SEX-SPECIFIC GROWTH IN THE EUROPEAN SHAG
*STICTOCARBO ARISTOTELIS**, A SEXUALLY DIMORPHIC
SEABIRD

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The European Shag *Stictocarbo aristotelis* is dimorphic in body size: males are 22% heavier than females. We used molecular techniques to sex of 25 male and 18 female chicks in colonies from the Cíes Islands (NW Spain). Discriminant functions were then obtained based on morphometric variables (culmen, head, wing and tarsus length) measured throughout the growth of the sexed birds. Once chicks were 25 days of age the discriminant functions accurately classified over 95% of cases, and at 30 days of 100% of cases. Using these functions we retrospectively sexed another 30 males and 35 females to examine the growth of the two sexes. The growth of the different variables was fitted to a logistic model. Culmen growth was found to be similar in both sexes. The asymptotic head size was larger in males but had the same growth constant as in females. The wing, tarsus and body mass asymptotes were larger in males, but females had a higher growth rate. The first principal component (PC1), extracted from a principal component analysis of the morphometric variables, may be considered as a synoptic descriptor of body size. The differentiation in mass growth between males and females started when the birds were 15 days old. However, body size (PC1) was not distinguished until they were 30 days old. During the first growth stage females were similar in body size to males due to their faster growth rate. This would suggest that the smaller sex (the females) has the same competitive ability as the larger sex and that the hierarchy in the early stages of growth would be contingent upon hatching order and not sex.

Key-words: *Stictocarbo [Phalacrocorax] aristotelis* - chick growth - sexually size dimorphism - sibling rivalry - discriminant analysis - body size - body mass.

* *Stictocarbo aristotelis*, formerly known as *Phalacrocorax aristotelis*

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INTRODUCTION

In dimorphic birds a number of studies have shown that sexual differences exist in growth dynamics (raptors: Newton 1978; Moss 1979; Bortolotti 1984; passerines: reviewed in Richter 1983): the smaller sex has a faster growth rate and an earlier fledgling age. However, Richner (1991) has reviewed the studies on differential growth between sexes of passerines and found that in dimorphic birds both males and females reach fledging mass at a similar age (see also Schaadt & Bird 1993). For species that show marked dimorphism at fledging, the smaller sex is at a relative
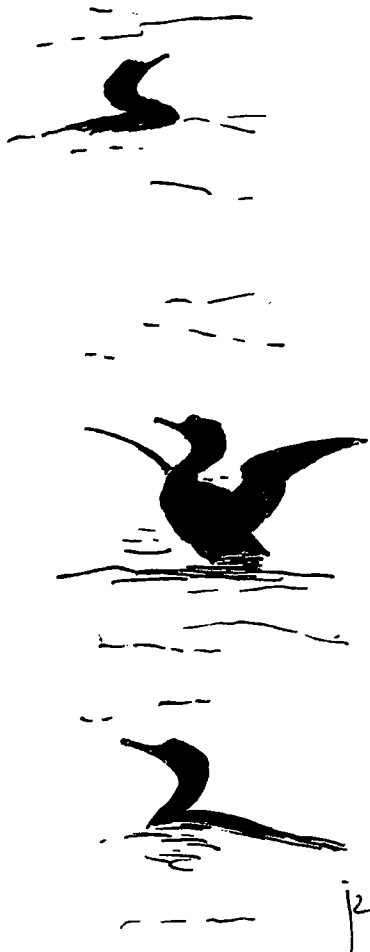
disadvantage when competing with its siblings in the nest, and must grow faster to compete with larger nest mates for resources (Bortolotti 1986; Schaadt & Bird 1993). The European Shag *Stictocarbo aristotelis* has intense intra-brood competition as shown by the high level of brood reduction and different growth rates within the brood (Amundsen & Stockland 1988; Velando 1997). Because this species is clearly dimorphic in size (males are 22% heavier than females during the breeding season, Snow 1960), sexually dimorphic growth patterns could be expected to compensate for size differences among nestlings.

