Osteological measurements and sexual dimorphism of the Madagascar Pochard *Aythya innotata* (Anseriformes: Anatidae)

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Abstract

Skeletal measurements of 20 adult specimens (10 males and 10 females) of the Madagascar Pochard (*Aythya innotata*) that died in captivity at a breeding center in Antsohihy, Madagascar, were used in this study. 28 osteological variables were employed to examine possible sexual dimorphism in this species. The results of the univariate analysis showed that two of the 28 variables differed between the sexes − greatest and medial length of coracoid with males being larger than females with a sexual size dimorphism (SSD) index between 3.5% and 4.1%. The results of a discriminant analysis based on significant differences of the two coracoid variables were used to construct a sexual discrimination equation (D), which correctly classified the two sexes for 83.3% of cross-validated grouped cases with 85.7% of males and 81.8% of females correctly assigned.

Keywords: morphometric characters, Madagascar Pochard, *Aythya innotata*, osteological specimens, sexual size dimorphism

Résumé détaillé

Fuligule de Madagascar, *Aythya innotata*, ou *onjy* en Malgache, est un canard plongeur endémique de Madagascar, classé dans la catégorie En danger critique d'extinction sur la liste rouge de l'UICN. Considéré comme éteint par certains chercheurs, il a été redécouvert en 2006 dans le lac Matsaborimena, au Nord-ouest de Madagascar. L'espèce présente un dimorphisme au niveau du plumage et de la masse corporelle. Dans cette étude, le dimorphisme sexuel de taille a été analysé chez 20 spécimens adultes (10 mâles et 10 femelles) morts en captivité dans un centre d'élevage à Antsohihy, Madagascar. Un test univarié bilatéral t-test a été effectué sur les 28 variables ostéologiques prélevées sur chaque spécimen pour examiner les différences morphométriques entre les mâles et les femelles. Des analyses discriminantes ont été réalisées sur les mesures squelettiques pour déterminer le sexe de Fuligule de Madagascar. Les résultats de l'analyse univariée ont montré que deux des 28 variables différaient entre les sexes − la longueur maximale et la longueur médiane du coracoïde, les mâles étant plus grands que les femelles avec un indice SSD entre 3,5 % et 4,1 %. Les résultats d'une analyse discriminante basée sur les différences significatives des deux variables de la coracoïde ont été utilisés pour construire une équation de discrimination sexuelle (D), qui a correctement classé les deux sexes pour 83,3 % des cas groupés validés par recoupement, avec 85,7 % des mâles et 81,8 % des femelles correctement affectés. La différence de taille sexuelle SSD trouvée dans cette étude indique probablement des différences intersexuelles possibles dans l'écologie et le comportement, informations qui sont essentielles pour des stratégies de conservation efficaces.

Mots clés : caractères morphométriques, Fuligule de Madagascar, *Aythya innotata*, spécimens ostéologiques, dimorphisme sexuel de taille

Introduction

The family Anatidae includes 175 species with a nearly worldwide distribution and including 12 species of the genus *Aythya*, referred to as pochards or scaups, distributed in the Americas, Asia, Australia, Eurasia,

Nomenjanahary, Z. B., Hansford, J. P., Samonds, K. E. & Goodman, S. M. 2023. Osteological measurements and sexual dimorphism of the Madagascar Pochard *Aythya innotata* (Anseriformes: Anatidae). *Malagasy Nature*, 18: 92-99.

New Zealand, Africa, and Madagascar (Clements *et al*., 2021). The Madagascar Pochard (*A. innotata*) is the only species of the genus found on Madagascar. This endemic bird is one of the most threatened species in the world and one of nine Malagasy wetland-associated birds that are Endangered or Critically Endangered (IUCN, 2022). One of the criteria that make Madagascar a recommended tourist destination is the existence of animal or plant species that are found nowhere else but on the island. In 2020, the tourism sector represents 10% of Madagascar's GDP. The Madagascar Pochard being one of the rarest bird species in the world, its presence on the island certainly contributes to the increase of the percentage of visitors coming to Madagascar every year. This endemic bird has therefore probably played an economic role mainly related to tourism and scientific research. Historically, the Madagascar Pochard was thought to be primarily restricted to the Lake Alaotra region (Webb, 1936; Langrand, 1990; Wilmé, 1994; Young & Kear, 2006), in the central-eastern part of the island, and in certain earlier publications classified as Extinct (Young & Kear, 2006). In 2006, 20-25 individuals were discovered on the southern foothills of the Tsaratanana Massif in northern Madagascar, specifically on Lake Matsaborimena, which would subsequently become the Bemanevika protected area (Rene de Roland *et al*., 2007; Rene de Roland & Young, 2022).

