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Sex-specific Growth in the Imperial Cormorant (*Phalacrocorax atriceps*): When Does Dimorphism Arise?

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Abstract.—Cormorants and shags (Phalacrocoracidae) are sexually monomorphic in plumage but dimorphic in size with males larger and heavier than females. Such size dimorphism has been capitalized upon for several species in the family to sex adults by using discriminant analysis applied on the morphometric measurements. Despite that, few studies have analyzed the development of sexual size dimorphism during chick growth. In this study, sex-specific growth was assessed in chicks of the Imperial Cormorant (*Phalacrocorax atriceps*) by analyzing the development of body mass, bill length, head length, tarsus length and wing length measured on 80 chicks sexed by DNA-based technics. Fieldwork was performed during the 2004 breeding season at Punta León, Patagonia, Argentina. In addition, discriminant analyses were performed to obtain functions to determine the sex of fledglings. Males had higher asymptotic values and growth rates than females for all measurements considered, even though the arising of dimorphism varied among morphometric characteristics (10-40 days). Discriminant functions to determine the sex of chicks at 30, 35 and 40 days of age were obtained. All functions included tarsus length and head length as variables, correctly classifying 88-94% of chicks. Our findings show the Imperial Cormorant to be an interesting model for evaluating the potential consequences of sexual size dimorphism on chick survival and fledging condition depending on brood sex composition. *Received 29 December 2016, accepted 8 February 2017.*

Key words.—cormorants, discriminant analysis, nonlinear mixed-effect models, Richards growth model, sexual size dimorphism.

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Cormorants (Phalacrocoracidae) are sexually monomorphic in plumage but dimorphic in size with males larger and heavier than females (Nelson 2005). Such size dimorphism has been capitalized upon for several species in the family to sex adults by using discriminant analysis applied on the morphometric measurements (Casaux and Baroni 2000; Quintana *et al.* 2003; Liordos and Goutner 2008; Riordan and Johnston 2013). Yet, few studies have analyzed the development of sexual size dimorphism during chick growth. These kinds of studies are needed because sex-specific differences in growth patterns can have effects on parental investment, sex-specific vulnerability, sibling dynamics, and, hence, fitness returns (Richner 1991; Uller 2006; Kalmbach and Benito 2007). To our knowledge, the only study that has characterized the development of sexual-size dimorphism in phalacrocoracid chicks was conducted by Velando *et al.* (2000) for the European Shag (*Phalacrocorax aristotelis*).

On the other hand, DNA-based techniques (Ellegren 1996) have been become the standard method for determining the sex of birds. These techniques have been widely adopted because they only require a small blood sample and provide a correct sex classification. However, DNA-based techniques require laboratory analyses that do not allow for sex determination *in situ*, which is sometimes required during the fieldwork (Casaux *et al.* 2008). Despite their potential utility, discriminant analyses that can be applied to fledglings of cormorants and shags are scarce (Velando *et al.* 2000; Casaux *et al.* 2008).

The Imperial Cormorant (*P. atriceps*) is a colonial seabird inhabiting southern South America (Nelson 2005). Males are larger (5-13% in linear measurements of morphometric characteristics) and heavier (~18%) than females (Svagelj and Quintana 2007), even though no information exists about the arising of such dimorphism during chick growth.

In this study, we assessed sex-specific growth in Imperial Cormorant chicks by analyzing the development of body mass, bill length, bill depth, head length, tarsus length and wing length throughout the rearing period. In addi-

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tion, discriminant analyses were performed to obtain functions to determine the sex of fledglings based on external measurements.

METHODS

Study Area

We conducted this study from October to December 2004 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). We checked nests every 1-3 days from the start of laying until completion of clutches. During egg hatching, we checked nests every 1-3 days (most daily) to establish hatching date and the identity of hatchlings, marking them on the tarsus with labeled fiber-tape bands. At an age of ~20 days, chicks were banded with numbered aluminum rings. During chick rearing, we checked nests every 3-5 days to obtain morphometric measurements of chicks until it proved impossible to capture them further, at an age of ~40 days. Also, we obtained blood samples to determine the sex of chicks by DNA-based techniques (Ellegren 1996). For each chick, we obtained three or four drops of blood from the leg during the first week of life. For a detailed description of molecular sexing techniques used in Imperial Cormorants, see Quintana *et al.* (2008). In total, we collected data on chick growth from 80 Imperial Cormorant nests.