Graves *et al.* (1993) sexed the chicks of this species using molecular biology techniques and reported that the sex ratio did not differ from parity, probably owing to the higher mortality rate in male chicks (the more demanding sex), a phenomenon that occurs in many species (Slagsvold *et al.* 1986; Teather & Weatherhead 1989; Griffiths 1992; Torres & Drummond 1997). The higher mortality of the more demanding sex might suggest that this sex is more vulnerable due to its higher energy requirements (Cooch *et al.* 1996). Therefore, the more demanding sex would be more likely to have a lower growth rate, leading to a drop in its survival rate. Growth patterns in the European Shag have been described for populations in Great Britain (Snow 1960; Nelson 1964; Pearson 1968) as well as in Norway (Barrett *et al.* 1986; Barrett 1989; Amundsen & Stokland 1988). However, none of these studies has taken the sex of the chicks into account. Nor are there any data available for sex differences in growth patterns in any sexually dimorphic seabird species.

We used molecular sexing techniques together with morphometric statistical models in order to develop a discriminant function for sexing European Shag chicks. This function allowed us to: (1) document the characteristics of growth in body mass and size for male and female European Shags, (2) assess the differences in the growth variability between sexes, (3) analyse the competitive value of the differences in growth patterns observed between the sexes.

METHODS

This study was carried out on the Cíes Islands (Ría de Vigo. Galicia, NW Spain) between March and June 1996. The Cíes Islands have a nesting population of around 1000 pairs of European Shags nesting in hollows underneath rocks (Velando 1997). Fifty-six nesting sites were tagged beginning in 1994 and visited periodically thereafter. The fieldwork was carried out in colonies that had not been visited during the incubation period in order to avoid disturbing the birds. During the hatching period, these colonies were visited daily or every other day (for ethical details see Velando 2000). During this period each visit lasted less than one hour to avoid cooling of the chicks when they are dependent on parental warmth (Østnes & Bech 1997). The date and time of hatching of each chick was recorded during daily visits when the hatching was either directly recorded or estimated from the stages prior to hatching (according to Stokland & Amundsen 1988).

The bill of each chick in the nest was marked with a different colour of indelible marker while they were in the process of breaking the shell or immediately after hatching. At five days after hatching they were tagged with a strip of Velcro across the tarsus and identified by colour. These strips were adjusted to tarsus size during the growth process. At 15 days of age, the chicks were tagged with metal rings provided by the Dirección General de Conservación de la Naturaleza (Ministerio de Medio Ambiente, Spain). During each visit chicks were weighed with a spring scale (to the nearest 1.0 g for birds weighing up to 100, to the nearest 5.0 g between 100 and 300 g, and to the nearest 10 g between 300 and 2000 g). A vernier calliper was used to measure, to the nearest 0.1 mm, the length of the exposed culmen (from the tip of the bill to the base of the feathers), head length (from the tip of the bill to the dorsal area of the skull) and tarsus length (total tarsal segment). Using a metallic tape with a stop the wing length was measured to the nearest 1.0 mm using the wing chord flattened method. The chicks were measured about seven times during

the first fifteen days of life and subsequently every four days until fledging. Once the chicks started moving in the hollows at about 20 days old, we used a rod with an aluminium hook at the tip to capture the chick.

Blood samples of 1-2 ml were taken from the tarsal vein of 43 chicks at 20 days of age. Blood-samples were stored in cryogenic tubes with 10 μl of EDTA and transported from the colonies to the laboratory in liquid nitrogen. The samples were kept at -80°C until they were shipped to the University of St. Andrews (Scotland) for analysis. The samples were shipped in 100 mM TRIS, 100 mM EDTA and 2% SDS at a ratio of 0.5-1:1 (blood : buffer). Sex was determined by a female specific band in shags for minisatellite probe 33.6 (Graves *et al.* 1993).

Forward stepwise discriminant analyses were carried out using the morphometric variables (culmen, head, wing and tarsus length) measured in the 43 sexed chicks. Several discriminant analyses were carried out using information from different age ranges. The growth of body mass and of the different morphometric variables was fitted to a logistic model that provided a better fit than the Gompertz and von Bertalanffy models (see Ricklefs 1968 for a description of the different models). The logistic model has the following form: $y = A/(1+Be^{kt})$, where y is the mass or morphometric variable, A is the asymptotic value, B the intercept at origin, k the growth constant (day^{-1}), and t the age (day). The growth constant (k) is representative for the overall growth rate and for the duration of the growth period (Ricklefs 1968; Richner 1991). The growth equations for mass and the different morphometric variables were fitted for all males and females and for individual chicks. The individual equations were used only for chicks that were also caught during the final growth stage and for which the fit accounted for over 98% of the variance.

