.78	52.45 \pm 2.02	54.23 \pm 1.01

TABLE 2. Components of variance in the size of the Imperial Cormorant eggs, partitioned among females, among clutches of a single female, and within a single clutch of a single female. In total, we included 287 eggs from 99 clutches laid by 33 females.^a

Effect			
Fixed	<i>F</i> -test	<i>P</i>	
Intercept	$F_{1,186} = 9096$	<0.001	
Order of laying	$F_{2,186} = 60.2$	<0.001	
Standardized date of laying	$F_{1,65} = 4.3$	0.040	
Random	Variance (± SD)	%	LRT ^b
Female	10.37±3.22	76.1	$\chi^2_1 = 305$, $P < 0.001$
Female (clutch)	0.18±0.43	1.4	$\chi^2_1 = 0.7$, $P = 0.42$
Residual	3.07±1.75	22.5	

^aThe order in which an egg is laid and standardized date of laying have a significant effect on egg size, being included in the minimum adequate model. Year ($F_{2,63} = 1.0$, $P = 0.36$) was excluded from the final model.

^bSignificances of random effects were tested with a likelihood-ratio test (LRT).

size to differences among females (repeatability), while differences between clutches of a single female (plasticity) accounted just for 1.4%. The residual variance (differences within a clutch) accounted for the remaining 22.5%. The repeatability of mean egg size was 0.894 ($F_{32,66} = 26.3$, $P < 0.001$).

INTER- AND INTRA-CLUTCH VARIATION IN EGG SIZE

The average total mass of three-egg clutches was 162.6 g, standard deviation 12.7 g (CV = 7.8%, $n = 389$), range 126.8–207.8 g. The heaviest three-egg clutch was 64% heavier than the lightest. Mean egg mass in three-egg clutches did not vary significantly by year (Table 3). Mean egg mass decreased as date of laying increased ($\beta = -0.61 \pm 0.17$; Table 3), although date of laying accounted for only <2% of mean egg-size variation. Neither the female's body size nor condition was related to mean egg size (Table 3).

In three-egg clutches, an egg's size decreased with the order in which it was laid (Table 3; first–second egg: $t = -3.3$, $P < 0.005$; first–third: $t = -21.3$, $P < 0.001$; second–third: $t = -18.0$, $P < 0.001$, Table 1). This pattern of intra-clutch variation was not related to year, date of laying, or the female's body size or condition (Table 3).

EFFECTS OF EGG MASS ON HATCHLING MASS, INCUBATION LENGTH, AND HATCHING SUCCESS

The mean mass of chicks weighed within 12 hr of hatching was 37.9 ± 0.4 g (range 26–54 g, $n = 124$). Egg mass positively

TABLE 3. General linear mixed model of size of Imperial Cormorant eggs. In total, we included 1167 eggs from 389 three-egg clutches laid by 296 females.

Effect		
Fixed	<i>F</i> -test	<i>P</i>
Inter-clutch variation in egg size		
Intercept	$F_{1,776} = 48\ 850$	<0.001
Year	$F_{2,90} = 1.1$	0.33
Standardized date of laying	$F_{1,92} = 12.4$	<0.001
Body size	$F_{1,38} = 0.4$	0.53
Body condition	$F_{1,39} = 3.2$	0.08
Inter-clutch variation in egg size		
Order of laying	$F_{2,776} = 274$	<0.001
Order × year	$F_{4,770} = 0.6$	0.64
Order × standardized date of laying	$F_{2,774} = 2.4$	0.09
Order × body size	$F_{2,416} = 0.7$	0.49
Order × body condition	$F_{2,418} = 1.5$	0.23
Random ^a	SD (95% CI)	LRT
Female	4.06 (3.72–4.43)	$\chi^2_1 = 1254$, $P < 0.001$
Female (clutch)	0.69 (0.43–1.09)	$\chi^2_1 = 7.2$, $P = 0.007$
Residual	1.71 (1.62–1.79)	

^aFemale and clutch nested in female were used as random-effect terms in the model. Significances of random effects were tested with a likelihood-ratio test (LRT).

affected hatchling mass ($F_{1,122} = 280$, $P < 0.001$, $n = 124$). The linear regression of hatchling mass on egg mass yielded the equation $y = 0.80x - 5.14$ ($r^2 = 0.70$; Fig. 1). Thus a difference of 1 g in egg mass corresponded to a difference of 0.8 g in hatchling mass.

