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Isometric beak morphology in *Phoenicopterus ruber roseus*, Phoenicopteriformes

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ABSTRACT   It is well documented that size of various body parts tends to correlate within the same individual. In the current study, we explore the relationship between body weight and some area and lineal beak measurements in a sample of 17 corpses of Greater flamingo *Phoenicopterus ruber roseus* (10 immatures and 7 adults), collected and after obtaining beak radiographic latero-lateral projections. On images, the following traits were obtained: area of rhinotheca –the sheath covering the maxilla- and gnathotheca –the sheath covering the mandibular-, rhamphotheca height, ocular area, ocular height, ocular width, height, width and area of nares. Our results suggest that some beak measurements are positively correlated with body weight, while nostril area is not. Specifically, rhinotheca and gnathotheca areas and rhamphotheca height were strongly coupled and largely correlated to body weight. The observed differences in beak dimensions are merely a consequence of body weight difference. It is suggested, that the cranial skeleton and musculature are closely linked at least developmentally, allowing for efficient functional integration, but genetic and functional tests must have been performed to reveal the exact nature of the flamingo beak change.
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Introduction

Bird beaks are relevant for foraging, parental care and singing (Shao et al. 2016) and being a highly malleable structure, it permits birds to adapt to different requirements (van Hemert et al. 2012) (Cheng et al. 2017).

The Greater flamingo (*Phoenicopterus ruber roseus*) is a species of the flamingo family. With its bent bill it filters out small shrimp, seeds, algae, plankton, tiny fish, fly larvae and mollusks (Zweers et al. 1995) (Deville et al. 2013). Its beak has a filter-like structure to remove food from the water before the liquid is expelled (Zweers et al. 1995), being the upper jaw movable and not rigidly fixed to its skull.

It is well documented that size of various body parts tends to correlate within the same individual. Although literature on beak morphology for Greater flamingo is abundant (Mascitti and Kravetz 2002) in the current study, we explore the relationship between body weight and some area and lineal beak measurements. We explore its beak structure employing an unusual tool, e.g., radiographic projection on which we obtained classical lineal measurements. The advantage of classical measurements is that they are obtained rapidly and that they can be taken on every parts of the body. This study offers a unique opportunity to understand how bill change arises in Greater flamingo. Here, we complement existing data on its external morphology and provide baseline data needed to understand the developmental mechanisms driving the observed changes.

Materials and methods

A sample of 17 corpses of *Phoenicopterus ruber roseus* (10 immatures and 7 adults), collected in one of the known breeding colonies of the species (Parc Natural del Delta de l'Ebre; Ebro Delta Natural Park, South Catalonia, Spain), were obtained from its wildlife recuperation center. After obtaining the body weight of each fresh corpse (BW), radiographic latero-lateral projections were obtained and the following traits were obtained with the Digimizer version 4.6.1 software (available at www.digimizer.com) on the rhamphotheca (beak): area of rhinotheca (the sheath covering the maxilla), area of gnathotheca (the sheath covering the mandibular), height of rhamphotheca, ocular area, ocular height, ocular width, height, width and area of nares (Fig. 1). A Multivariate Analysis of Variance (MANOVA) test was done to detect differences between immature and adult animals. A Principal Components Analysis (PCA) from var-covar matrix was done to gener-

Table 1. Main descriptive statistics. Body weight in kg. The rest of values in cm or cm^2.

	Body weight	Area of rhinotheca	Area of gnathohteca	Height of rhamphotheca	Ocular area	Ocular height	Ocular width	Area of nares	Height of nares	Width of nares
W	0.951	0.950	0.903	0.944	0.954	0.974	0.919	0.953	0.933	0.936
P	0.476	0.457	0.077	0.362	0.518	0.888	0.143	0.508	0.246	0.272
Min	0.83	12.85	18.45	2.91	1.90	1.48	1.39	1.19	0.61	2.51
Max	3.40	18.49	34.71	4.43	2.60	1.88	1.82	2.04	0.81	3.31
Mean	1.85	16.37	26.08	3.73	2.26	1.68	1.67	1.59	0.70	2.84
Stand. dev.	0.59	1.58	3.29	0.33	0.22	0.12	0.10	0.21	0.06	0.24
Std. error	0.14	0.38	0.80	0.08	0.05	0.03	0.02	0.05	0.02	0.06
CV (%)	31.98	9.68	12.60	8.84	9.87	7.16	6.08	13.03	8.91	8.49

W: Shapiro-Wilk's *W*, CV: Coefficient of Variation

ate a morphospace of beak shape variation.

Data analysis were performed with PAST version 2.17c software (Hammer et al. 2001). Classical morphological measurements were transformed into log-shape ratios in order to control for the size effect on the body parts measured (Cardini and Polly 2013). Following this method, the overall size of each individual was defined as the mean of the log transformed measurements. Each measurement was then standardized by subtracting the overall size of the individual to the log-transformed measured value, and Pearson's correlation was applied (Bookstein 1991). Allometry was studied regressing body weight against normalized data.

Results and discussion

As no statistical differences appeared between immatures and adults (Wilk's $\lambda = 0.191$, p = 0.245), values were mixes for ulterior analysis. Main descriptive statistics appear in Table 1 and correlation coefficients in Table 2.