In order to analyse the sexual differences by age, the weight of chicks were analysed every five days. As chicks were not measured at identical ages, the body-mass of each chick was estimated every five days based on the individual logistic model. All logistic models were carried out by non linear model estimation with the Levenberg-Marquardt algorithm (Nouris 1994). The logistic growth curves are symmetrical with regard to the inflection point y = $A/2$, and the instantaneous growth rate is obtained by derivation of the original equation: $g = dy/dt = ky (1-y/A)$. The maximum instantaneous growth rate (g_{max}) is located at the point of inflection, $g_{max} = (KA/2) (1-A/2A) = KA/4$ (for further details see Richner 1991).

A principal component analysis was carried out using the correlation matrix of the morphometric variables, including all the data measured for each chick studied. The first principal component (PC1) accounted for 97% of the variance, with an eigenvalue of 3.89 and a Pearson correlation coefficient of 0.995 with culmen length, 0.998 with head length, 0.946 with wing length and 0.950 with tarsus length. PC1 can be seen as a synoptic descriptor of body size and its increase during the first 40 days of life was fitted to a cubic polynomial model for males, females and individual chicks. A logistic model was not used given that most of the chicks examined did not reach the asymptotic value of all the morphometric variables before the end of the study. A cubic model was used since it provided a good fit for the first 40 days and the purpose of this fit was to estimate the PC1 scores for each chick every five days, and not the parameters of the model.

Comparisons between sexes of growth equation parameters (asymptote, growth rate, and maximum instantaneous growth rate) and body mass and size (PC1) of the chicks every five days were carried out by student's t-tests. The differences between males and females in the variability of the asymptote and growth rate of the individual logistic models were tested by comparing standardised absolute residuals which represent the difference between the fitted parameter for each chick and the one obtained in the overall fitting for each sex, by means of a t-test. The normality of the distributions of variables was checked by the Kolmogoronov-Smirnov test. All statistical analyses were performed using SPSS for Windows 6.3.1 (Norusis 1994).
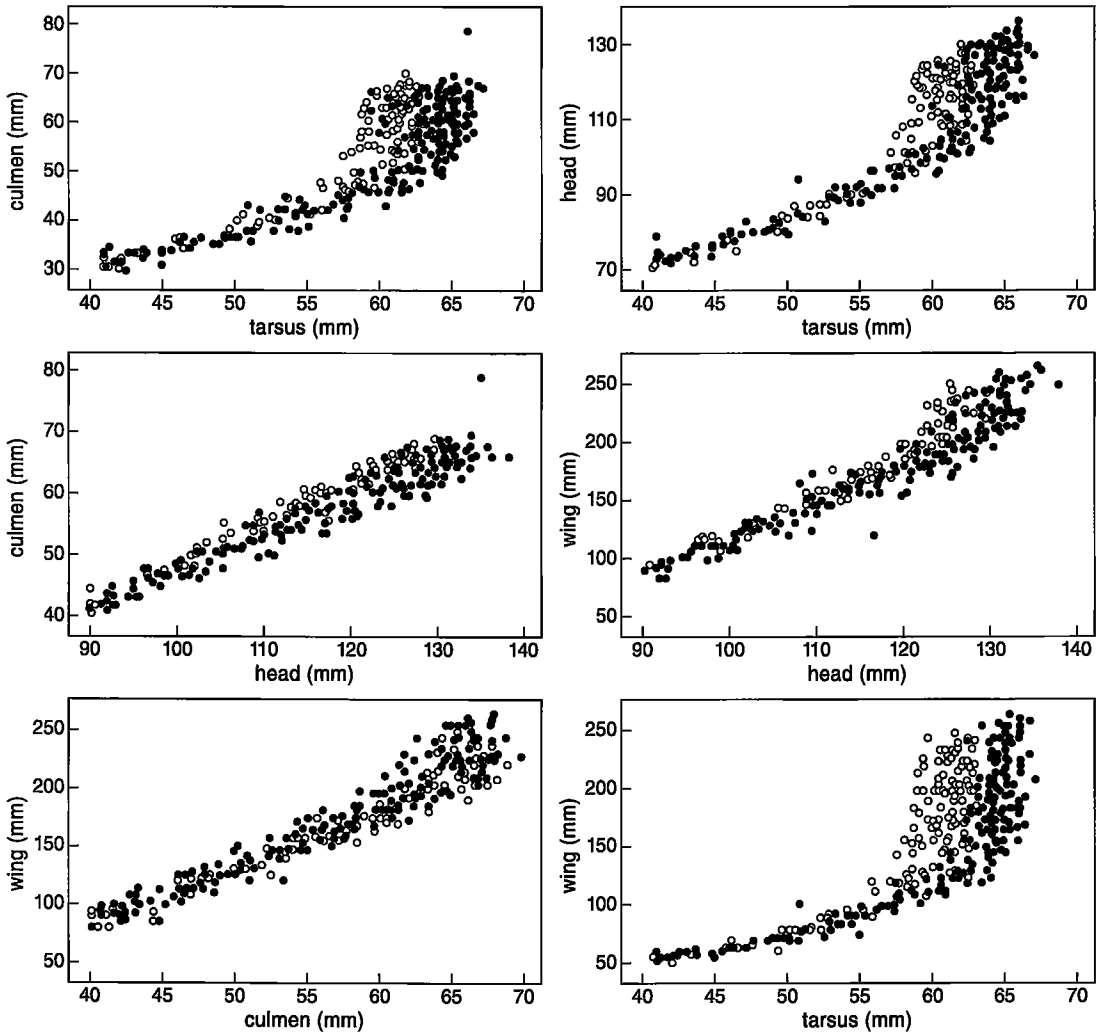
Fig. 1. Bivariate plots of the different morphometric variables measured throughout the growth of 25 male (closed circles) and 18 female (open circles) European Shag chicks sexed using molecular techniques.