Morphometric Measurements

Six measurements were taken: body mass, bill length (exposed culmen), bill depth (minimum depth), head length (from the tip of the bill to the posterior ridge), tarsus length (from the middle of the midtarsal joint to the distal end of the tarsometatarsus), and wing length (the length of flattened and extended wing). For bill, head, tarsus and wing measurements, we used a digital caliper (nearest 0.01 mm). For wing length measurements larger than ~100 mm, a ruler (nearest 1 mm) was used. We recorded body mass using 100 g, 300 g, 600 g, 1,000 g and 2,500 g spring scales. Imperial Cormorants exhibit brood reduction with last-hatched chicks in three-hatchling broods usually starving to death mainly within the first week of life (Svagelj 2009; Svagelj and Quintana 2011a, 2011b). To minimize disturbance in nests with more than one chick, body mass was the only characteristic measured during the first week at these nests. For each chick, mass at hatching was calculated from egg mass using the equation: *Hatchling mass = 0.80 x Egg mass – 5.14* (Svagelj and Quintana 2011b). To simplify statistical analyses and to avoid for lack of independence among chicks of the same nest, we only considered one chick per nest (that with higher number of morphometric measurements) in our statistical analyses. As a consequence, growth data analyzed here corresponds to 80 chicks (42 males and 38 females) with 690 measurements in body mass ($\bar{x}$ = 8.6, SD = 1.5 measurements per chick), while bill, head, tarsus and wing comprised 436 measurements ($\bar{x}$ = 5.5, SD = 1.5 measurements per chick). Finally, we excluded bill depth from further analyses because our early measurements on this characteristic were inconsistent and unreliable.

Data Analyses

We analyzed chick growth using nonlinear mixed models (Pinheiro and Bates 2000). These models allow the simultaneous inclusion of growth parameters as fixed effects, describing the average growth curve and the influence of predictor variables, as well as random effects allowing for random individual variation around the average values. Thus, individual growth curves can be derived, and chick size at a particular age, estimated. Growth data were fitted to Richards equation (Richards 1959) using the parameterization proposed by Tjørve and Tjørve (2010): $y_t = A\ (1+((W_0/A)^{(1-d)}-1)\ \exp(-Kt/d^{d/(1-d)}))^{1/(1-d)}$. In this parameterization, y_t is size at age t, and A, W_0, $K$and d are the upper asymptote (i.e., adult size), intersection value on the y-axis (i.e., size at hatching), maximum relative growth rate and shape parameter, respectively. Sex of chicks (male or female) was included as a predictor variable for each growth parameter (i.e., A, W_0, $K$and d), and growth parameters from chick identity were included as random effects. Significance of sex was evaluated using an F statistic, while significance of random effects was evaluated using likelihood ratio tests, with non-relevant factors being discarded. Because bill, head, tarsus and wing measurements were scarce during the first week, we fixed the size at hatching (W_0) for these characteristics (mean values at hatching: bill length = 9.5 mm, head length = 32 mm, tarsus length = 13.5 mm, wing length = 16 mm; W. S. Svagelj and F. Quintana, unpubl. data). In addition, we fixed the asymptotic values (A) of wing length for males and females (298 and 283 mm, respectively; Svagelj and Quintana 2007) because wing length continues to growth beyond the time the chicks can be caught. Finally, growth models in body mass exhibited heteroscedasticity, which was modeled considering a variance function where variance increases linearly with the fitted values (Pinheiro and Bates 2000).

To analyze the arising of sexual size dimorphism, we derived estimators from individual growth curves at different ages and compared them between sexes. Using a t-test, we compared body mass between sexes at 3, 6, 9, 12, 15, 20, 25, 30, 35 and 40 days of age, while bill, head, tarsus and wing lengths were compared at 10, 15, 20, 25, 30, 35 and 40 days. Using the parameterization proposed by Tjørve and Tjørve (2010), the maximum absolute growth rate (g_{max}) takes a value of $g_{max} = A\ K$. For all measurements considered, we compared g_{max} between sexes using a t-test.