The mean length of incubation of third eggs monitored daily during laying and hatching was 27.9 ± 0.1 days (range 26–30 days, $n = 42$). Egg mass affected the length of incubation ($F_{1,40} = 22.2$, $P < 0.001$, $n = 42$) according to the equation $y = 0.11x + 22.25$ ($r^2 = 0.36$), so that the incubation period is extended by 0.11 days per 1-g increase in egg mass (Fig. 2).

The overall probability of hatching of eggs that completed the incubation period was 0.88 ± 0.01 ($n = 918$ eggs). The model that best explained the variation in probability of hatching included both the linear and quadratic terms for egg size (likelihood-ratio test, comparison with null model: $\chi^2_2 = 11.2$, $P = 0.0036$). The probability of hatching successfully was positively correlated with egg mass (egg mass: $\beta = 0.73 \pm 0.28$; $\chi^2_1 = 6.0$, $P = 0.014$; Fig. 3). However, there was evidence that extremely large eggs also suffered low hatchability

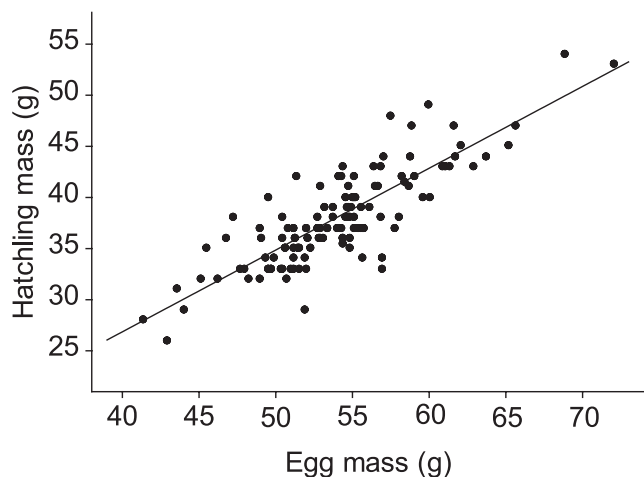


FIGURE 1. Relationship between the mass of eggs and the mass of hatchlings of the Imperial Cormorant ($n = 124$).

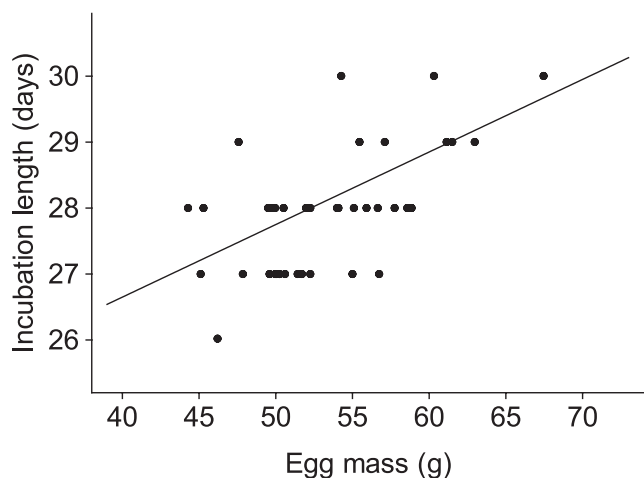


FIGURE 2. Duration of incubation in relation to egg mass for third eggs of the Imperial Cormorant ($n = 42$).