RESULTS

Of the 43 chicks sexed for analysis 25 were males and 18 females. The morphometric data compiled throughout the growth period of these birds (Fig. 1), produced discriminant functions to sex the remaining chicks studied. Depending on the variable used differences between the sexes were detected at 15-20 days of age; 95% of the chicks were correctly classified at 25 days and 100% after 30 days (Table 1). A total of 108 chicks were sexed, 65 (30 males and 35 females) using the discriminant function for chicks over 30 days old and 43 using the molecular technique.

Logistic curves were fitted individually for the growth in body mass and morphometric variables pertaining to each chick (Table 2) and for all the chicks of each sex (Fig. 2). Body mass and tarsus
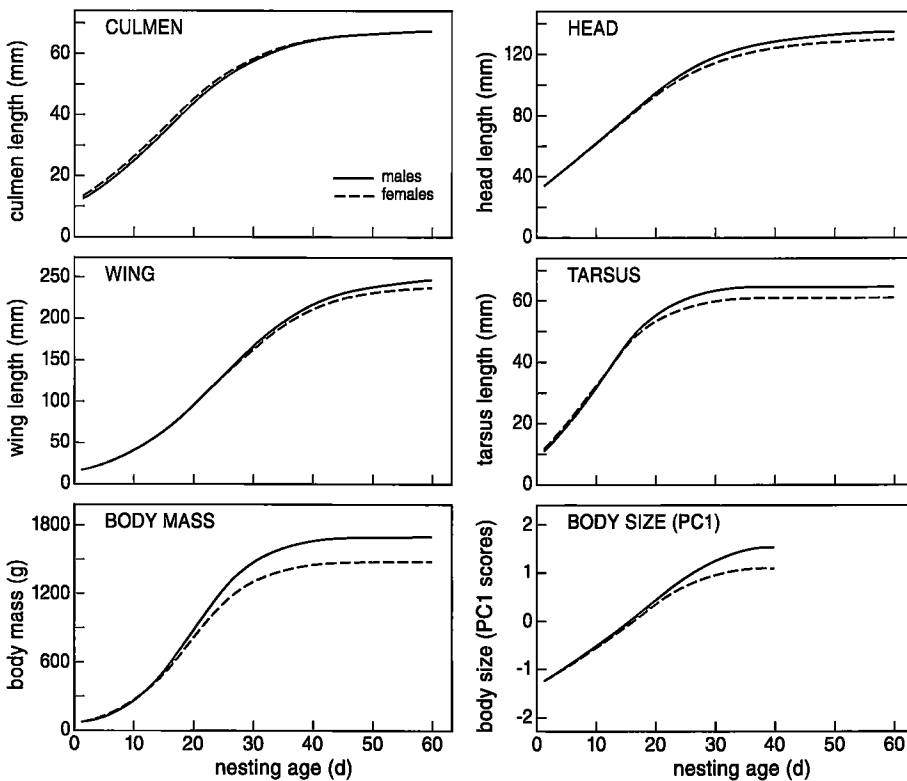
Fig. 2. Comparison of the male (solid line) and female (dashed line) European Shag chicks for the logistic models (see Ricklefs 1968) fitted for the morphometric growth (culmen, head, wing and tarsus length) and body mass and of the cubic polynomial model fitted (up to 40 days of age) to the growth rate of the first principal component (PC1, synoptic variable that describes body size based on different morphometric variables)

