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Allometry as evidence of sexual selection in monochromatic birds: the case of the Coscoroba Swan (Anseriformes: Anatidae)

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ABSTRACT. The Coscoroba Swan, *Coscoroba coscoroba* (Molina, 1782), is a poorly known aberrant Anserine endemic to South America. We captured adult birds (189 male, 157 female) from the largest population in Brazil at the Taim Ecological Reserve, State of Rio Grande do Sul, Brazil. Different patterns between sexes can reflect differences in selection, and positive allometry may indicate that a character is sexually selected. We used body weight and 10 morphological measurements to examine allometric differences between males and females of *C. coscoroba*. Males were consistently larger than females. Analysis of scaling relationships against body mass showed that nostril, tail, wing and bill height were positively allometric (i.e., heavier birds had relatively larger character lengths), but there were no sexual differences in allometric slopes. However, for a given mass, mature females had longer tails, longer wings (up to metacarpophalangeal articulation) and shorter heads than males. In the light of current debate in the literature, we discuss whether such positively allometric traits and sexual differences in scaling may be indicative of sexual selection. Although Coscoroba Swan is a monogamous species, increasing the size of some attributes may confer some advantage for mate selection or male-male competition and, contrary to other studies, we suggest that positively allometric slopes alone should not be considered as evidence for sexual selection of the considered traits.

KEY WORDS. Monomorphic; natural selection; waterfowl, scaling.

The "allometry" or "scaling" of morphological characters in vertebrates has long been a subject of interest (Gould 1966, Reiss 1991). However, we still have relatively little understanding of the relationship between static allometry, or variation in shape among individuals of the same species and developmental stage, and sexual dimorphism (Green 2000, Bonduriansky 2007, Cuervo & Møller 2009). Using standard morphological measurements, the relative variation of each character in relation to a reference body size measurement may be compared in order to examine scaling patterns within and between sexes. Characters subjected to strong sexual selection in a given sex are expected to be exaggerated in size, leading to sexual dimorphism, but are also likely to be positively allometric (i.e., larger individuals have even larger attributes than expected from their body size – Green 1992, 2000, Kodric-Brown *et al.* 2006).

Recent studies have indicated that positive allometry does not seem to be a reliable indicator of sexual selection and have shown variable scaling relationships for characters thought to be sexually selected (e.g., Bonduriansky 2007, Cuervo & Møller 2009). In fact, the scaling parameter for a certain character reflects the trade-offs between resource allocation, natural selection and sexual selection, and thus directional selection of sexual traits does not necessarily lead to positive allometry (Bonduriansky 2007). However, more studies on scaling relationships for traits lacking extreme exaggeration are necessary in order to evaluate the connection among relative variation of morphological traits, functional responses and evolutionary consequences, both for secondary sexual and non-sexual characters (Bonduriansky 2007).

The Coscoroba Swan, *Coscoroba coscoroba* (Molina, 1782) is unusual among the Anatidae in South America, and is found from the Falkland Islands and Tierra del Fuego north through Chile and Argentina, Uruguay and southern Brazil and Paraguay (Kear 2005). The Coscoroba is traditionally considered to be a swan, but molecular studies suggest it is more closely related to the aberrant Cape Barren goose, *Cereopsis novaehollandiae* Latham, 1802 (see Donne-Goussé *et al.* 2002). It is monochromatic, but males are generally larger than females (see below and Calabuig *et al.* 2011).

In monogamous species, such as the *C. coscoroba*, sexual dimorphism is often less exaggerated than in related polygamous species (e.g., Figuerola & Green 2000, Horrocks *et al.* 2009). Yet, in species with high levels of parental care and variability in quality of partners, mutual mate choice is typically important (Clutton-Brock & Vincent 1991, Clutton-Brock & Parker 1992, Johnstone *et al.* 1996, Kraaijeveld *et al.* 2004). Like true swans, the Coscoroba Swan displays high levels of parental care, but unlike true swans (Kraaijeveld *et al.* 2004) it does not have obvious secondary sexual characteristics, and very little is known about the ecology of the species (see Kear 2005, Calabuig *et al.* 2010).

The objective of this study was to investigate the relationship between sexual dimorphism and static allometry in the Coscoroba, in particular: a) to identify characters that were sexually dimorphic, before and after controlling for general structural size, and b) to compare allometric slopes for different characters between the sexes, and to identify positively allometric characters. We also examine the role that sexual selection may have in explaining our results.