Finally, we applied linear discriminant analyses (Tabachnick and Fidell 1996) on the morphometric data to obtain combinations of characteristics (discriminant functions) that best distinguish the sexes at 30, 35 and 40 days of age. We chose those ages to derive our predictive discriminant functions because: 1) chicks can be easily captured up to 30 days of age and capture probability progressively decreases thereafter;

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and 2) power of discriminant functions would increase with chick age. As chicks were not measured exactly at those ages, values were derived from individual growth curves. Because wing length may be affected by wingtip wear, we excluded that characteristic from our discriminant analyses. The effectiveness of the discriminant functions was assessed in terms of the percentage of birds of known sex that were classified correctly. For each age, we evaluated seven possible models (i.e., all possible combinations using bill length, head length and tarsus length as predictor variables), choosing the model with the highest percentage of birds of known sex correctly classified. For each age, we provided the best discriminant function obtained with their *F*-value, Wilks' Lambda, and the percentage correctly classified for each sex and for all birds pooled. Chicks with a discriminant score higher than 0 were classified as males, and those with a lower score as females.

Statistical analyses were carried out using packages from statistical software R (R Development Core Team 2016), including nlme (Pinheiro *et al.* 2016) and MASS (Venables and Ripley 2002). Results are presented as mean ± SE. All tests were two-tailed, and differences were considered significant at $P < 0.05$.

RESULTS

Males showed higher asymptotic values (*A* parameter) than females for all measurements considered (Table 1; Figs. 1 and 2). Neither maximum relative growth rate (*K*) or shape parameter (*d*) differed between sexes (all $P > 0.05$).

The arising of sexual size dimorphism varies among morphometric characteristics (Figs. 1 and 2). Males were heavier than females from 15 days onward (Table 2; Fig. 1). Head and

Table 1. Final Richards's growth models for body mass, bill length, head length, tarsus length and wing length of Imperial Cormorant chicks. Sex (male or female) was included in the starting models as a predictor variable modeling *A* (adult size), W_0 (size at hatching), *K* (maximum relative growth rate) and *d* (shape parameter). Parameters noted with asterisks were fixed and not modeled by sex. Only significant effects of the predictor variable that remained in the final models are shown. Models were fitted as nonlinear mixed models.

	Parameter	Predictor Variable	Estimate ± SE	*t*	*P*
Body mass	*A*	Intercept	1,971 ± 32	$t_{606} = 62.2$	< 0.001
		Sex (Males)	226 ± 35	$t_{606} = 6.5$	< 0.001
	W_0	Intercept	38 ± 1	$t_{606} = 33.7$	< 0.001
	K	Intercept	0.038 ± 0.001	$t_{606} = 50.1$	< 0.001
	d	Intercept	1.26 ± 0.03	$t_{606} = 37.3$	< 0.001
Bill length	*A*	Intercept	54.9 ± 0.5	$t_{353} = 108.5$	< 0.001
		Sex (Males)	3.5 ± 0.6	$t_{353} = 5.7$	< 0.001
	W_0*	Intercept	9.5	—	—
	K	Intercept	0.029 ± 0.001	$t_{353} = 86.6$	< 0.001
	d	Intercept	2.26 ± 0.07	$t_{353} = 31.3$	< 0.001
Head length	*A*	Intercept	130.3 ± 0.8	$t_{353} = 171.5$	< 0.001
		Sex (Males)	7.7 ± 0.8	$t_{353} = 9.4$	< 0.001
	W_0*	Intercept	32.0	—	—
	K	Intercept	0.025 ± 0.001	$t_{353} = 105.0$	< 0.001
	d	Intercept	2.22 ± 0.08	$t_{353} = 26.8$	< 0.001
Tarsus length	*A*	Intercept	66.4 ± 0.2	$t_{353} = 272.3$	< 0.001
		Sex (Males)	3.4 ± 0.3	$t_{353} = 10.3$	< 0.001
	W_0*	Intercept	13.5	—	—
	K	Intercept	0.047 ± 0.001	$t_{353} = 123.7$	< 0.001
	d	Intercept	4.11 ± 0.11	$t_{353} = 37.7$	< 0.001
Wing length					
Males	*A**	Intercept	298	—	—
	W_0*	Intercept	16	—	—
	K	Intercept	0.024 ± 0.001	$t_{186} = 90.7$	< 0.001
	d	Intercept	1.86 ± 0.04	$t_{186} = 45.7$	< 0.001
Females	*A**	Intercept	283	—	—
	W_0*	Intercept	16	—	—
	K	Intercept	0.025 ± 0.001	$t_{168} = 80.0$	< 0.001
	d	Intercept	1.91 ± 0.05	$t_{168} = 41.3$	< 0.001