length had the greatest growth constant. Culmen and wing length had a similar growth constant while head length had the lowest growth constant.

The culmen length was the only variable in which the growth constant and the asymptotic size did not differ between males and females (Table 2). The head growth constant was also similar between the sexes, but males had display a larger asymptotic size. The growth constants of the wing, tarsus and body mass were greater in females than males, and they therefore reached the asymptote at an earlier age and at a significantly lower level than in males. The growth curves of the tarsus in males and females could be differentiated prior to the age of 20 days, while

differences in body mass were seen at around 20 days of life. Head and wing lengths started to show sex-related differences at 30 and 40 days respectively (Fig. 2). Body mass was significantly greater in males than in females from the age of 15 days ($P < 0.01$) with a difference that ranges from 5.9% at the age of 15 days to 14.8% at 35 days (Table 3). The body sizes estimated for males and females based on the individual models (PC1) could only be differentiated statistically ($P < 0.05$) from age 30 d onwards, with males having a 5% larger size than females.

The maximum instantaneous growth rates (g_{max}) of the culmen, wing and head were similar in the two sexes ($P > 0.05$, Table 2). In contrast,

Table 1. Results of the forward stepwise discriminant analyses carried out for European Shag chicks based on morphometric variables (culmen, head tarsus and wing length in mm) measured throughout the growth period. 25 males and 18 females were previously sexed using molecular biology techniques. Functions are shown for chicks over 25 days of age ($n = 207$, with an average of 4.8 measurements per chick) and 30 days of age ($n = 159$, 3.7 measurements per chick).

Variable	Step	Coefficient	λ	df	P <	%	y^a
Chicks over 25 days of age							
Tarsus	1	0.812	0.30	1, 204	0.0001		
Culmen	2	-0.237	0.27	2, 203	0.0001		
Head	3	0.121	0.25	3, 202	0.0001	97.1	51.447
Chicks over 30 days of age							
Tarsus	1	0.749	0.29	1, 157	0.0001		
Culmen	2	-0.213	0.27	2, 156	0.0001		
Head	3	0.234	0.23	3, 155	0.0001		
Wing	4	-0.018	0.22	4, 154	0.0001	100	59.543

[a]The discriminant functions take the following form: $y = a\,\text{var}_1 + b\,\text{var}_2 + ... + k\,\text{var}_n$, where y is the discriminant coefficient and a, b, ... k are the coefficients of each morphometric variable var_n. The order of entry (step), coefficient of each variable, Wilks' λ statistic and its probability are shown. Additionally the cut-off point (y) is given (chicks classified as males when $y >$ cut-off point and as females when $y <$ cut-off point) and the percentage of cases correctly classified for each function (%).
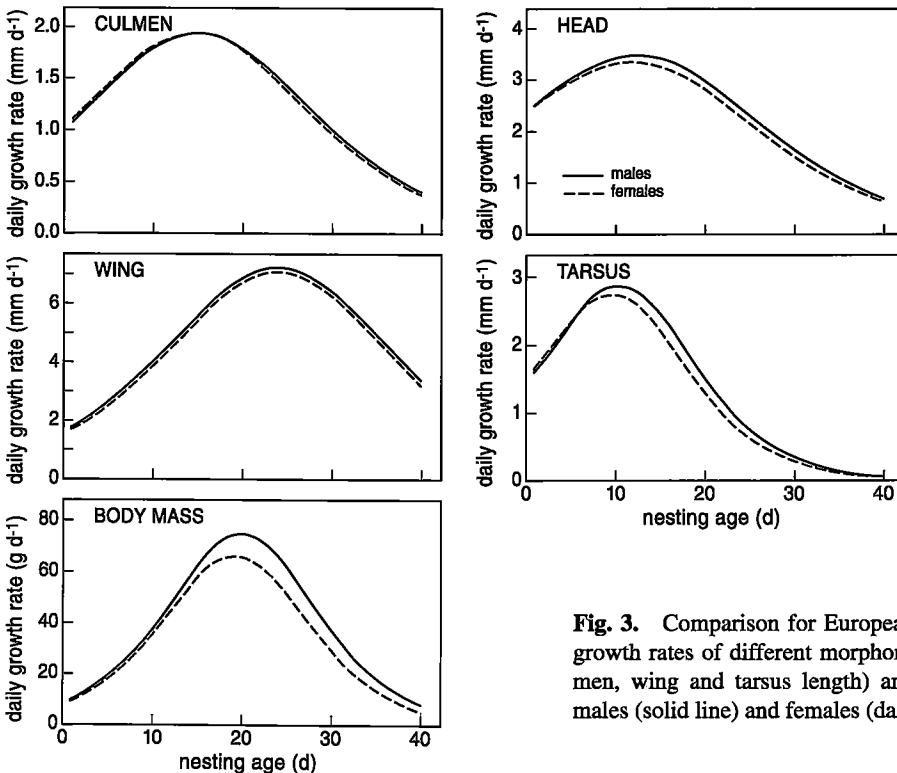