MATERIAL AND METHODS

All individuals were captured at the "Estação Ecológica do Taim" Reserve which is located in the southern coastal plain of Brazil (~32°33'S, 52°32'W) within the most important area for Coscoroba Swan in Brazil. Birds were captured by hand, from a boat, in 2005, 2006, 2007, and 2008, during the wing moult period (between August and January), when they are flightless. All the individuals considered in our analysis were mature (>2 years old). We captured 346 individuals (189 males, 157 females).

We weighed the birds (50 g precision) and measured 10 morphological variables. Total length of head to the occipital-tip of the bill (TLH), maximum height of the bill (HBI), maximum width of the bill (WBI), nostril (distal edge of a nostril to the end of the bill), total culmen (TCU) and tarsus length were measured with a calliper (± 0.1 mm). Tail (from the preen gland), wing without the feathers (metacarpophalangeal articulation), forearm length from the front of the folded wrist to the proximal extremity of the ulna (Ferrer & De le Court 1992) and length of neck (LNE) were measured with a ruler marked in millimetres.

Before releasing, the tarsus of each animal was marked with a numbered, metal ring (rings from Centro Nacional de Pesquisa para Conservação das Aves Silvestres – Instituto Chico Mendes de Conservação da Biodiversidade (CEMAVE-ICMBio)).

Three milliliters of blood were taken from the wing vein of each bird, (using plastic 3 ml syringes equipped with 21-ga needles) and samples were stored in Vacutainer tubes with EDTA and kept cool in ice, until processing. We used molecular methods to determine the sex of each specimen (see Calabuig *et al.* 2011 for details).

To compare sexes, we used all 11 morphological variables in a multivariate ANOVA (MANOVA). We used residuals from each analysis to check the normality assumption. None of the 11 variables showed significant deviation from normality according to the Kolmogorov-Smirnoff test with Lilliefor's correction, or from homogeneity of variance tested with Levene's test. Consequently, no transformations were used.

Length of neck (LNE) was excluded from further analyses due to a large measurement error. Following the standard approach in scaling studies (e.g., Green *et al.* 2001, Warton *et al.* 2006, Arnold & Green 2007, Peig & Green 2009), the allometric slopes of each linear measure in relation to mass were calculated using reduced major axis (RMA, also known as standardised major axis or SMA) regression models to place the line of best fit in bivariate plots of log transformed data. The results of ordinary least squares regression (OLS) and RMA regressions are increasingly divergent as r decreases, and slopes become seriously underestimated by OLS methods (McArdle 1988, Warton *et al.* 2006, Arnold & Green 2007). The RMA slope is equal to the ratio between the standard deviations of Y and X (and also to the OLS slope divided by r). See McArdle (1988) for methods used to calculate the statistical significance of the deviation between observed RMA slopes and those expected under the null hypothesis of isometry. For the purpose of this paper, we consider isometry to be where, in log-log bivariate plots, linear measures scale with a slope of one third against mass (i.e., mass is proportional to the cube of length). Since slopes did not differ significantly between males and females (see below), sexual differences in elevation (i.e., intercepts) were tested by comparing the means of the residual scores for each sex from a common RMA regression slope (see Warton *et al.* 2006). This constituted a test for a difference between sexes in the relative size of different characters. We preferred this test to least-squares methods such as ANCOVA owing to the existence of error in both dependent and predictor variables (see Warton *et al.* 2006).

Statistical analyses were carried out with Statistica 6.0 software (Statsoft Inc., Tulsa). Differences were considered significant at $p < 0.05$.

RESULTS

Using all variables in a MANOVA, adult male swans are larger than adult females (Wilks = 0.29, F = 77.7, $p < 0.01$). Values of body mass and all linear measures were significantly higher for males than females (Table I). TLH, tarsus and forearm were the most sexually dimorphic characters in terms of statistical significance.

RMA regression with body weight, nostril, wing and tail length showed significant positive allometry for both sexes (Table II and Figs 1-3). For mature males, HBI also showed significant positive allometry. However, no significant difference was observed in allometric slopes between the sexes for any morphometric measures (Table II).

When common slopes were fitted for all mature birds in regressions of linear measures on body mass, there were differences in elevation between sexes for three measures. For a given body mass, females had lower TLH but longer wings and longer tails (Table III, Figs 2 and 3).

DISCUSSION

Our results indicate interesting deviations from isometry in *C. coscoroba*, with nostrils, tails and wings showing positive allometry. Important differences in scaling relationships were also found among females and males. For a given body mass, the wing and tail of females were relatively larger, whereas their heads were comparatively shorter. All morphometric measurements showed a clear dimorphism according to gender and followed a size gradient in which male characters were, on average, larger than their corresponding female counterparts.