Since its rediscovery, Durrell Wildlife Conservation Trust, Wildfowl & Wetlands Trust, The Peregrine Fund Madagascar, and Asity Madagascar in collaboration with the Malagasy government, have worked closely to implement action plans for the rewilding and protection of this species (Young *et al*., 2013). A captive breeding center of Madagascar Pochard in Antsohihy (Sofia Region), Madagascar, was created in 2011 to maintain a viable captive population of this species and with the intent to reintroduce them into the wild (Woolaver *et al*., 2015). In December 2018, 21 captive-bred Madagascar Pochards were released on Lake Sofia, a Ramsar site, and also in the Sofia Region, which was identified as a potential high-quality reintroduction site to establish a second population (Asity Madagascar & BirdLife International, 2021); and from 2018-2022, 111 birds have now been released (Young, pers. comm.). The following year, two broods of ducklings were observed on the lake, confirming that the released birds had successfully bred. The total wild population is now about 50 individuals, and around 90 captive birds held in the Antsohihy captive-breeding facilities (Sargent, 2021). The lake where the pochard was rediscovered is now part of the Paysage Harmonieux Protégé de Bemanevika protected area (IUCN category V) managed by The Peregrine Fund Madagascar and also in the Sofia Region (Goodman *et al*., 2018); however, the site is considered to contain habitat of insufficient quality for the long-term survival of the species (Bamford *et al*., 2015). Additionally, ecological studies of the remaining known wild population of the Madagascar Pochard have revealed that this site of rediscovery, Lake Matsaborimena, is far from ideal habitat for this species. The lake is too deep for ducklings to properly feed and the benthic substrate is poor in invertebrates, the principal food of this species. These factors limit recruitment of young into the breeding population and the lake probably only has the capacity to support the current small existing population (Bamford *et al*., 2015). Thus, conservation managers are faced with the challenge of identifying suitable reintroduction sites for captive bred individuals from the Antsohihy center. Potential insights into this critical question can be based on historical and subfossil sites where this species once occurred and, hence, providing data into its past geographic distribution. In order to advance on possible identification of remains from subfossil sites, comparative skeletal material is required, as well as details on osteological variation, which are provided herein.

Opportunities to protect and enhance suitable areas of habitat for this species require data on its preferred niche and quality of potential reintroduction sites. Incorporating natural history information into the choice of the best reintroduction sites for rewilding is important, particularly in light of current and future climate change, overlaid on anthropogenic habitat changes. Little is known about these aspects for the Madagascar Pochard (Rene de Roland & Young, 2022) and given that the 2006 rediscovery of this species took place hundreds of kilometers outside its putative historical geographic range clearly underlines that field research is wanting for developing a reintroduction and habitat restoration strategy.

Data on its former distribution are extremely limited. Another possible source of such information might be from extensive subfossil waterbird bone remains found at different sites on the island and dating from the Quaternary. To date this species has not been identified from this material and a first step in advancing on the possible discovery of Madagascar

Pochard remains held in various paleontological museums is the preparation of comparative skeletal material of this species. To our knowledge only a single skeletal specimen of this taxon was previously available, and held at the Field Museum of Natural History of Chicago (FMNH 360032). In the context of this study additional comparative osteological material of this species was prepared and used to quantify different measurements and examine patterns of possible sexual dimorphism.