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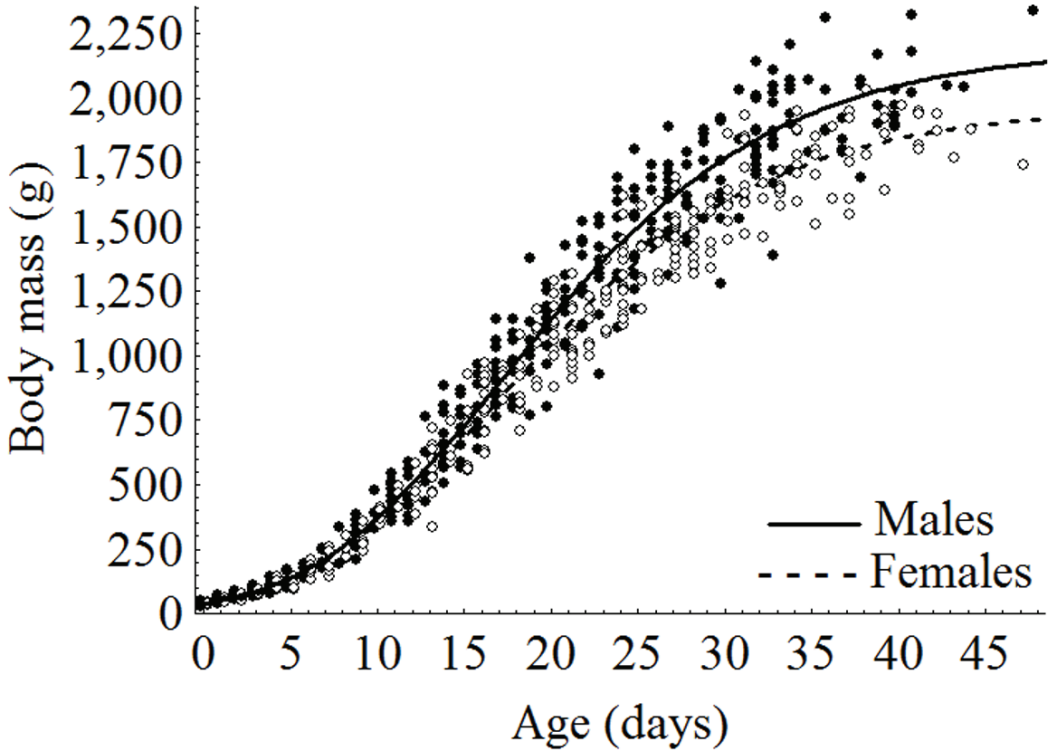

Figure 1. Growth curves in body mass for Imperial Cormorant chicks according to sex (males: solid line, females: dashed line). Measured values are shown as filled (males) and empty (females) circles. Growth curves were obtained from nonlinear mixed models applied to the Richards equation.

bill lengths exhibited sexual dimorphism beginning at 10 and 15 days of age, respectively (Table 3; Fig. 2A, 2B). Tarsus length diverged between 15 and 20 days (Table 3; Fig. 2C), while wing length differed from 40 days onward (Table 3; Fig. 2D). Maximum absolute growth rate (g_{max}) of males was higher than for females for all measurements considered (Table 4).

For chicks that were 30, 35 and 40 days of age, the best classification of sex was obtained by including tarsus length and head length as discriminatory variables (Table 5). Correct classification rates increased with chick age, from 88% at 30 days to 94% for chicks 40 days old (Table 5).