Miller *et al.* (1988) suggested for Tundra swans, *Cygnus columbianus* (Ord, 1815) that similar dimorphism among adult birds is the result of selection for large body size in males. In general, large size may be selected in male swans, geese and the Cape Barren Goose because they are responsible for nest protection (e.g., Scott 1972,Veselovsky 1973, Hawkins 1986, Whitehead & Tschirner 1990) or owing to the need to defend females against extra-pair copulations (e.g. Mineau & Cooke 1979, McKinney *et al.* 1983, Welsh & Sedinger 1990, Gauthier & Tardif 1991, Choinière & Gauthier 1995). As in the Cape Barren goose, male and female coscorobas form long-term pair bonds

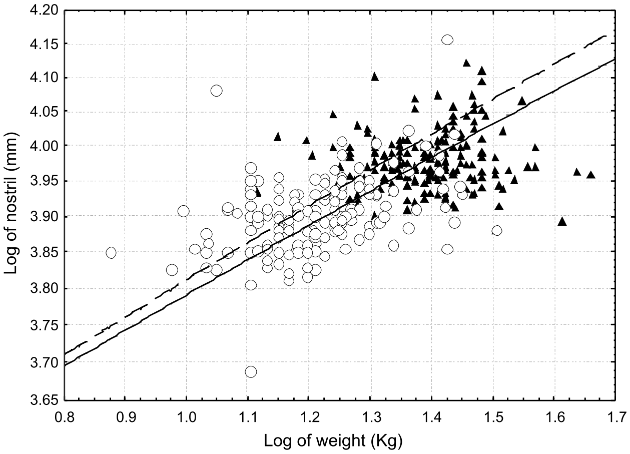

Figure 1. Nostril length against mass (log$_e$ transformed) for male and female Coscorobas. Scaling lines are plotted for both sexes using RMA regression (females: y = 3.3+0.512*x, males: y = 3.31+0.481*x). The slopes and elevations were not different between sexes (Tables II and III). (○) Females, (▲) males.

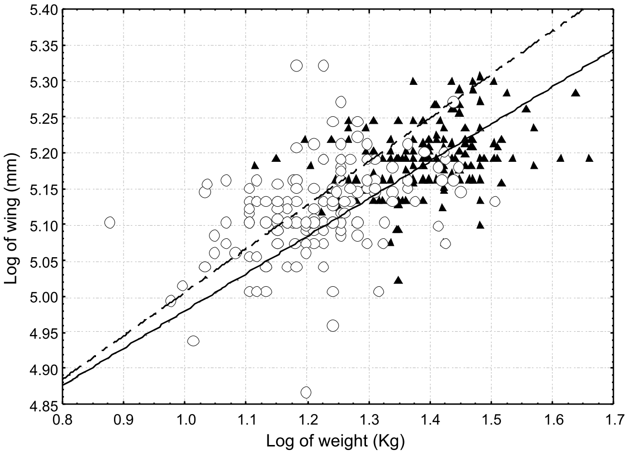

Figure 2. Wing length (tip to metacarpophalangeal articulation) against mass (log$_e$ transformed) for male and female Coscoroba swans. Scaling lines are plotted for both sexes using RMA regression (females: y = 4.4+0.606*x, males: y = 4.46+0.52*x). The slopes were not significantly different (Table II), but elevation was significantly greater for females ($p < 0.01$, Table III). (○) Females, (▲) males.

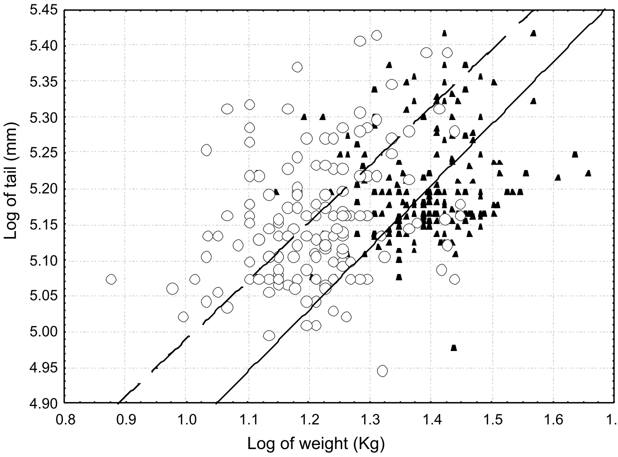

Figure 3. Tail length against mass (log$_e$ transformed) for male and female Coscoroba swans. Scaling lines are plotted for both sexes using RMA regression (female: y = 4.11+0.87*x, males: y = 4.07+0.811*x). The slopes were not significantly different, but elevation was significantly greater for females ($p < 0.001$, Table III). (○) Females, (▲) males.