Sexual dimorphism is the existence of distinct male and female forms within a species. Many bird species exhibit sexual dimorphism in terms of plumage dichromatism and body size (Svagelj & Quintana, 2007). Differences in body size between the sexes, termed sexual size dimorphism (SSD), are a common feature of many organisms, from vascular plants to invertebrates and vertebrates, including birds (Svagelj & Quintana, 2007; Nepshinsky *et al.*, 2021). In many bird species, SSD is widespread (Anderson, 1994) and in the majority of cases with males being slightly or significantly larger than females (Ganbold *et al.*, 2019). The origin and maintenance of SSD has been explained as the result of sexual selection, especially with regards to mate choice, selection on reproductive life history traits, and intersexual ecological divergence (Hood, 2000; Pincheira-Donoso *et al.*, 2021). Many Anseriformes exhibit SSD at different levels (Livezey, 1996; Handley *et al.*, 2016). Herein, we determine if the Madagascar Pochard displays SSD based on osteological measurements.

Materials and methods

Sample preparation

Twenty specimens of adult Madagascar Pochard preserved in formaldehyde were obtained from the Pochard Captive Breeding Center, in Antsohihy, Madagascar, where they died in captivity from various causes. Of the 20 specimens, 13 (6 males, 7 females) were reared in captivity from eggs laid in the wild and collected in 2009; and 7 specimens (4 males, 3 females) were bred in captivity. Large portions of feathers, flesh, and organs were removed from the carcasses, and the balance of the roughed-out skeletons were cleaned using water maceration.

Specimens and measurements

The study material includes full skeletons of 20 individuals (10 males and 10 females). All long bone measurements were made with a digital caliper to an accuracy of 0.1 mm. Photographs were also taken to document morphological aspects of long bones (Figure 1). Using the definitions and descriptive terms in Von Den Driesch (1976), the following measurements were made: humerus - greatest length (GLH), breadth of the proximal end (BpH), breadth of the distal end (BdH), and smallest breadth of the corpus (SCH); radius - greatest length (GLR) and smallest breadth of the corpus (SCR); ulna - greatest length (GLU) and diagonal of the distal end (DidU); carpometacarpus - greatest length (GLC), breadth of the proximal extremity (BpC), and diagonal of the distal end (DidC); phalanx 1 - greatest length anterior to the 2nd digit (GLP); coracoid - greatest length (GLCo), medial length (LmCo), and breadth of the facies articularis basalis (BFCo); scapula - greatest length (GLS) and cranial diagonal (DicS); femur - greatest length (GLF), breadth of the proximal end (BpF), breadth of the distal end (BdF), and smallest breadth of the corpus (SCF); tibiotarsus - greatest length (GLT), axial length (LaT), and depth of the distal end (DdT); tarsometatarsus - greatest length (GLTa), breadth of the proximal end (BpTa), breadth of the distal end (BdTa), and smallest breadth of the corpus (SCTa) (see Figure 1).

Statistical analysis

The normality and homogeneity of the variances of the variables were checked before performing the analyses. For all variables, coefficient of variation (CV) [CV = 100SD / $\bar{x}$] were calculated for each sex and averaged between them to indicate the degree of variability. A univariate two-tailed t-test and discriminant analysis were performed to examine morphometric differences between males and females. Despite the relatively small number of specimens used in this study, we suggest that 10 specimens of each sex provide a meaningful level of statistical comparison.

According to Rensch's rule, the magnitude of SSD increases with overall body size in taxa where males are larger than females (Rensch, 1960). A larger SSD value indicates a greater difference between males and females. Herein, the SSD index was calculated according to Weidinger and Franeker (1998): $SSD = \{(\bar{x}_m - \bar{x}_f) / \bar{x}_f)\} \times 100$, where $\bar{x}_m$ and $\bar{x}_f$ are the mean values of males and females, respectively. Discriminant function analysis (DFA) was performed to determine if morphometric measurements could be used to reliably determine the sex of Madagascar Pochard. The performance of each individual measure as a discriminant variable (univariate DFA)