DISCUSSION

We found sex-specific differences in the growth of Imperial Cormorants with sexual dimorphism in size arising early during the chick rearing period. Males had higher asymptotic values and absolute growth rates than females for all measurements considered, even though the arising of dimorphism varied among morphometric characteristics. Sexual dimorphism in head length began at 10 days of age, body mass and bill length at 15 days and tarsus length at 20 days, while wing length differed from 40 days onward.

Sex-specific differences in growth patterns can affect vulnerability of sexes, sibling dynamics and parental investment. The larger sex is often more vulnerable to poor conditions during chick growth. To achieve their greater size, individuals of the larger sex are likely to have higher energy demands during growth, which in turn might make them more vulnerable to a shortage of resources, leading to increased mortality and reduced fledging mass (Kalmbach and Benito 2007). On the other hand, in contrast to the intrinsic disad-

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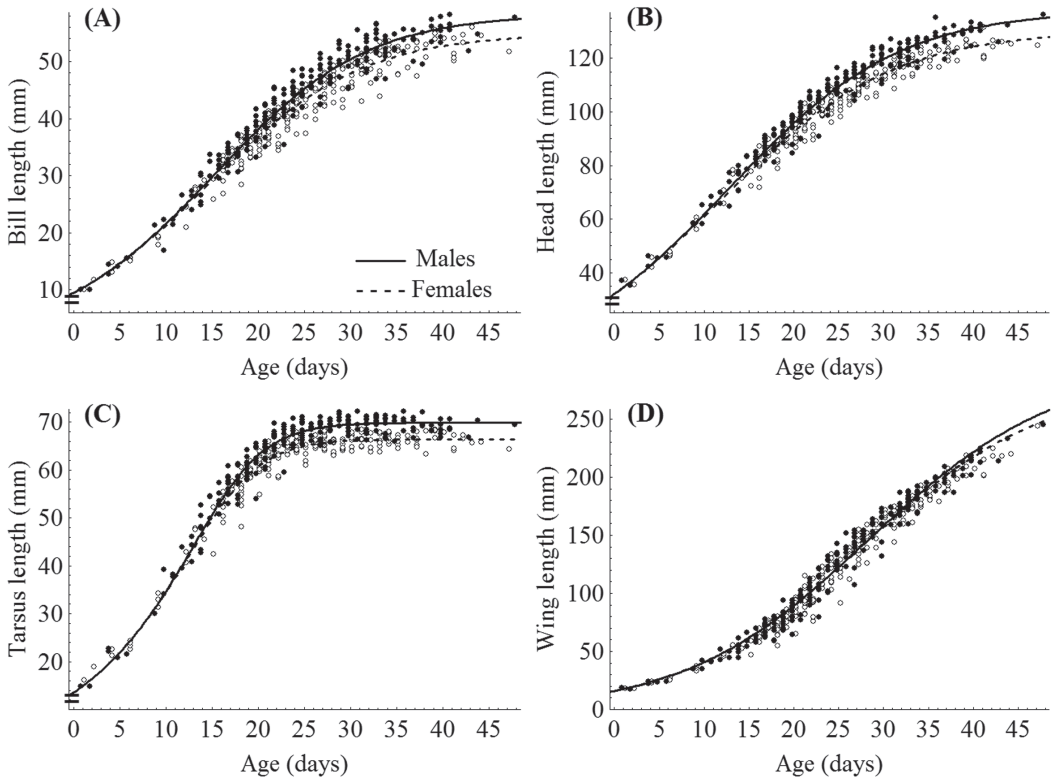

Figure 2. Growth curves for Imperial Cormorant chicks according to sex (males: solid line, females: dashed line) for (A) bill length, (B) head length, (C) tarsus length and (D) wing length. Measured values are shown as filled (males) and empty (females) circles. Growth curves were obtained from nonlinear mixed models applied to the Richards equation.

vantage of a higher vulnerability, individuals of the larger sex generally have a competitive advantage within the brood at the behavioral, extrinsic level (Uller 2006; Kalmbach and Benito 2007). Such sexual differences in competitive ability can be more or less pronounced depending not only on the degree of dimorphism but on other factors such as brood sex composition or sibling hierarchy in the brood. In this study, we characterized the sexual differences in chick growth of Imperial Cormorants, which will allow us in the future to evaluate the potential consequences of such dimorphism that arise during chick rearing. In the Imperial Cormorant, both parents play an active role in nest defense, incubation, brood care and lastly chick feeding duties for more than 2 months (Svagelj and Quintana 2011a, 2011b; Svagelj *et al.* 2012). Therefore, sex-specific growth is likely to have a differential effect on chick survival and fledging condition depending on brood sex composition, and additional studies are needed to assess their consequences.