Fig. 3. Comparison for European Shags of the daily growth rates of different morphometric variables (culmen, wing and tarsus length) and the body mass in males (solid line) and females (dashed line).

Table 2. Parameters of the logistic equations (asymptote A, growth constant k, and maximum instantaneous growth rate g_{max}) fitted to describe individual growth in body mass (in g) and of different morphometric variables (in mm) $\pm$ SE of European Shag chicks, obtained from the individual fit to 55 males and 53 females. The significance of t-test used to compare parameters between sexes are indicated (n.s. $= P > 0.05$, * $= P < 0.05$, ** $= P < 0.01$, *** $= P < 0.001$).

	A			k			g_{max}		
	male	female		male	female		male	female	
Culmen	68.3 ± 0.4	68.1 ± 0.4	n.s.	0.114 ± 0.001	0.115 ± 0.001	n.s.	1.94 ± 0.02	1.96 ± 0.01	n.s.
Head	136.3 ± 0.3	130.9 ± 0.5	***	0.103 ± 0.001	0.105 ± 0.002	n.s.	3.44 ± 0.02	3.49 ± 0.06	n.s.
Wing	254.0 ± 1.5	242.8 ± 1.5	***	0.115 ± 0.001	0.118 ± 0.001	**	7.30 ± 0.05	7.20 ± 0.04	n.s.
Tarsus	65.7 ± 0.2	62.0 ± 0.2	***	0.174 ± 0.001	0.178 ± 0.001	*	2.87 ± 0.02	2.76 ± 0.02	***
Body Mass	1722 ± 14	1473 ± 16	***	0.176 ± 0.002	0.184 ± 0.003	**	75.91 ± 0.82	67.73 ± 0.70	***

Table 3. Comparison of body mass and size of male and female chicks ($n = 55$ and 53, respectively) of the European Shag throughout the growth period. The significance of t-test used to compare parameters between sexes are indicated (n.s. $= P > 0.05$, * $= P < 0.05$, ** $= P < 0.01$, *** $= P < 0.001$).

Age in days	Male	Female	
Body Mass (g)[a]			
10	269 ± 2.9	2.63 ± 4.3	n.s.
15	540 ± 7.5	510 ± 8.2	**
20	902 ± 10.5	837 ± 10.9	***
25	1248 ± 11.9	1126 ± 11.1	***
30	1486 ± 12.3	1311 ± 11.5	***
35	1614 ± 12.8	1406 ± 13.0	***
Body Size (PC1 scores)[a]			
10	-0.48 ± 0.01	-0.49 ± 0.02	n.s.
15	-0.01 ± 0.01	-0.02 ± 0.02	n.s.
20	0.48 ± 0.01	0.46 ± 0.02	n.s.
25	0.91 ± 0.02	0.87 ± 0.03	n.s.
30	1.23 ± 0.02	1.17 ± 0.03	*
35	1.39 ± 0.03	1.32 ± 0.04	*

[a]Mean values ± SE are shown every five days, estimated from the growth equations fitted for each chick following a logistic model in the case of body mass and a cubic polynomial model up to 40 days of life in the case of body size (represented by PC1, extracted from a principal component analysis of morphometric variables).

however, this parameter was greater in males than in females for the tarsus and body mass growth ($P < 0.001$). Table 4 presents a comparison between sexes of the individual variability in growth constants and the asymptotic values of body mass and the different morphometric variables. Significant differences ($P < 0.05$) were found between males and females only in the case of the asymptotic size of the head and body mass growth constant. Both of these were more variable in females than in males.