Our results suggest that some beak measurements are positively correlated with body weight, while nostril area is not. Specifically, rhinotheca and gnathotheca areas and rhamphotheca height, were strongly coupled, and largely correlated to body weight. This relationship means that beak size is highly constrained to evolve in the particular way of body weight. Similar to the present findings, Palacios and Tubaro (2000) demonstrated a positive correlation between body mass and beak length in woodcreepers. Similarly, Clegg and Owens (2002) found that there was a significant general trend toward heavier BW with larger bill size in island-dwelling birds. By contrast, Laiolo and Rolando (2003) reported no significant correlations between BW and bill size in 28 species of crow. The different findings may relate to between-species differences in foraging and beak functionality. In fact, among wild birds, body weight and beak size may found related to competition, adaptation, or both (Fahey et al. 2007).

Furthermore, beak mandibular area evolves cohesively with ocular dimensions. Size is also an important consideration when assessing ocular area variation. Larger flamingos would have access to larger feed volumes due to their increased gape and greater absolute muscular power, and size is further related to morphology via allometry, e.g., the tendency of traits to vary with size throughout a morphological structure. In fact, allometry has been demonstrated as a key contributing factor to craniofacial form across a range of animal groups. Moreover, our results reconsider the view that the beak and braincase act as independent modules. When the configurations are divided in subsets that separately the beak and the ocular conformations, we find that orbitary socket morphology is more conservative (less variable) than the beak.

To assess the effect of allometric (size) signal in our dataset we conducted a PCA on the residuals of the regression
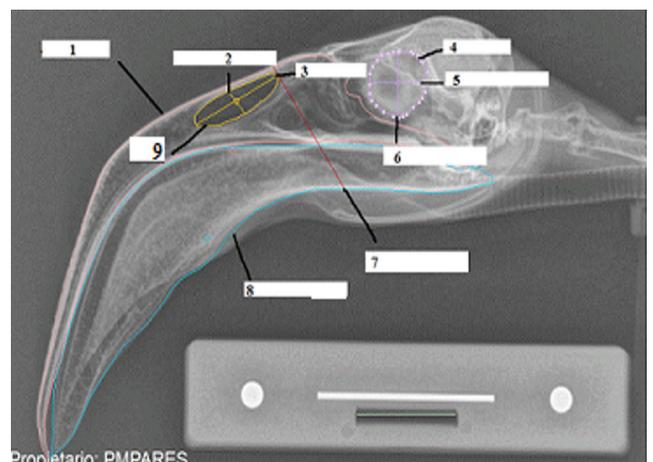
Figure 1. Measurements on the rhamphotheca (beak): area of rhinotheca (1), height (2) and width (3) of nares, ocular area (4), ocular width (5) and height (6), height of rhamphotheca (7), area of gnathotheca (8) and area of nares (9).

Table 2. Correlation values for analyzed traits. Pearson's coefficients appear under the diagonal, *p*-values above. Significative values appear in bold. Bonferroni corrected values.

	Body weight	Area of rhinotheca	Area of gna-thohteca	Height of rham-photheca	Ocular area	Ocular height	Ocular width	Area of nares	Height of nares	Width of nares
Body weight		0.000	0.004	0.000	0.069	0.496	0.460	0.005	0.062	0.072
Area of rhinotheca	0.972		0.001	0.000	0.078	0.585	0.556	0.006	0.069	0.047
Area of gnathotheca	0.666	0.711		0.116	0.187	0.237	0.278	0.083	0.384	0.933
Height of rhamphotheca	0.792	0.793	0.396		0.014	0.436	0.597	0.003	0.090	0.006
Ocular area	0.452	0.438	0.336	0.582		0.346	0.991	0.075	0.046	0.946
Ocular height	-0.177	-0.143	-0.303	-0.202	-0.244		0.016	0.143	0.072	0.104
Ocular width	0.192	0.154	-0.279	0.138	-0.003	0.574		0.854	0.004	0.061
Area of nares	-0.642	-0.639	-0.433	-0.673	-0.444	0.371	0.048		0.857	0.452
Height of nares	-0.462	-0.451	-0.225	-0.424	-0.490	-0.447	-0.662	-0.047		0.096
Width of nares	-0.447	-0.488	-0.022	-0.636	-0.018	-0.408	-0.464	0.196	0.416	

of biometrical data against body weight. PC1 represented 74.04% of the variation, while PC2 decreased to 12.22%. When the allometric effect was analyzed a significative signal was present ($r^2 = 0.699$, $F_{10,6} = 36.71$, p = 0.00013).

Birds adapt to different consumptions either by increasing bill dimensions independently of body size or by increasing all the body and bill characters isometrically until a desirable bill size (width and/or depth) (Clabaut et al. 2009). Greater flamingo is an example of this latter adaptation: beak traits are increased equally. This would indicate a close and continued relationship between skeletal bill morphology and jaw musculature (but no functionality, as indicated by negative correlations with nares area), due to increased demands for space and attachment sites for the musculature. Detected correlation that would support the hypothesis of integration between these tissues, many beak morphological descriptions being coupled with a corresponding change in jaw musculature, too (Foster et al. 2008; Riyahi et al. 2013). Therefore, we suggest that the cranial skeleton and musculature are closely linked at least developmentally, allowing for efficient functional integration. Further genetic and functional tests must have been performed to reveal the exact nature of the flamingo beak change.

Thus, in addition to be an interesting model system for the study of change in beak morphology, flamingos offer an exciting and unique opportunity to understand the mechanism of an adaptive musculo-skeletal integration in birds.

Acknowledgements

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