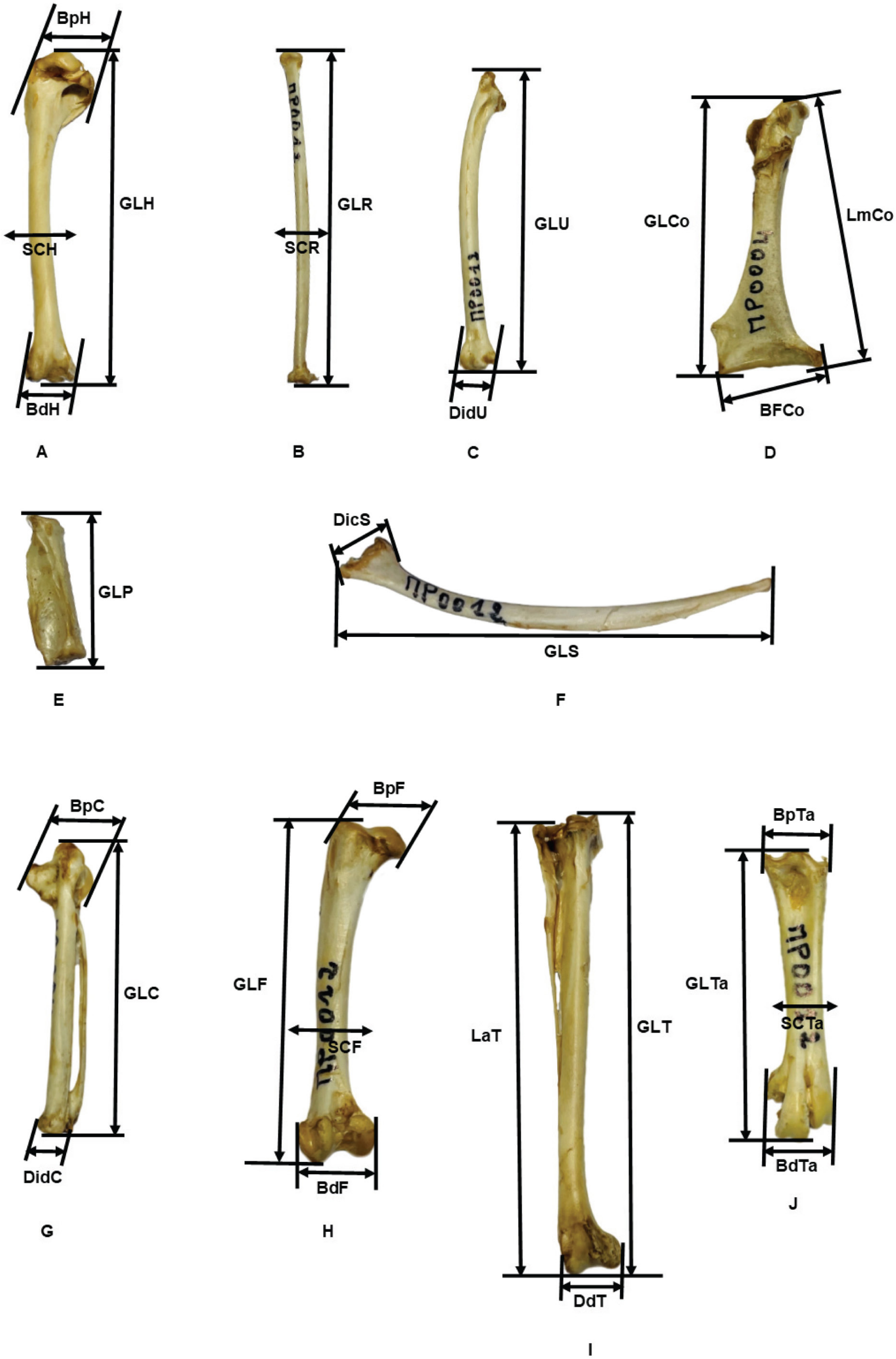

Figure 1. Measurement of the skeletal elements of Madagascar Pochard. **A**) humerus, **B**) radius, **C**) ulna, **D**) coracoid, **E**) phalanx, **F**) scapula, **G**) carpometacarpus, **H**) femur, **I**) tibiotarsus, and **J**) tarsometatarsus. (Photos by Zafindratsaravelo B. Nomenjanahary.)

was evaluated. In addition, Wilks' Lambda was used to determine if the discriminant function analysis was significant ($P < 0.0018$) between males and females. Advanced discriminant analyses were applied to obtain the combinations of features (discriminant functions) that best distinguished the sexes (Phillips & Furness, 1997). The descriptive statistics reported for each variable consisted of the sample size (n), mean (x̄), standard deviation of the mean (SD), and range (minimum – maximum). All statistical analyses were performed with the program R 4.0.5 (R Development Core Team, 2021) using the MASS package (Venables & Ripley, 2002) for multivariate analysis.