(egg mass²: $\beta = -0.0062 \pm 0.0025$; $\chi^2_1 = 5.2$, $P = 0.022$; Fig. 3). The model including both the linear and quadratic terms for egg size fitted our data significantly better (likelihood-ratio test, $\chi^2_1 = 5.2$, $P = 0.022$) than did the simpler model including the linear term of egg mass (model parameters: intercept = -0.97 , egg mass = 0.056 ; comparison with null model: $\chi^2_1 = 6.0$, $P = 0.014$). The probability of egg hatching was not influenced by year ($\chi^2_2 = 5.8$, $P = 0.06$), date of laying ($\chi^2_1 = 0.1$, $P = 0.77$), or order of laying ($\chi^2_2 = 1.9$, $P = 0.38$).

EFFECT OF INTRA-CLUTCH VARIATION IN EGG SIZE ON BROOD REDUCTION

Only 11 third chicks (7%) fledged from 163 three-hatchling broods (median survival time = 6 days). The average deviation in egg size between the third egg and the other eggs in

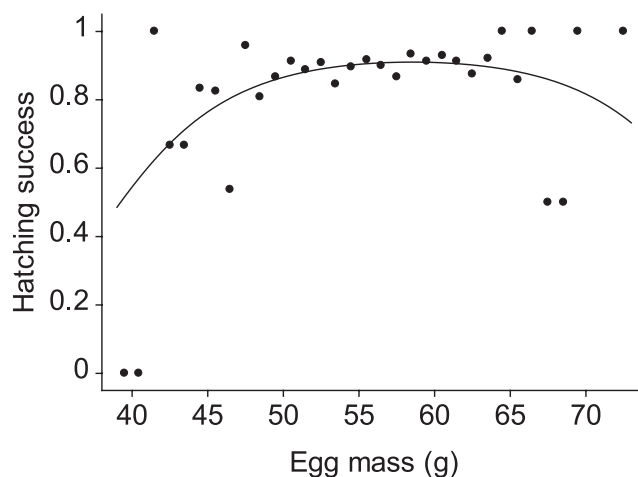


FIGURE 3. Adjusted curve of probability of hatching of Imperial Cormorant eggs in relation to their mass ($n = 918$). Parameters of the adjusted curve (intercept = -19.0 , egg mass = 0.73 , egg mass² = -0.0062) were estimated from a generalized linear model with a binomial family distribution and logit-link function (see text). Circles show the mean probability of hatching of eggs belonging to various size categories (integer values of mass, in grams).

a clutch was -2.3 g (SD = 2.2 g, $n = 163$), ranging from -8.6 to 3.3 g. It was not related ($\beta = -0.025 \pm 0.042$; $\chi^2_1 = 0.4$, $P = 0.55$) to survival time of the third chick. However, the third chick's survival time increased with egg size ($\beta = -0.052 \pm 0.022$; $\chi^2_1 = 5.7$, $P = 0.02$). Thus the chance of death decreased by 5% ($e^{-0.052} = 0.95$) with each additional gram of egg mass. Survival time of the third chick also increased with the previous death of an elder sibling ($\beta = -1.46 \pm 0.29$; $\chi^2_1 = 33.5$, $P < 0.001$) and decreased as the asynchrony of hatching increased ($\beta = 0.22 \pm 0.06$; $\chi^2_1 = 11.1$, $P < 0.001$). Survival time varied by year (median of 6, 6, and 8 days for 2004, 2005, and 2006, respectively; $\chi^2_2 = 8.6$, $P = 0.01$) and was not related to the date of laying ($\beta = 0.21 \pm 0.12$; $\chi^2_1 = 3.1$, $P = 0.08$).