The daily growth rates in head and wing length and body mass were higher in males than females throughout the growth period (Fig. 3). The culmen and tarsus, however, grew faster in females during the first few days. All of the maximum daily increases of the morphometric variables occurred prior to the peak in daily body mass increase, except in the case of the wing. However, no great differences were found between males and females in the timing of the daily increase peaks. Maximum peak of body mass growth occurs in females a day before males, with a difference of 9 g.

DISCUSSION

We used the same method as Richner (1991) to study the sex differences in growth of birds, but

Table 4. The mean value ± SE is presented of the absolute standardised residuals of asymptote (*A*) and growth constant (*k*) of male and female European Shag chicks (*n* = 55 and 53, respectively). The residuals represent the absolute difference between the individual fit for each chick and the overall fit for each sex. The significance of *t*-test used to compare parameters between sexes are indicated (n.s. = *P* > 0.05, * = *P* < 0.05).

	Residuals of *A*			Residuals of *k*		
	Male	Female		Male	Female	
Culmen	0.73 ± 0.09	0.81 ± 0.09	n.s.	0.69 ± 0.09	0.85 ± 0.10	n.s.
Head	0.66 ± 0.08	0.91 ± 0.10	*	0.57 ± 0.09	0.77 ± 0.13	n.s.
Wing	0.82 ± 0.09	0.78 ± 0.09	n.s.	0.73 ± 0.10	0.89 ± 0.08	n.s.
Tarsus	0.83 ± 0.09	0.78 ± 0.08	n.s.	0.70 ± 0.11	0.78 ± 0.09	n.s.
Body Mass	0.74 ± 0.08	0.83 ± 0.09	n.s.	0.63 ± 0.08	0.89 ± 0.10	*

we came to a different conclusion. In his review of sex-specific growth of dimorphic birds he reported that most birds have a similar growth rate and reach the asymptote at the same age, yet his study lacked statistical tests. In our study we found significant differences in growth dynamics between the sexes.

Males had a greater asymptote in body mass and all the morphometric variables, except culmen, than females. The lack of an asymptotic size difference between the sexes in the culmen may be attributed to the feeding habits of the European Shag. Shags use their bill like a pair of tweezers to capture fish (Lumsden & Haddow 1946).

Throughout the season fish of 10 cm in length are consumed by both males and females (Velando & Freire 1999), the lack of a sex-difference being in accordance with the lack of sexual dimorphism in bill size (see Calvo & Bolton 1997).

We found clear differences between the sexes in the growth constants of European Shags, particularly during the early stages of growth. Using both the growth constant (*k*) and the maximum instantaneous growth rate (g_{max}), it is possible to compare growth between the sexes (Richner 1991, see his Fig. 1). When g_{max} is less in the smaller sex and both sexes reach asymptotic size at the same age, k is similar in both sexes. If g_{max} is similar in both sexes, but the smaller sex has a greater *k* value, then the smaller sex reaches the asymp-

tote slightly earlier due to a faster early growth but the inflection point occurs at the same age. When the smaller sex has higher values of g_{max} and *k*, it grows faster and the inflection point occurs earlier, with the asymptote being reached much earlier. Finally, the smaller sex may have a greater *k* value but a smaller g_{max} in which case the asymptote is reached after the larger sex, but growth is similar during the early stages.

In the European Shag we found that females reached asymptotic size in head length and wing length, slightly earlier than males (Table 2). Thus, for head length both sexes had similar *k* and g_{max} values. The wings grow faster in females, but have the same instantaneous rate at the inflection point. In tarsus length and mass, females reached the asymptote at the same time or slightly later than males but growth in the early stages was similar. Moreover in females, the tarsus and mass had a maximum peak in daily increase one day earlier than males and the daily growth rates of the tarsus and culmen were slightly higher during the first few days (Fig. 3). The differences between the sexes in body mass were already established at the age of 15 days, but it was not until the day 30 that they were evident in body size (PC1). Thus in the early stages of growth females were similar in size to males while weighing less (Table 3).