Results

Skeletal measurements were made from the 10 male and 10 female skeletal specimens of the Madagascar Pochard. There was no significant difference between the left and right bones for a given element for any individual. Subsequently, measurements from the right-hand side were used in the analyses, and summary data are presented in Table 1. Most of the descriptive statistics indicated that males are on average larger than females with a general mean difference of 0.1 mm to 1.8 mm. The coefficient of variation is low for all measurements, ranging from 1.2% to 4.4%.

Of the 28 measured variables, only two showed statistically significant evidence of sexual dimorphism (Table 2). The Bonferroni correction was determined from 28 simultaneous tests to calculate the significance level, which was set at 0.0018. This threshold was obtained from 0.05 / 28. As shown in Table 2, mean greatest length of coracoid for males (range 46.9-48.8 mm) was 1.6 mm larger than in females (range 44.9-47.4 mm) and mean medial length of coracoid for males (range 44.2-46.3 mm) was 1.8 mm larger than in females (range 41.9-44.5 mm). The level of size dimorphism for both measurements was 3.5% to 4.1%.

DFA equations retained the GLCo and LmCo variables as the best predictors. Wilk's Lambda multivariate analyses revealed that DFAs was significant (Table 3). The results of discriminant analysis based on the statistically significant differences of these two osteological measurements were used to construct a sexual discrimination equation (D, with an associated cut-off value of 76.47): D = 0.21 GLCo + 1.05 LmCo. The sexual discrimination equation was employed to identify the two sexes with 83.3% of cross-validated grouped cases correctly classified, since positive D scores

Table 1. Morphometric datasets for the Madagascar Pochard. Mean (x̄), minimum values (Min), maximum values (Max), standard deviation (SD), and coefficient of variation (CV). See Materials and methods for definitions of measurement acronyms.

Morphometric character (mm)	Male (n = 10)				Female (n = 10)				CV (%)
	x̄	Min	Max	SD	x̄	Min	Max	SD	
GLH	78.3	76.0	79.7	1.3	76.7	74.1	77.9	1.1	1.5
BpH	17.4	16.7	18.0	0.5	17.1	16.3	17.6	0.4	2.6
BdH	11.5	11.1	11.7	0.2	11.2	10.9	11.5	0.2	1.8
SCH	5.2	5.0	5.4	0.2	5.2	5.1	5.4	0.1	2.9
GLU	67.0	65.7	68.6	1.1	66.0	65.3	66.8	0.5	1.2
DidU	7.7	7.5	7.9	0.1	7.6	7.4	7.8	0.1	1.3
GLR	62.5	61.0	63.7	1.1	61.5	59.4	62.4	0.9	1.6
SCR	2.3	2.1	2.5	0.1	2.3	2.1	2.5	0.1	4.4
GLC	41.7	40.8	42.7	0.7	40.7	39.2	41.2	0.6	1.6
BpC	10.1	9.5	10.7	0.3	9.9	9.7	10.3	0.2	2.5
DidC	5.5	5.2	5.6	0.1	5.4	5.2	5.6	0.1	1.8
GLP	16.6	16.2	16.8	0.2	16.4	15.5	16.8	0.4	1.8
GLCo	47.9	46.9	48.8	0.9	46.3	44.9	47.4	0.7	1.7
LmCo	45.3	44.2	46.3	0.9	43.5	41.9	44.5	0.7	1.8
BFCo	16.9	16.1	17.5	0.4	16.5	15.9	17.3	0.4	2.4
GLS	62.7	61.5	63.8	0.8	61.8	60.7	63.4	1.0	1.5
DicS	10.3	9.9	10.8	0.3	10.1	10.0	10.3	0.1	2.0
GLF	42.0	40.6	43.0	0.8	41.3	39.1	42.3	1.0	2.2
BpF	10.0	9.6	10.3	0.2	9.7	9.4	9.9	0.2	2.0
BdF	9.4	8.9	9.6	0.2	9.2	8.8	9.4	0.2	2.2
SCF	3.7	3.5	3.8	0.1	3.7	3.6	3.8	0.1	2.7
GLT	71.8	69.7	72.4	0.9	70.4	69.0	72.3	1.1	1.4
LaT	66.0	64.4	67.1	0.9	65.2	63.4	66.8	0.9	1.4
DdT	8.3	8.0	8.4	0.1	8.1	7.6	8.4	0.3	2.5
GLTa	33.3	32.3	33.9	0.5	32.6	31.0	33.6	0.8	2.0
BpTa	7.8	7.5	8.1	0.2	7.7	7.4	7.9	0.2	2.6
BdTa	8.5	8.2	8.8	0.2	8.3	7.8	8.6	0.2	2.4
SCTa	4.4	4.2	4.5	0.1	4.3	4.0	4.4	0.1	2.3