DISCUSSION

PHENOTYPIC VARIATION, REPEATABILITY, AND PLASTICITY IN EGG SIZE

In the population of the Imperial Cormorant we studied, egg size varied widely, the largest egg being more than twice as heavy as the smallest. We found that most of the total phenotypic variation in egg size (76.1%) is attributable to variation between females. With respect to the repeatability of both egg size (0.761) and mean egg size (0.894), these values are the highest reported for any bird species in the wild (see Christians [2002] for a full review of egg-size variation in birds). The high repeatability of egg size we noted for the Imperial Cormorant could be a consequence of genetic differences but also of permanent nongenetic (environmental) differences among individuals (see Boag and van Noordwijk

1987, Falconer and Mackay 1996), such as differences arising from nutritional constraints during nestling ontogeny or consistent differences among individuals in foraging skills. A more detailed analysis in this regard is beyond the scope of this paper, and further studies of this population, estimating heritability in egg size and assessing genetic and environmental factors, are needed. In addition, our results emphasize the importance of egg-size repeatability over mean egg-size repeatability because the latter ignores some of the phenotypic variation within an individual (i.e., variation within a clutch) and hence overestimates the repeatability (Flint et al. 2001).

We have also shown the lack of phenotypic plasticity (adjustment to environmental conditions) of individual females (1.4%), despite substantial variation in egg size within a clutch (22.5%). In environments where reproductive output and survival vary, plasticity in life-history traits should evolve (Hirshfield and Tinkle 1975). Therefore, phenotypic plasticity should be favored in a varying environment, whereas specialization (i.e., low phenotypic plasticity) should be selected in a relatively constant environment (Endler 1986). Kontiainen et al. (2008) showed a high plasticity (22.4%) in egg size for the Ural Owl (*Strix uralensis*), a bird depending mainly on rodents whose population density varies strikingly in a rather regular 3-year cycle. By contrast, southern marine ecosystems in general, and the area exploited by Imperial Cormorants from Punta León in particular, are usually characterized by their stability (Acha et al. 2004, Rivas et al. 2006). The primary productivity of the coast of northern Patagonia is moderately high throughout the year, with a seasonal peak in spring and summer (Acha et al. 2004, Rivas et al. 2006). Moreover, during the breeding season, the Imperial Cormorants of Punta León feed in a small area of high productivity (Quintana et al. 2011) associated with a seasonal marine tidal front to the southeast of the Valdés Peninsula (Rivas et al. 2006). Therefore, the lack of phenotypic plasticity in egg size in the Imperial Cormorant at Punta León is likely a consequence of the exploitation of a highly predictable food source in a relatively stable marine ecosystem.

INTER-CLUTCH VARIATION IN EGG SIZE

In the Imperial Cormorant, we found inter-clutch variation in egg size unrelated to the female's body condition. Our results did not support the idea that proximate nutritional constraints on the Imperial Cormorant may be the factor causing variation between clutches in egg size (see Introduction). In several species of birds (mostly small passerines), a clutch's total mass may represent 100% or even more of the female's mass (Perrins 1970). In our study, the average mass of a three-egg clutch (i.e., the modal size; Svagelj and Quintana 2011) of the Imperial Cormorant was 162 g, representing only 8.3% of the average body mass of a breeding female. Thus, although egg production should be costly per se, for females of the Imperial Cormorant it does not impose a major cost.

INTRA-CLUTCH VARIATION IN EGG SIZE

Our results provided evidence of a general pattern of intra-clutch variation in egg size in the Imperial Cormorant, regardless of year, date of laying, body size or condition of the female. In most clutches, egg size decreased as the eggs were laid, with last (third) eggs being ~5% smaller than earlier eggs within a clutch.

Pierotti and Bellrose (1986) suggested that intra-clutch variation in egg size may be caused by variation in the female's energy reserves. In accordance with this hypothesis, Slagsvold and Lifjeld (1989) found that the female's body condition affected the size of last eggs more than it did first eggs. In our study, the interaction term of an egg's position in sequence \times female's body condition was not significant, so body condition was not supported as the factor causing the pattern within a clutch. Our results agree with Meijer and Drent (1999), who stated that, in birds, the egg mass is more or less independent of the female's body condition.