Table 2. Body mass (mean ± SE) of Imperial Cormorant chicks according to sex (males: $n = 42$, females: $n = 38$) and age of chicks (in days). Estimated values were obtained from the individual growth curves derived from a nonlinear mixed model applied to the Richards equation. Significance was evaluated using a *t*-test.

	Body Mass (g)			
Age (days)	Males	Females	t_{78}	P
3	86 ± 1	86 ± 1	0.5	0.607
6	174 ± 3	171 ± 3	0.8	0.432
9	312 ± 7	302 ± 6	1.1	0.272
12	502 ± 11	479 ± 9	1.6	0.108
15	729 ± 14	688 ± 11	2.3	0.027
20	1,135 ± 17	1,052 ± 14	3.7	< 0.001
25	1,493 ± 18	1,367 ± 14	5.4	< 0.001
30	1,759 ± 18	1,598 ± 13	7.1	< 0.001
35	1,936 ± 18	1,749 ± 13	8.4	< 0.001
40	2,045 ± 17	1,842 ± 13	9.3	< 0.001

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Table 3. Bill length, head length, tarsus length and wing length (mean ± SE) of Imperial Cormorant chicks according to sex (males: $n = 42$, females: $n = 38$) and age of chicks (in days). Estimated values were obtained from the individual growth curves derived from nonlinear mixed models applied to the Richards equation. Significance was evaluated using a *t*-test.

	Bill Length (mm)				Head Length (mm)			
Age (days)	Males	Females	t_{78}	P	Males	Females	t_{78}	P
10	21.6 ± 0.2	21.2 ± 0.2	1.8	0.075	61.8 ± 0.3	60.8 ± 0.4	2.0	0.045
15	29.8 ± 0.3	28.9 ± 0.3	2.4	0.018	79.2 ± 0.5	77.2 ± 0.5	2.9	< 0.01
20	38.1 ± 0.3	36.6 ± 0.3	3.3	< 0.01	95.6 ± 0.5	92.4 ± 0.5	4.2	< 0.001
25	45.2 ± 0.3	43.1 ± 0.3	4.4	< 0.001	109.2 ± 0.5	104.9 ± 0.5	6.0	< 0.001
30	50.4 ± 0.3	47.8 ± 0.4	5.3	< 0.001	119.4 ± 0.5	114.1 ± 0.4	8.0	< 0.001
35	53.8 ± 0.3	50.9 ± 0.4	6.0	< 0.001	126.4 ± 0.5	120.3 ± 0.4	10.3	< 0.001
40	55.8 ± 0.3	52.7 ± 0.4	6.4	< 0.001	131.0 ± 0.4	124.3 ± 0.3	12.5	< 0.001
	Tarsus Length (mm)				Wing Length (mm)			
	Males	Females	t_{78}	P	Males	Females	t_{78}	P
10	34.5 ± 0.3	34.6 ± 0.3	-0.1	0.903	41 ± 0.4	41 ± 0.4	0.0	0.993
15	50.3 ± 0.5	49.8 ± 0.5	0.8	0.429	62 ± 1	62 ± 1	0.0	0.982
20	62.6 ± 0.4	60.7 ± 0.4	3.7	< 0.001	90 ± 1	90 ± 1	0.0	0.977
25	67.9 ± 0.3	65.0 ± 0.2	8.2	< 0.001	123 ± 1	122 ± 1	0.2	0.843
30	69.4 ± 0.2	66.1 ± 0.2	10.7	< 0.001	158 ± 1	157 ± 1	0.6	0.549
35	69.8 ± 0.2	66.4 ± 0.2	11.4	< 0.001	192 ± 1	189 ± 1	1.5	0.151
40	69.9 ± 0.2	66.4 ± 0.2	11.5	< 0.001	221 ± 1	216 ± 1	2.9	< 0.01