In the European Shag, body mass growth rate had the widest individual variability in females, the smaller sex. In the Bald Eagle *Haliaetus leu-*

cocephalus and Osprey *Pandion haliaetus* nestlings (Bortolotti 1986; Schaad & Bird 1993), the male is the smaller sex and also showed the greatest variability. The lower variability in the growth rate of the larger, more demanding sex would appear to contradict their higher -energy requirements (Cooch *et al.* 1996). However, the results could be biased because only surviving nestlings were included. If variability in growth affects males more than females, then males having low growth rates would have a lower survival rate than females and would not be included in the variability estimation. Therefore, in order to determine the effect of variability on the growth and mortality rates of each sex it would be necessary to carry out experiments in which food availability is manipulated.

In a pelecaniform bird, the Blue-Footed Booby *Sula nebouxii*, the hierarchy between siblings is established during the early stages of growth, with the first hatched dominant, regardless of whether the smaller sex occupies the first or second position (Drummond *et al.* 1991; 1992). In European Shags hatching asynchrony is the most important factor affecting the hierarchy in the brood (Stockland & Amundsen 1988). In experimental 'doubly-asynchronous' broods, chicks suffered a reduced growth rate and higher mortality (Amundsen & Stockland 1988). In the Cíes Islands many chick died occurred during each of the four years of the study (Velando *et al.* 1999). In the early stages of growth the larger chick successfully completed for meals (Velando 1997). The first hatched chick has more advantages, and the differences in growth dynamics in European Shag chicks would suggest that females have the same competitive ability as males and that the hierarchy in the early stages of growth would be contingent upon hatching order and not sex.

ACKNOWLEDGEMENTS

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SAMENVATTING

Bij de Kuifaalscholver *Stictocarbo aristotelis* zijn mannetjes 22% zwaarder dan vrouwtjes. In dit artikel wordt gedetailleerd beschreven hoe deze grootteverschillen tussen mannetjes en vrouwtjes tijdens de groei tot stand komen. Omdat bij kuifaalscholverkuikens de sexen in eerste instantie niet uit elkaar te halen zijn, werd bij 43 kuikens afkomstig van kolonies op de Cíes Eilanden (Noordwest-Spanje) de sexe bepaald op grond van een DNA-test. Bij deze kuikens werd om de paar dagen de snavellengte, de totale koplengte, de vleugellengte, de lengte van de tarsus en het lichaamsgewicht gemeten. Vervolgens werd met behulp van discriminant analyses gekeken op welke leeftijd de afmetingen van mannetjes en vrouwtjes uit elkaar begonnen te lopen. Bij kuikens van 25 dagen waren de grootteverschillen tussen mannetjes en vrouwtjes reeds zodanig dat in meer dan 95% van de gevallen, de zogenaamde discriminant functie op grond van de afmetingen de sexe correct voorspelde. Bij een leeftijd van 30 dagen was het onderscheid compleet. De gegevens over de groei van de verschillende lengtematen en het gewicht werden samengevat met behulp van logistische groeivergelijkingen. De snavellengte van volgroeide Kuifaalscholvers verschilde niet tussen de sexen, en ook het groeipatroon was gelijk. De totale koplengte van mannetjes was groter dan die van vrouwtjes, maar er was geen verschil in groeisnelheid. Hoewel de uiteindelijke vleugel- en tarsuslengte en het lichaamsgewicht van vrouwtjes kleiner waren dan die van mannetjes, was de groeisnelheid bij vrouwtjes groter. De eerste principale component van de lichaamsmaten (PC1) kan beschouwd worden als de meest algemene maat voor de lichaamsgrootte. Het lichaamsgewicht van mannetjes en vrouwtjes begon al op een leeftijd van 15 dagen uit elkaar te lopen, maar dat was bij de PC1 pas op een leeftijd van 30 dagen het geval. Dit suggereert dat hoewel vrouwtjes uiteindelijk kleiner van stuk blijven dan mannetjes, ze met hun vergelijkbare lichaamsgrootte in het nest 'hun mannetje kunnen staan' als het gaat om het veroveren van het aangebracht voer waar ze met hun broertjes om moeten knokken. (TP)