Table I. Means, standard errors and sample sizes for body mass (kg) plus ten morphometric variables (in mm) for the Coscoroba Swan according to sex. Results for univariate ANOVAs between sexes for each measurement are also shown.

	Combined		Male			Female			ANOVAs		
Variable	Mean	SE	Mean	SE	N	Mean	SE	N	F	df	p
MASS	3.7	0.03	4.0	0.03	188	3.3	0.03	154	288.5	1, 340	<0.01
TCU	68.8	0.20	70.9	0.20	189	66.1	0.24	156	252.0	1, 343	<0.01
NOSTRIL	51.8	0.17	53.5	0.17	189	49.7	0.22	156	201.7	1, 343	<0.01
HBI	25.3	0.08	26.1	0.09	188	24.3	0.10	156	196.5	1, 342	<0.01
WBI	30.0	0.06	30.7	0.06	189	29.1	0.08	156	244.8	1, 343	<0.01
TLH	136.0	0.29	139.9	0.21	189	131.1	0.27	157	736.7	1, 344	<0.01
TARSUS	101.0	0.35	105.3	0.29	189	95.6	0.35	156	477.5	1, 343	<0.01
WING	174.6	0.62	179.9	0.61	188	167.9	0.91	157	133.9	1, 343	<0.01
FOREARM	206.1	0.61	213.1	0.58	188	197.5	0.67	157	337.3	1, 343	<0.01
TAIL	178.4	0.83	181.9	0.99	187	173.5	1.26	152	19.4	1, 337	<0.01
LNE	336.0	1.45	351.0	1.58	187	317.9	1.66	156	205.7	1, 341	<0.01

Table II. Scaling of mature Coscoroba Swan morphometric measurements against body mass using Reduced Major Axis (RMA) regression. The deviation of the RMA slope from that expected under isometry (1/3) was tested for statistical significance for each measurement and sex (T_1, T_2) as well as slope difference between sexes ($T_{1,2}$).

Measurement	Females (N = 154)				Males (N = 188)				Female vs Male slopes	
	RMA slope	R^2	Intercept	T_1	RMA slope	r^2	Intercept	T_2	$T_{1,2}$	p
TCU	0.405	0.138	3.70	1.00	0.439	0.009	3.65	1.45	0.34	0.210
Nostril	0.512	0.160	3.30	2.36**	0.481	0.007	3.31	2.02*	0.30	0.142
HBI[1,2]	0.478	0.050	2.60	1.85	0.514	0.018	2.55	2.48**	0.33	0.760
WBI[1]	0.305	0.189	3.00	0.34	0.314	0.132	2.98	-0.28	0.05	0.595
TLH	0.232	0.232	4.60	1.38	0.230	0.080	4.62	-1.47	0.03	0.151
Tarsus	0.423	0.118	4.04	1.08	0.419	0.060	4.07	1.21	0.03	0.570
Wing[2]	0.606	0.164	4.40	3.69***	0.520	0.103	4.46	6.68***	0.86	0.572
Forearm[2]	0.388	0.152	4.82	1.17	0.413	0.068	4.80	1.13	0.25	0.438
Tail[1,2]	0.867	0.084	4.11	6.85***	0.811	0.035	4.07	6.60***	0.54	0.884

[1]for females, N = 153; [2] for males, N = 187; Both body mass and the linear measure were $\log_e$ transformed. The deviation of the RMA slope from that expected under isometry (1/3) was tested for statistical significance, as was the difference between slopes for the two sexes (*$p < 0,05$, ** $p < 0.01$, *** $p < 0.001$).

Table III. Differences in elevation between sexes of mature Coscoroba Swan for Reduced Major Axis (RMA) regression of morphometric measurement against body mass ($\log_e$ transformed). Differences between the sexes in the residuals for a common regression line were tested using a t-test (after Warton *et al.* 2006).

RMA regression		Residuals						
		Males			Females			
Variable (log)	Y = Intercept +β*X	Mean	SE	N	Mean	SE	N	t-value
TCU	Y = 3.7+0.406*X	-0.001	0.004	188	0.002	0.004	154	0.54
NOSTRIL	Y = 3.34+0.462*X	-0.003	0.004	188	0.005	0.005	154	1.30
HBI	Y = 2.64+0.451*X	-0.003	0.004	187	0.006	0.005	153	1.47
WBI	Y = 3.01+0.296*X	-0.001	0.002	188	0.002	0.003	153	0.71
TLH	Y = 4.52+0.296*X	0.006	0.002	188	-0.006	0.002	154	3.84***
TARSUS	Y = 3.99+0.476*X	0.003	0.004	188	-0.007	0.004	154	1.83
WING	Y = 4.52+0.489*X	-0.009	0.004	187	0.009	0.005	154	2.93**
FOREARM	Y = 4.79+0.409*X	0.003	0.003	187	-0.001	0.004	154	0.61
TAIL	Y = 4.36+0.625*X	-0.032	0.006	186	0.040	0.008	150	7.53***

** $p < 0.01$, *** $p < 0.001$.

and look after their goslings. The male is primarily a guardian and helps with nest building but not with incubation.