Table 2. T-test results of morphometric differences between male and female Madagascar Pochard, including t-statistic (t), degrees of freedom (df), and sexual size dimorphism (SSD). See Materials and methods for definitions of measurement acronyms. Significantly different (*).

Morphometric character	t	df	*P*-values	SSD (%)
GLH	-2.8	16.1	0.01	
BpH	-1.2	16.6	0.2	
BdH	-2.6	17.4	0.02	
SCH	0.76	12.6	0.5	
GLU	-2.7	12.6	0.02	
DidU	-2.9	17.9	0.009	
GLR	-2.2	17.5	0.04	
SCR	-0.4	17.9	0.7	
GLC	-3.5	17.2	0.002	
BpC	-1.5	15.1	0.2	
DidC	-2.1	17.2	0.05	
GLP	-1.4	11.4	0.2	
GLCo	-4.2*	13.4	0.0009	3.5
LmCo	-4.4*	12.6	0.0008	4.1
BFCo	-2.1	17.9	0.05	
GLS	-1.6	9.4	0.1	
DicS	-1.9	7.9	0.1	
GLF	-1.5	15.2	0.1	
BpF	-3.1	17.9	0.006	
BdF	-2.3	17.8	0.03	
SCF	0.9	16.4	0.4	
GLT	-2.6	13.9	0.02	
LaT	-1.9	17.9	0.06	
DdT	-2.1	13.8	0.05	
GLTa	-2.7	15.8	0.02	
BpTa	-0.9	17.7	0.3	
BdTa	-2.5	15.5	0.02	
SCTa	-2.1	17.5	0.05	

Table 3. Accuracy of each measurement for sexing Madagascar Pochard. See Materials and methods for definitions of measurement acronyms.

Morphometric character	Wilk's Lambda	*F*-value	Accuracy (%)
GLH	0.7	7.9	68.4
BpH	0.9	1.5	57.9
BdH	0.7	6.9	70.0
SCH	0.9	0.6	36.8
GLU	0.7	6.0	72.2
DidU	0.7	8.5	75.0
GLR	0.8	5.0	65.0
SCR	0.9	0.1	55.0
GLC	0.6	12.5	80.0
BpC	0.9	2.3	70.0
DidC	0.8	4.4	80.0
GLP	0.9	1.9	66.6
GLCo	0.5	18.7	88.9
LmCo	0.4	20.9	88.9
BFCo	0.8	4.4	75.0
GLS	0.9	0.5	60.0
DicS	0.9	1.2	72.7
GLF	0.9	2.4	68.4
BpF	0.6	9.8	70.0
BdF	0.8	5.4	75.0
SCF	0.9	0.7	42.1
GLT	0.7	6.5	81.3
LaT	0.8	3.9	65.0
DdT	0.8	4.5	70.0
GLTa	0.7	7.2	80.0
BpTa	0.9	0.9	55.0
BdTa	0.7	6.4	85.0
SCTa	0.8	4.5	70.0

indicated males and negative D scores indicated females, with 85.7% of the males and 81.8% of the females being correctly assigned.