We found that egg-size variation within a clutch did not affect the survival time of the third chick. Both hatchling mass and incubation length were positively related to egg size. While hatchling mass increased on average 0.8 g per gram of egg mass, incubation was 0.11 days longer per gram of egg. During the first 24 hr of life, chicks of the Imperial Cormorant gain an average of ~9 g (Svagelj and Quintana, unpubl. data). Therefore, if two eggs in a clutch differ in size by ΔM g, and they are incubated at the same time, the smaller egg hatches 0.11 ΔM days earlier than the larger one. When the large egg hatches, the differences in mass should be $(0.8\Delta M - 0.11 \times 9\Delta M) = -0.19\Delta M$ g. Therefore, the smaller size of chicks hatched from small eggs appears compensated for by postnatal growth during the time provided by the shorter incubation period. Although this result is in agreement with the hypothesis of Parsons (1972), as a decline in egg size through laying of a clutch may serve to reduce asymmetry in the size of siblings within Imperial Cormorant broods, the net effect of variation in egg size on asymmetry of sibling size was negligible (<2 g) in relation to the species' highly asynchronous hatching (average interval between hatching of first and third eggs 4.3 days, Svagelj 2009). Therefore, in the Imperial Cormorant the adaptive value of intra-clutch variation in egg size appears low and insufficient to support either the hatchling-size (Howe 1976) or hatching-asynchrony (Parsons 1972) hypotheses.

Alternatively, intra-clutch variation in the size of Imperial Cormorant eggs could be adaptive, females investing fewer resources in those eggs with poorer prospects for survival. Quinn and Morris (1986) proposed that intra-clutch variation in egg size could be a consequence of females saving energy, in which females benefit by investing less in those eggs with lower prospects for survival and hence lower returns in fitness. Within an Imperial Cormorant brood, survival of a chick decreases steadily with order in which it hatched: chicks from only 15% of third eggs fledge (Svagelj 2009). Thus, in

the Imperial Cormorant, intra-clutch variation in egg size appears to be in accordance with the idea of energy saving.

In addition, as proposed by Williams et al. (1993), physiological constraints rather than the female's nutritional status and/or adaptive causes could be responsible for the pattern of intra-clutch variation in egg size in birds. Hormonal mechanisms controlling ovulation and incubation (Leblanc 1987) or constraints in rates of yolk or albumen production (Bolton 1991) could be explored in future studies.

EFFECTS OF EGG MASS ON HATCHING SUCCESS AND SURVIVAL TIME OF THE THIRD CHICK

Both extremely small and extremely large Imperial Cormorant eggs hatch less frequently than intermediate-sized ones. In general, small eggs do not hatch as well as larger ones (Perrins 1996, Valkama et al. 2002) because of the nutritional and/or thermoregulatory advantages large eggs have over smaller ones (Serrano et al. 2005). Although it is unclear why extremely large eggs of the Imperial Cormorant suffer lower hatchability, a lower efficiency of incubation due to the increase in the volume of clutches consisting of three extremely large eggs could explain that pattern. Our results suggest a stabilizing selection acting on egg size at the level of the individual egg. Selection on egg size, however, appears to operate only on the extremes of egg size, being neutral for most of the range. For example, while the predicted probability of hatching of most eggs (94.1%) was >0.8 (range 47–72 g, Fig. 3), only 5.5% (88/1588) of the extremely small and 0.3% (5/1588) of the extremely large eggs would be selected against with respect to reduced hatchability.

Finally, we found egg size to be related positively to the time of survival of the third chick, suggesting that a chick hatched from a large egg may benefit by hatching with more nutrients and water reserves, which help increase its resistance to starvation (Ankney 1980). Svagelj (2009) showed that the third egg of the Imperial Cormorant provides an insurance value (sensu Dorward 1962, Mock and Forbes 1995) for those broods in which one of the older chicks dies previously at an early age. Therefore, investing in a large third egg benefits females of the Imperial Cormorant by keeping the insurance chick alive and conserving its insurance value longer.

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