In this study, we analyzed chick growth using nonlinear mixed models applied to the Richards equation. Growth curves showed a good fit to measured values throughout chick growth, and estimated asymptotes were close to the real values of adults for all measurements considered (Svagelj and Quintana 2007). From the methodological perspective, the combination of nonlinear mixed models with the Richards equation represents a flexible and powerful analytical tool that deserves future consideration. Nonlinear mixed models can deal with any lack of statistical independence among data, also allowing a regressive approach that considers predictor variables modeling growth parameters (Pinheiro and Bates 2000). Thus, the effect of predictor variables such as hatching order, hatching asynchrony, brood size, laying date or parental body condition can be evaluated for each growth parameter. On the other hand, the Richards equation is a very attractive growth model because traditionally used models, such as logistic, Gompertz, and von Bertalanffy, all have fixed forms with inflection points fixed at a given relative value (i.e., at a percentage of the upper asymptote), while Richards model does not have this constraint (Tjørve and Tjørve 2010). Moreover, all of these traditional models represent particular cases of the Richards equation (Tjørve and Tjørve 2010).

Table 4. Maximum absolute growth rate (g_{max}, as mean ± SE) of Imperial Cormorant chicks according to sex (males: $n = 42$, females: $n = 38$) for body mass, bill length, head length, tarsus length and wing length. Maximum absolute growth rate was calculated as $g_{max} = A\,K$, which were obtained from the individual growth curves derived from nonlinear mixed models applied to the Richards equation. Significance was evaluated using a *t*-test.

	Males	Females	t_{78}	P
Body mass (g day^{-1})	82.8 ± 1.0	74.5 ± 0.7	6.8	< 0.001
Bill length (mm day^{-1})	1.70 ± 0.02	1.60 ± 0.02	4.5	< 0.001
Head length (mm day^{-1})	3.52 ± 0.03	3.32 ± 0.03	4.9	< 0.001
Tarsus length (mm day^{-1})	3.26 ± 0.03	3.14 ± 0.03	2.8	< 0.01
Wing length (mm day^{-1})	7.12 ± 0.02	6.95 ± 0.03	5.3	< 0.001

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Table 5. Accuracy of sexing Imperial Cormorant chicks using discriminant functions for chicks at 30, 35 and 40 days of age. All functions include tarsus length (TL) and head length (HL) as predictors. Values represent percentages correctly classified for each sex (males: $n = 42$, females: $n = 38$) and for all birds pooled.

Discriminant Function	Wilks' Lambda	$F_{2,77}$	P	Males	Females	Total
DF_{30} = (0.643 x TL) + (0.052 x HL) - 49.71	0.403	57.0	< 0.001	83	92	88
DF_{35} = (0.507 x TL) + (0.155 x HL) - 53.71	0.353	70.5	< 0.001	90	92	91
DF_{40} = (0.329 x TL) + (0.276 x HL) - 57.66	0.308	86.5	< 0.001	90	97	94

Velando *et al.* (2000) applied discriminant analyses to chicks of European Shags, correctly classifying 97% of chicks at an age of 25 days, and 100% of chicks at 30 days. In the Antarctic Cormorant (*P. bransfieldensis*), a species closely related to Imperial Cormorants, Casaux *et al.* (2008) determined the sex of chicks older than 45 days using a discriminant function originally developed for adults. That discriminant function included tarsus and bill measurements, and correctly classified 98% of adults and 92% of chicks (Casaux and Baroni 2000; Casaux *et al.* 2008).

Our results suggest that the use of discriminant functions is a suitable method to determine the sex of chicks of the Imperial Cormorant from 30 days of age onward. Overall effectiveness in the classification of chicks ranged from 88-94%, rates slightly lower than those obtained for adults (94-97%; Svagelj and Quintana 2007). Our discriminant functions included tarsus and head lengths, two measurements easy to take in the field. Classification rates increased with age of chicks, probably because head length is still growing and dimorphism increasing, between 30 and 40 days. While less accurate than DNA-based techniques, our discriminant functions exhibited reasonable classification rates and can be directly applied in the field to sex chicks of known age.

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