Positive allometry is most likely to evolve when an increase in relative trait size leads to a greater mating success for larger individuals (Bonduriansky 2007). Dimorphic, sexually selected characters tend to have positively allometric slopes (Green 1992, Kodric-Brown *et al.* 2006). Thus, scaling relationships have been proposed as a potential means to distinguish between sexual and natural selection as causes of dimorphism (Green 2000).

However, according to more recent research, a link between sexual selection and positive allometry only seems clear for exaggerated sexual characters (e.g., tails of peacocks or widowbirds) of the kind absent in Coscoroba swans. A recent review of less extreme secondary sexual characters suggested that sexual selection does not consistently result in positive allometry, and that nonsexual traits sometimes show positive allometry (Bonduriansky 2007). Various mechanisms have been proposed which could generate such a wide diversity of allometries for both sexual and non-sexual characters, although there is currently a general lack of empirical data to distinguish between them (Bonduriansky 2007). Cuervo & Møller (2009) showed that ornamental feathers tend to have particularly high allometric slopes. However, non-ornamental tail feathers also tended to be positively allometric (although to a lesser extent), and Cuervo & Møller (2009) support the view of Bonduriansky (2007) that positive allometry should not be considered as diagnostic of a sexually selected character.

This study extends the currently limited knowledge on scaling patterns in Anatidae (Green 2000, Green *et al.* 2001) and shows that positive allometry can be observed in monomorphic species in characters which have never been considered as ornaments. The limited data available suggests that, amongst the Anatidae, allometries do not appear to show consistent patterns. For example, head length is isometric in the Coscoroba Swan, negatively allometric in the Eurasian Teal *Anas crecca* Linnaeus, 1758 (Green *et al.* 2001), and positively allometric in male Marbled Teal, *Marmaronetta angustirostris* (Ménétries, 1832) (Green 2000).

There is little evidence available from field studies to assess the role of sexual selection in explaining the limited sexual dimorphism and positive allometry recorded in the Coscoroba Swan. Although this is a monogamous species, increasing the size of some attributes may confer some advantage for mate selection or male-male competition. The tail appears crucial when pivoting and to enable the "up-ending" or "tipping" feeding technique regularly used by this species, but it may also be a sexually selected character important for signalling. Wings are used in male-male combat (authors, pers. obs.) but wing growth is most likely to be constrained by the biomechanics of flight. Across the Anatidae, folded wing (a different measure of wing than ours) shows positive interspecific allometry (Green *et al.* 2001), as does wingspan for all flying birds (Rayner 1985). This is consistent with a possible biomechanical explanation for the positive allometry for wing in Coscoroba. Tail morphology may also be an adaptation to biomechanics (Matyjasiak *et al.* 2009).

Although female Coscoroba swans have relatively longer wings and tails for a given mass, we have no other reason to believe they are subject to greater sexual selection than males. The measures of nostril and height of the bill should mainly reflect bill adaptations for feeding (see Ferns *et al.* 2005), although the bill may also have a significant courtship role since the Coscoroba Swan has displays based on head movements (see Horrocks *et al.* 2009), and perhaps breathing during flight might influence bill morphology. However, further research is required to establish the importance of the different characters addressed in this study for mate choice, foraging ecology etc in this species.

We used body mass as an overall measure of structural size (Peig & Green 2009), but mass typically changes during wing moult, increasing in some Anatidae but decreasing in others (Hohman *et al.* 1992).There is no information as yet on seasonal changes in body mass in Coscoroba Swan. Such changes can even vary between the sexes (Hohman *et al.* 1992), such that it is feasible that our analyses of elevation (Table III) would give different results at a different stage of the annual cycle. However, the finding that females have relatively shorter heads compared with their wings and tails would not change.

Contrary to Green (2000), we suggest that positively allometric slopes alone should not be considered as evidence for sexual selection of the considered traits. Nevertheless, more studies such as ours are required before we can begin to understand the conditions that generate negative allometry, positive allometry or isometry in birds (see Bonduriansky 2007, Cuervo & Møller 2009 for more discussion).

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