Discussion

Traditionally, SSD has been described using measures of body size (Hood, 2000), primarily univariate variables such as external measurements or body mass. On the basis of body mass of captive Madagascar Pochards, Woolaver *et al*. (2015) showed that males are heavier (626-780 g) than females (476-740 g). According to Young (2013), the wings and tarsi of males are also slightly larger than those of females. To our knowledge, no information was previously available on the skeletal morphometric characteristics of the Madagascar Pochard.

We were able to determine the presence of SSD in the Madagascar Pochard, specifically significant differences between the two sexes in greatest length of coracoid (GLCo) and medial length of coracoid (LmCo), with males being larger than females. Body mass for each sex was estimated by the method of Campbell and Marcus (1992) using femoral least-shaft circumference. These estimates indicate that male Madagascar Pochard have an average body mass of 483 g (448-551 g) and females 454 g (416-490 g). The level of sexual dimorphism found in this species is similar to many other Anseriformes species (Cramp *et al*., 1978). The low amplitude of SSD (3.5-4.1%) is indicative of subtle size differences between males and females.

Our results confirm previous work on the presence of SSD in this species, with males being heavier than females (Young, 2013; Woolaver *et al*., 2015). The body mass reported by Woolaver *et al*. (2015) and mentioned above based on captive birds at the breeding center are distinctly heavier than our estimates, which is presumably associated with different health states and dietary considerations. Size differences between males and females is observed in virtually all *Aythya* species occurring elsewhere in the world (Cramp *et al*., 1978; Michot & Woodin, 2005). In general, the presence of sexual dimorphism in a given bird species indicates social polygamy and/or differences between male and female provisioning of the young (Owens & Hartley, 1998). However, despite the significant size difference between the two sexes, all *Aythya* spp. are thought to maintain monogamous pair bonds (Cramp *et al*., 1978).

In the Madagascar Pochard, the only post cranial element that shows sexual dimorphism is the coracoid. The coracoid is part of five bones (sternum, furcula, coracoid, scapula, and humerus) that form the shoulder girdle and is closely related in birds with different types of flight (Close & Rayfield, 2012; Mitchell *et al*., 2017). Of the bones that comprise the shoulder girdle, the coracoid has been described as being partially mobile during wing flapping because it supports the furcula (Jenkins *et al*., 1988; Baier *et al*., 2013). Sexual dimorphism in coracoid size can therefore help explain the difference in wing size between males and females of this species identified by Young (2013).

Discriminant function was developed using only two morphometric variables: GLCo and LmCo, which resulted in 83.3% correct sexual classification. Wing length was previously determined to be the most discriminating variable between sexes in Anatidae such as Muscovy ducks (Yakubu, 2011). The accuracy of sex determination by morphometry depends on the degree of dimorphism; for example, in some highly dimorphic birds, the discriminant function is able to predict sex correctly in over 90% of individuals (Leal *et al*., 2019). Due to the low degree of dimorphism in Madagascar Pochard, other techniques such as plumage coloration may be more effective in sexing this species in the field.

As the Madagascar Pochard is classified as Critically Endangered by the International Union for Conservation of Nature (IUCN, 2022), the ability to identify bones of this species among subfossil remains in Madagascar's Quaternary deposits will be valuable to better understand its previous geographical distribution and by extrapolation help formulate conservation strategies. The SSD difference found herein indicate possible intersexual differences in ecology and behavior

Acknowledgments

Funding and logistical support for this project were provided by Durrell Wildlife Conservation Trust (DWCT), Zoological Society of London (ZSL), and Association Vahatra. Additional funding support was provided by Research England. The research and the transfer of the specimens were conducted with the authorization of the Direction des Aires Protégées, des Ressources Naturelles et des Ecosystèmes and Direction Régionale de l'Environnement et du Développement Durable. The authors gratefully acknowledge Durrell Madagascar and the waterbird breeding center in Antsohihy, particularly Leslie Wilmet, Rinah Razafindrabe, and Solofoniaina Fernandez Arsenel for providing access to preserved specimens. We thank Glyn Young for his comments on an earlier version of this manuscript.

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